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## Article

# Middle Pleistocene Hippopotamuses from the Italian Peninsula: An Overview

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**Abstract:** Our work presents an updated overview of the Italian Middle Pleistocene records of hippopotamuses, including the two species *Hippopotamus antiquus* and *Hippopotamus amphibius*. In addition to reviewing several well-known fossils in the literature, a large number of samples are described herein for the first time. Following the recent results published in the literature, where the skull from the Middle Pleistocene of Cava Montanari (ca. MIS 13) was confirmed to belong to *H. amphibius*, one of the aims of this work was to investigate the *H. antiquus*–*H. amphibius* transition. A morphological analysis applied to a large sample confirmed the validity of the arrangement of the enamel ridges of the external surfaces of the lower canines as a diagnostic character for specific identifications. Finally, biometric analyses allowed us to test the size variability during the Middle Pleistocene, which confirmed that *H. antiquus* was generally larger than *H. amphibius*. Nevertheless, the remains of *H. antiquus* dated to ca. 600 ka show a reduced size when compared to older fossils of the same taxon, probably as a response to severe glacial conditions that occurred during MIS 16.

**Keywords:** Quaternary; Mediterranean Europe; *Hippopotamus*; taxonomy; biochronology; large mammals; Epivillafranchian; Galerian



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## 1. Introduction

The Middle Pleistocene was an important period for the evolution of European terrestrial ecosystems, which experienced a progressive transformation toward modern biodiversity [1,2]. This evolution was driven by substantial changes in the Earth's climate system, with a progressive yet not gradual increase in the amplitude of climate oscillations (from 41 ka to approximately 85–125 ka; [3,4]). These climatic changes started during the late Early Pleistocene and continued during the Middle Pleistocene [5–7]. This phase is known in the literature as the Middle Pleistocene Revolution (MPR) or the Early–Middle Pleistocene Transition (EMPT, 1.2–0.4 Ma) [8–10]. The end of the EMPT coincides with the Mid-Brunhes Event (MBE, ca. 424 ka; MIS 12–11 transition), an event that, from a climatic perspective, marks the consolidation of the glacial cycles ruled by a 100 kyr periodicity, the longest cyclicity recognized during the Quaternary.

These intense climatic oscillations caused a renewal of large mammal faunas, reflected in the identification of two European Land Mammal Ages (ELMAs), the Epivillafranchian for the late Early Pleistocene (ca. 1.2–0.8 Ma) and the Galerian for the latest Early to early Middle Pleistocene (ca. 0.8–0.4 Ma), witnessing multiple mammal dispersals, including those of species that still live in Europe (e.g., *Cervus elaphus*, *Sus scrofa*) or that disappeared

only during the early Late Pleistocene (*Palaeoloxodon antiquus*), but also the survival of late Villafranchian holdovers [2,10–18]. The Acheulean technocultural complex also spread into Europe during the EMPT (e.g., [13,15,18]). Finally, multiple key bioevents occurred in Europe shortly before or coinciding with the MBE (the end of the EMPT), among which was the diffusion of *Bos primigenius*, *Equus hydruntinus*, *Dama clactoniana*, and *Canis lupus* [19–22].

The hippopotamuses occupied Europe for a long time, with their first dispersal recognized during the Early Pleistocene (ca. 2.2 Ma, “Hippo Event” *sensu* [23] and references therein). During the Villafranchian, hippopotamuses were dispersed across the continent, but their fossil record is limited to a few European localities [24–29]. Late Early Pleistocene hippopotamuses were often extremely abundant and widely spread, as documented, for instance, by the impressive record of Untermassfeld [30,31], on the one hand, or the fossil from Westbury Cave [29], which testifies to the diffusion of these animals into Britain, on the other.

The evolution of European Quaternary hippopotamuses has been long disputed, with diverging taxonomic opinions expressed by different authors [24–27,32–35]. Excluding the Mediterranean islands, the model proposed by [36] was adopted in many works (e.g., [13,22,29,31,37–40], but see [35]). This model involves only two species: *H. antiquus* (= *H. major* = *H. amphibius antiquus* = *H. tiberinus* = *H. ex gr. antiquus*) and *H. amphibius* (= *H. incognitus* = *H. amphibius incognitus*).

These two forms, however, morphologically differ in cranial and mandibular features [24,26,40,41], while a distinction based on postcranial bones was proposed by [26] but followed only by a few authors ([40] and references therein).

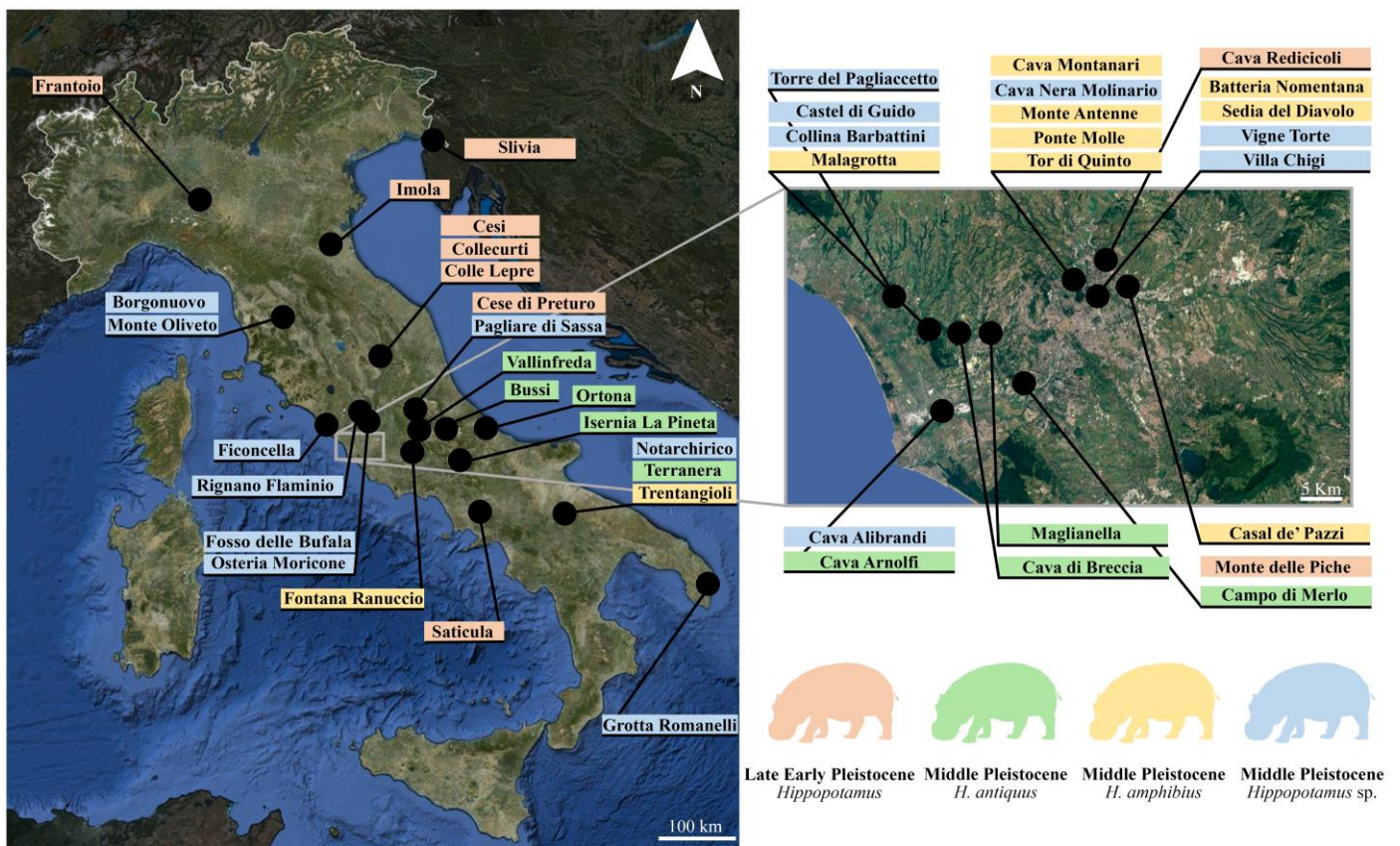
Dental remains display a large intraspecific variability in the development cusps, cingula, and valleys, which are, therefore, hardly useful for taxonomic assignments [24,26]. One of the features proposed for the distinction between *H. antiquus* and *H. amphibius* was the configuration of the enamel ridges and grooves on the external surfaces of the lower canines [24,42]. According to [42], the canine enamel ridges of *H. antiquus* are prominent and convergent, whereas in *H. amphibius*, they are characterized by parallel development. Later, [26] argued that the two distinct morphotypes are observed with the same frequency in *H. antiquus*. However, [26] did not provide specific details on the specimens used to score this character, and since he attributed all Middle Pleistocene European hippopotamuses to *H. antiquus* (= *H. tiberinus*), it cannot be ruled out that this interpretation is biased by the inclusion in his sample of specimens actually belonging to *H. amphibius*. Indeed, [22] recently reviewed the chronostratigraphic setting of Cava Montanari and confirmed the attribution of a skull known from the site to *H. amphibius*. With an age of ca. 500 ka, the Cava Montanari skull implies that the appearance of *H. amphibius* in the European Middle Pleistocene record is another bioevent that occurred during the end of the EMPT, confirming the hypothesis previously proposed by several authors [24,34,36,39,41].

This work offers an updated overview of the Italian Middle Pleistocene and, to give perspective on the subject, selected late Early Pleistocene occurrences of hippopotamuses, comprising both *H. antiquus* and *H. amphibius*. Fossils from a number of localities are presented herein for the first time. Finally, size variability during the Middle Pleistocene is investigated, testing the existence of differences between species or evolutionary trends across time.

## 2. An Overview of the Late Early to Late Middle Pleistocene Hippopotamus Record

The Italian hippopotamus record from the late Early Pleistocene is quite sparse and known from few localities (Figure 1, Table 1).

Of great importance are the remains recovered from Colle Curti (or Collecurti), where 402 specimens were found (90.7% of the total mammal fossils collected at the site; [43]). The sample includes three skulls, a real rarity in the European record that, in addition to other remains, allowed researchers to explore and to define the variability of the Epivillafranchian hippopotamuses [26,43]. This locality is definitely a reference point for *H. antiquus* of Europe.



**Figure 1.** Geographic positions of the main late Early to late Middle Pleistocene sites in the Italian Peninsula yielding *Hippopotamus* remains.

Another important area for hippopotamuses is the late Early Pleistocene basin of Scoppito-Madonna della Strada, where several fossil-bearing sites were discovered. The first local fauna was collected from Cese di Preturo, where hippopotamuses were initially described by [44]. These fossils were examined by [26], who confirmed the presence of *H. antiquus* (the author also attributed several specimens to *H. tiberinus*, today a synonym of *H. antiquus*). The sample was also studied by [45], confirming again its attribution to *H. antiquus*. Other fossils recovered from the Scoppito-Madonna della Strada basin were collected in the Cava Santarelli succession, and they were referred to *H. antiquus* by [45]. Additional remains were found at Civitatomassa, Coppito, and Genzano di Sassa, listed by [45] and ascribed to *H. antiquus*. In the Scoppito-Madonna della Strada basin, a rich mammal sample was recovered from Pagliare di Sassa, including some isolated hippopotamus remains [46]. These fossils were considered of limited taxonomic value and attributed to *Hippopotamus* sp. cf. *H. antiquus* by [46]. Later, the sample from Pagliare di Sassa was attributed to *Hippopotamus* ex gr. *H. antiquus* by [45] and *H. antiquus* by [47].

In sum, at Scoppito-Madonna della Strada basin, hippopotamuses were documented from three late Early Pleistocene deposits, Cese di Preturo, Cava Santarelli, and Genzano di Sassa (between ca. 1.3 and 1.1 Ma), and from three early Middle Pleistocene sites, Civitatomassa, Coppito, and Pagliare di Sassa.

Early Pleistocene mammals were discovered at Saticula, a lacustrine deposit located in the intramontane basin in the north-western part of the Caudina valley [48]. The sample included a partially articulated skeleton and other isolated fossils attributed to *H. antiquus* [48].

**Table 1.** Hippopotamuses from the late Early Pleistocene to the Middle Pleistocene sites in the Italian Peninsula, with chronological attribution, previous and present taxonomical attribution, references, and present location of the material. Light pink—Epivillafranchian specimens of *H. antiquus*; green—Middle Pleistocene specimens of *H. antiquus*; light orange—Middle Pleistocene specimens of *H. amphibius*; blue—Middle Pleistocene specimens with open nomenclature. MIS = Marine Isotopic Stage.

Sites	Previous Attribution	References for Previous Attribution	Geochronology	Age (Ma)	MIS	References for Chronological Assignment	Analyzed in This Work	Current Attribution
Cese di Preturo	<i>Hippopotamus antiquus</i>	[26]	late Early Pleistocene	1.3–1.1		[26,45]		
Cava Santarelli	<i>Hippopotamus antiquus</i>	[45]	late Early Pleistocene	1.3–1.1		[26,45]		
Colle Curti	<i>Hippopotamus antiquus</i>	[26,43]	late Early Pleistocene	1.1		[26,43]		
Saticula	<i>Hippopotamus antiquus</i>	[48]	late Early Pleistocene	1.1		[48]		
Cesi	<i>Hippopotamus</i> sp.	[49]	late Early Pleistocene	ca 1.0		[49]		
Colle Lepre	<i>Hippopotamus</i> ex gr. <i>H. antiquus</i>	[34]	late Early Pleistocene	1.0		[34]		
Frantoio	<i>Hippopotamus</i> sp.	[50]	late Early Pleistocene	0.99		[50]		
Slivia	<i>Hippopotamus</i> sp.	[51,52]	late Early Pleistocene	ca. 0.9		[51,52]		
Imola	<i>Hippopotamus amphibius</i> (?)	[53]	late Early Pleistocene	0.85–0.8	21/20	[54]		
Cava Redicicoli	<i>Hippopotamus</i> cf. <i>antiquus</i>	[40]	late Early Pleistocene	ca. 0.8	20/19	[40,55]		
Monte delle Picche	<i>Hippopotamus</i> sp.	[56]	late Early Pleistocene	ca. 0.8	20/19	[56]		
Bussi	<i>Hippopotamus antiquus</i>	[57]	early Middle Pleistocene	0.78–0.6	19–15	[57]	X	<i>Hippopotamus antiquus</i>
Ortona	<i>Hippopotamus antiquus</i>	[34,58]	early Middle Pleistocene	0.78–0.7	19–17	[34]		
Vallinfreda	<i>Hippopotamus antiquus</i>	[24,59]	early Middle Pleistocene	0.78–0.7	19–17	[59]	X	<i>Hippopotamus antiquus</i>
Campo di Merlo	<i>Hippopotamus antiquus</i>	[36]	early Middle Pleistocene	ca. 0.7	18–17	[60]	X	<i>Hippopotamus antiquus</i>
Cava Alibrandi	<i>Hippopotamus</i> sp.	[61]	early Middle Pleistocene	ca. 0.7	18–17	[55]	X	<i>Hippopotamus</i> sp.
Cava Arnolfi	<i>Hippopotamus antiquus</i>	[36]	early Middle Pleistocene	ca. 0.7	18–17	[55]	X	<i>Hippopotamus antiquus</i>
Monte Oliveto	<i>Hippopotamus</i> sp. cf. <i>H. antiquus</i>	[62]	early Middle Pleistocene	0.8–0.6	19–15	[62]		
Notarchirico	<i>Hippopotamus antiquus</i>	[15]	early Middle Pleistocene	0.7–0.65	17	[15]	X	<i>Hippopotamus</i> sp.
Pagliare di Sassa	<i>Hippopotamus</i> sp.	[46]	early Middle Pleistocene	ca. 0.7–0.6	18–17	[45,46]		
Borgonuovo	<i>Hippopotamus</i> sp.	[63]	early Middle Pleistocene	ca. 600	15	[64]		

Table 1. Cont.

Sites	Previous Attribution	References for Previous Attribution	Geochronology	Age (Ma)	MIS	References for Chronological Assignment	Analyzed in This Work	Current Attribution
Cava di Breccia—Casal Selce 2	<i>Hippopotamus antiquus</i>	[2]	early Middle Pleistocene	0.615–0.611	15	[2,55]	X	<i>Hippopotamus antiquus</i>
Isernia La Pineta	<i>Hippopotamus antiquus</i>	[26]	early Middle Pleistocene	ca. 600	15	[65]	X	<i>Hippopotamus antiquus</i>
Maglianella	<i>Hippopotamus antiquus</i>	[36]	early Middle Pleistocene	ca. 600	15	[55]		
Terranera			early Middle Pleistocene	ca. 600	15	[66]	X	<i>Hippopotamus antiquus</i>
Cava Montanari	<i>Hippopotamus amphibius</i>	[22]	Mid Middle Pleistocene	ca. 540–460	13	[22]		
Cava Nera Molinario	<i>Hippopotamus</i> sp.	[55]	mid Middle Pleistocene	ca. 500	13	[55]	X	<i>Hippopotamus</i> sp.
Ficoncella	<i>Hippopotamus</i> sp.	[67]	mid Middle Pleistocene	499–441	13	[67]		
Fosse della Bufala	<i>Hippopotamus</i> cf. <i>antiquus</i>	[68]	mid Middle Pleistocene	ca. 600–500	15	[68]		
Monte Antenne	<i>Hippopotamus amphibius</i>	[69]	Mid Middle Pleistocene	ca. 500	13	[55]	X	<i>Hippopotamus amphibius</i>
Osteria Moricone	<i>Hippopotamus</i> cf. <i>antiquus</i>	[68]	mid Middle Pleistocene	ca. 600–500	15	[68]		
Ponte Molle	<i>Hippopotamus</i> ex gr. <i>antiquus</i>	[70]	Mid Middle Pleistocene	ca. 540–460	13	[70]	X	<i>Hippopotamus</i> cf. <i>amphibius</i>
Rignano Flaminio	<i>Hippopotamus</i> cf. <i>amphibius</i>	[71]	mid Middle Pleistocene	ca. 500	13	[71]	X	<i>Hippopotamus</i> sp.
Tor di Quinto	<i>Hippopotamus</i> sp. and <i>Hippopotamus antiquus</i>	[72]	mid Middle Pleistocene	ca. 500	13	[41]	X	<i>Hippopotamus amphibius</i>
Trentangioli			early Middle Pleistocene	ca. 500	13	This work	X	<i>Hippopotamus amphibius</i>
Castel di Guido	<i>Hippopotamus</i> sp.	[73]	mid Middle Pleistocene	ca. 400	11	[73–75]		
Collina Barbattini	<i>Hippopotamus</i> sp. and <i>Hippopotamus antiquus</i>	[60,76,77]	mid Middle Pleistocene	ca. 400	11	[60,75,76]	X	<i>Hippopotamus</i> sp.
Fontana Ranuccio	<i>Hippopotamus amphibius</i>	[78]	mid Middle Pleistocene	ca. 400	11	[79]		
Malagrotta	<i>Hippopotamus</i> sp.	[80]	mid Middle Pleistocene	ca. 400	11	[60,75,80]		
Serbaro di Romagnano	<i>Hippopotamus amphibius</i>	[81]	mid Middle Pleistocene	ca. 400	11	[82,83]	X	<i>Hippopotamus</i> sp.
Batteria Nomentana	<i>Hippopotamus (Tetraprotodon) major</i>	[84]	late Middle Pleistocene	0.370–0.290	9–8	[41]	X	<i>Hippopotamus amphibius</i>
Sedia del Diavolo	<i>Hippopotamus</i> cf. <i>amphibius</i>	[24]	late Middle Pleistocene	0.370–0.290	9–8	[41]	X	<i>Hippopotamus amphibius</i>

Table 1. Cont.

Sites	Previous Attribution	References for Previous Attribution	Geochronology	Age (Ma)	MIS	References for Chronological Assignment	Analyzed in This Work	Current Attribution
Vigne Torte	<i>Hippopotamus</i> sp.	[72]	Late Middle Pleistocene	0.370–0.290	9–8	[41]	X	<i>Hippopotamus</i> sp.
Villa Chigi	<i>Hippopotamus amphibius</i>	[72]	Late Middle Pleistocene	0.370–0.290	9–8	This work	X	<i>Hippopotamus</i> sp.
Grotta Romanelli—ISU1-2	<i>Hippopotamus antiquus</i>	[26]	late Middle Pleistocene	0.320–0.200	9–7	[85]	X	<i>Hippopotamus</i> sp.
Casal de' Pazzi	<i>Hippopotamus</i> cf. <i>amphibius</i>	[86]	late Middle Pleistocene	ca. 240	7	[86]		
Torre del Pagliacetto—upper level	<i>Hippopotamus</i> sp.	[26,87]	late Middle Pleistocene	0.270–0.240	7	[88]		

Hippopotamus remains were also found at Cesi, a site located in the Colfiorito basin, near the aforementioned locality of Collecortu [49]. The state of preservation of the limited number of dental and postcranial bones prevents their specific identification [49]. In the same area, other hippopotamus remains were accidentally discovered at Colle Lepre, thanks to agricultural activities [34]. The sample, including cranial fragments, teeth, and postcranial bones, was ascribed to *H. gr. H. antiquus* [34].

An interesting mammal record was collected from the Frantoio deposit, located in the proximity of the Arda river [50]. Two hippopotamus femurs, belonging to juvenile individuals, were identified, but considering the limited taxonomic value of the remains, they were attributed to *Hippopotamus* sp. [50].

A key site for the Italian Land Mammal Biochronological scheme is Slivia, which gave the name of the last Epivillafranchian faunal unit ([11], Galerian in [1]). The deposit consists of an ossiferous breccia developed in a karst cavity, which was exposed by quarry activities during the XX century [51]. Hippopotamus remains collected during illegal excavations [51] were presented by [52]. The authors ascribed them to *H. amphibius*, but later, they were considered *Hippopotamus* sp. by [51].

Four remains were found at Imola: a fragment of a mandible, two fragments of a lower canine, and a pelvis [53]. The authors attributed, with uncertainty, the sample to *H. amphibius* (?).

The rich sample of Cava Redicicoli was recently examined by [40], who attributed the remains to *H. cf. antiquus*. The sample included several complete postcranial bones, in addition to a number of dental remains, which allowed the expansion of the knowledge on Epivillafranchian hippopotamus variability.

A fragmentary femur was found at Monte delle Piche, a deposit located in an area of Rome discovered during the XIX century ([56] and references therein). Due to its state of preservation, the femur was attributed to *Hippopotamus* sp. [56].

In the Middle Pleistocene, the hippopotamuses were widely dispersed in the Italian Peninsula, especially in the Rome basin (Figure 1; Table 1).

Five postcranial bones recovered at Monte Oliveto were attributed to *Hippopotamus antiquus* (*H. major* considered synonym of *H. antiquus*) [62].

A complete mandible and other isolated remains were accidentally found at Ortona during construction works [58]. The fossils were ascribed to *H. antiquus* by [34].

An interesting record comes from the lacustrine level of Maglianella, a locality in the area of Rome described by [89]. The deposit was located approximately along the Maglianella Road at the level of the intersection with the Aurelia Statal Road (ca. 11 km of the Aurelia Statal Road). One articulated skeleton with its skull and other remains, including two crania, were found at Maglianella. The first skull was considered by [25] to be the holotype of *Hippopotamus tiberinus*, and the other two crania were subsequently described to expand the known variability of this form [26]. As aforementioned, *H. tiberinus* is now considered a synonym of *H. antiquus* (see [36] for discussion). Nonetheless, the Maglianella record offers an important insight into the morphological variability of Middle Pleistocene hippopotamuses, and more generally, the site yielded one of the latest occurrences of *H. antiquus* in the Italian Peninsula.

Another important skull attributed to *H. amphibius* was found at Tor di Quinto (urban area of Rome), but for a long time, remained of uncertain geographical provenance and stratigraphical context and hence was not properly considered in reconstructing the evolution of Quaternary hippopotamuses. Fabiani & Maxia [90] first described the hippopotamus skull and indicated it was recovered from Cava Montanari ("Cava" means quarry in Italian). Subsequently, other authors doubted the provenance of the skull and suggested it could have been collected from another quarry (always opening in the Tor di Quinto area), Cava Nera Molinario, ascribed to the Middle Pleistocene (MIS 13, [24,37,41]). The skull from Tor di Quinto, nowadays part of the historical collection of the MUST, was recently restudied after the end of the restoration work carried out in 2021 [22]. The results of this work confirmed its taxonomic attribution as *H. amphibius* and supported the

hypothesis published by [90], where Cava Montanari was indicated as the toponym of its provenance. This, integrated with sedimentological analysis and the revision of historical and updated geological and topographic maps, allowed the specimen to be chronologically attributed to the Middle Pleistocene, precisely between 560 ka and 460 ka [22]. According to these recent results, the Cava Montanari skull represents the earliest attested occurrence of *H. amphibius* in Europe.

Hippopotamus remains were also collected from the Cretone basin, where several deposits were identified [68]. Fossils were found at Fosso delle Bufala and Osteria Moricone (one specimen at each site) and attributed to *Hippopotamus* cf. *antiquus* [68]. The authors identified a first phalange but did not specify which site the specimen came from (Fosso della Bufala or Osteria Moricone). A second phalange was also recovered from this area, but no data were reported on this specimen.

Aureli and coauthors [67] reported the presence of *Hippopotamus* sp. from La Ficoncella, but without information about the findings.

Along the Via Aurelia, in the area of Rome, several sites dated to the mid-late Middle Pleistocene have been discovered, and several of these also yielded hippopotamus remains (Figure 1; Table 1). The first is Castel di Guido, the most important site in this area for both the quality of the fossil record and the human presence documented based on an isolated fossil and a considerable number of artifacts [91]. The mammal sample was described by [73], who attributed a fragment of an incisor and a distal epiphysis of the fourth metacarpal to *Hippopotamus* sp.

The second locality is Malagrotta, where vertebrate remains were described by [80]. Similarly to other Middle Pleistocene deposits, the two remains, a fragment of a vertebra and a fragment of a metacarpal, were ascribed to *Hippopotamus* sp.

The third locality is Torre del Pagliacetto (or Torre in Pietra), where hippopotamus material was collected from the upper level. Four dental fragments were attributed to *H. amphibius* [87]. According to [26], these specimens possess no diagnostic features for specific attribution.

Fossil remains from other sites located along the Via Aurelia are described in our work (see Section 4).

Hippopotamus material was found at Fontana Ranuccio, one of the most important localities for human evolution in Quaternary Europe (e.g., [79,92]). Initially, a single canine fragment was ascribed to *Hippopotamus* sp. by [93]. Several fieldwork activities were carried out later in the work of [93], and a rich vertebrate sample was recovered (a total of 1360 mammal remains [78]). According to [78], 11 isolated specimens were attributed to *H. amphibius*.

The latter site of the urban area of Rome is Casal de' Pazzi, excavated in the 1980s, and nowadays, part of the deposit is still preserved in a museum aptly named Casal de' Pazzi Museum (see [94] for discussion). The hippopotamus sample, consisting of a fragment of an upper canine, a fragment of a lower canine, a lower deciduous tooth, and two lower third molars, was ascribed to *H. amphibius* [86].

Three other Middle Pleistocene records are excluded from this work since the fossils were not fully described, and/or their chronostratigraphic setting needs to be revised.

The first is Pignataro Interamna, initially described by [95]. The findings included a nearly complete mandible of a hippopotamus, in addition to other postcranial remains. The sample, now stored at the American Museum of Natural History of New York, was attributed to *H. amphibius* (*H. antiquus* for [26]). Additional dental and postcranial remains, also ascribed to common hippopotamuses, were collected during the 1930s and are currently stored at the Paleontological Museum of the Naples University Federico II [96]. These specimens need to be re-examined, as does their chronostratigraphic assessment.

The second is the Mercure basin, where hippopotamus remains were collected in different localities [97]. For instance, several authors [96,98,99] reported the presence of hippopotamus teeth from the lignite bed of Fornaci, attributed to *H. amphibius*. At Calorie, isolated teeth were ascribed to *H. antiquus* [97]. These fossils are dispersed among different

repositories, including the Civic Museum of Natural History of Milan, the Paleontological Museum of the Naples University Federico II, and the Natural Museum of Pollino. Fossils collected in the Mercure basin were generally dated to the early Middle Pleistocene (0.7–0.5 Ma; [100] and references therein). Nevertheless, a review of the fossil materials and a better definition of their chronostratigraphic contexts is needed.

The last important sample excluded from this work is the skeleton recovered from Sant’Oreste (MPUR/V 1950). The material of Sant’Oreste is preserved at the Earth Science University Museum (MUST), and the skeleton MPUR/V 1950 is displayed in the vertebrate hall (now closed for restoration work). According to [25], the skeleton represented the paratype of *H. tiberinus*. By contrast, Petronio [36] stated that the skull is slightly deformed due to taphonomic processes, and several parts were reconstructed during restoration work carried out during the second part of the XX century. In 2021, a new restoration project started on mammal skeletons displayed at the MUST, including MPUR/V 1950 from Sant’Oreste. This work is still in progress, and therefore, the material is excluded from our review.

### 3. Materials and Methods

The fossil remains described in this work were recovered from a number of Italian localities and are preserved in different museums and/or institutions (Figure 1, Table 1): 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): Batteria Nomentana, Campo di Merlo, Cava Alibrandi, Cava Arnolfi, Collina Barbatini, Monte Antenne, Ponte Molle, Rignano Flaminio, Sedia del Diavolo, Tor di Quinto Vallinfreda, Vigne Torte and Villa Chigi; Laboratorio PaleoFactory, Sapienza Università di Roma (PF): Bussi, Cava di Breccia di Casal Selce, Grotta Romanelli; Museo Archeologia Nazionale “Mario Torelli” (MANV; Venosa): Notarchirico, Terranera and Trentangioli; Museo di Paleontologia e Preistoria “Piero Leonardi” (MPPL): Isernia La Pineta; Istituto Italiano di Paleontologia Umana (IsIPU, Anagni): Cava Nera Molinaro, Collina Barbattini, Grotta Romanelli; Museo delle Civiltà (MUCIV, Roma): Grotta Romanelli; Museo di Storia Naturale di Verona: Serbaro di Romagnano; and Collegio San Giuseppe—Istituto De Merode: Ponte Molle. Other comparative materials were also considered: Cava Redicicoli (MUST, IsIPU), Monte delle Picche (MUST), and Saticula (PF). Extant material of *H. amphibius* was also studied: one complete mounted skeleton and one complete skull displayed at the Museo di Anatomia comparata “Battista Grassi”, Sapienza Università di Roma, and the skull from PF. In addition to the material directly examined, we considered literature data on Italian Quaternary hippopotamuses and extant *H. amphibius* (see Table 1). We also included the material of *H. amphibius* from Barrington (Britain) as representative of this species for size comparison.

The taxonomic attribution of the hippo specimens was carried out by morphological and biometric comparisons of the studied materials with corresponding specimens of other fossils and extant hippopotamuses [24,26,33].

Following [26], six dental variables were 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.

The measurements reported by [33] on extant hippopotamuses were excluded since they were taken differently from [26] and later studies.

Size variations in fossil and extant hippopotamuses were investigated by comparing the maximum length of the upper first ( $M^1$ ), second ( $M^2$ ), and third molars ( $M^3$ ), and the lower first ( $M_1$ ), second ( $M_2$ ), and third molars ( $M_3$ ). We grouped the Italian fossils of *H. antiquus* from the Early Pleistocene in the Villafranchian and Epivillafranchian samples (following the Mammal Ages identified in the Italian biochronological scheme). We considered the sample from the Britain locality of Barrington (the only fossil group recovered from a site not located in Italy) as representative of fossil *H. amphibius*. Finally, extant specimens of *H. amphibius* were also included.

A standard bivariate plot of the  $M_2$  length vs.  $M_3$  length of fossil and extant hippopotamuses was also generated in order to investigate possible size differences among groups.

#### 4. Newly Studied Hippopotamus Material in Italy

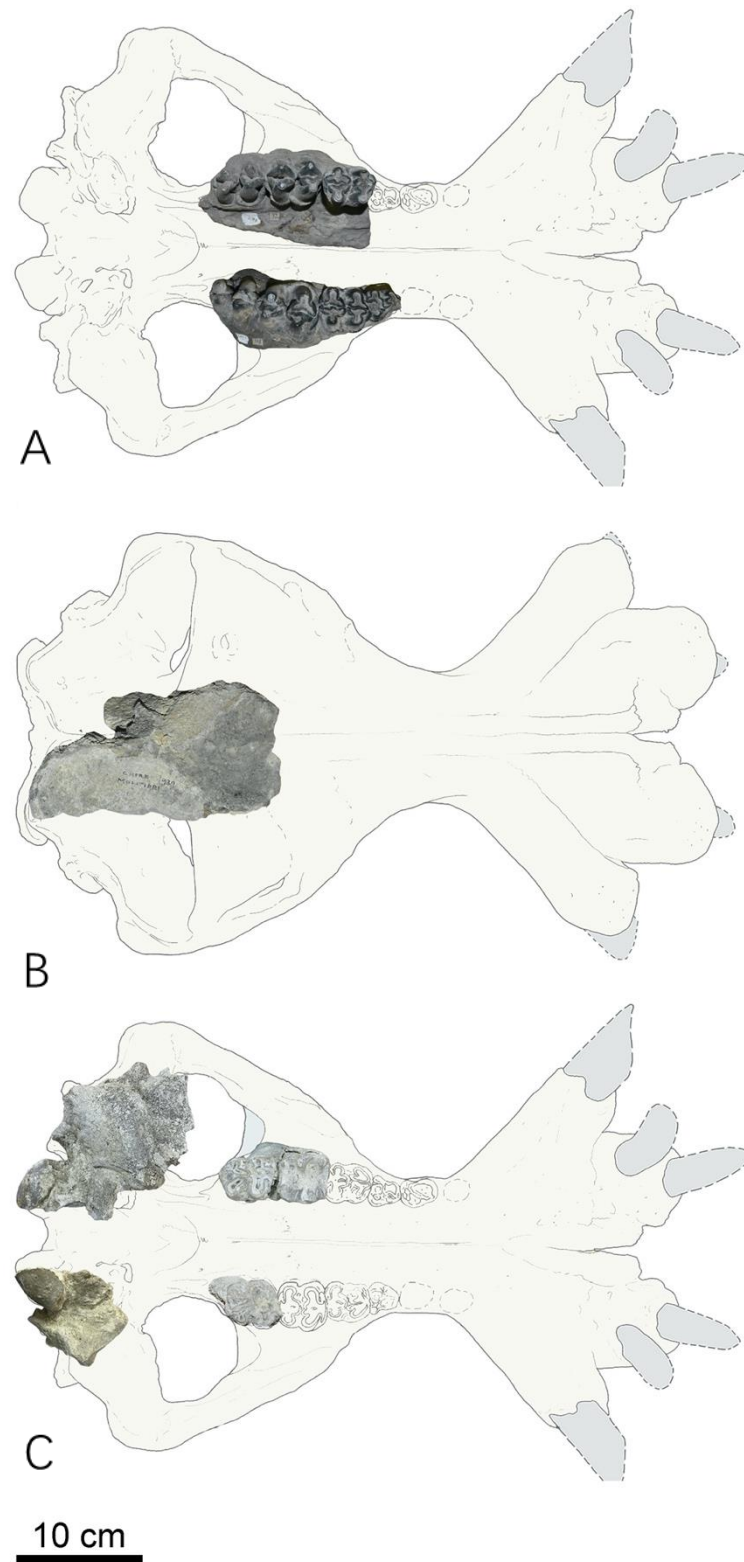
##### 4.1. Vallinfreda

The material was accidentally discovered in yellowish sands near Vallinfreda village by a farmer during the XIX century [59]. The hippopotamus sample included several specimens, among which was a cranium that was probably broken at the time of discovery [101]. The authors of [24] only studied the complete mandible, attributing it to *Hippopotamus* cf. *antiquus*. The authors of [59] carried out a systematic review of the fossils found in the Oricola–Carsoli intramontane basin and their chronostratigraphic setting. The authors attributed the fossils to the early Middle Pleistocene (Ponte Galeria FU). The study of all remains from Vallinfreda confirms that in the MUST collection are preserved specimens belonging to the same damaged cranium mentioned by [101], the right and left maxillaries, and a fragment of the left premaxillary and maxillary (including  $I^2$  and  $C^X$ ; Figures 2 and 3). It cannot be excluded that the mandible was associated with the cranium, since the teeth of these four specimens possess a similar degree of wear. The sample shows features that are generally observed in *H. antiquus*: a concave profile of the mandibular corpus in lateral view and parallel grooves on the external surfaces of the canines [22,24,42].

##### 4.2. Venosa Basin

The Venosa Basin is characterized by the preservation of long archeological sequences in volcano–sedimentary complexes linked to the eruptive activity of the Vulture stratovolcano, mainly dated to the Middle Pleistocene [102]. Notarchirico, discovered in 1979, is one of the most important and best-known sites of the area, yielding a 7 m thick sequence of fluvial sediments including eleven archeological and paleontological levels [103]. Recent  $^{40}\text{Ar}/^{39}\text{Ar}$  ages and ESR dates have revised the chronology of the sedimentary sequence excavated by Marcello Piperno [103] and constrained archeological levels  $\alpha$  to F to between ca. 610 and 675 ka (MIS 16, [104]). According to the new chronostratigraphic setting, the hominin femur fragment found in level  $\alpha$  is the oldest human finding in the Italian Peninsula. New excavations coordinated by one of the authors (MHM), authorized by the Soprintendenza Archeologia Belle Arti e Paesaggio of the Basilicata Region, began in 2016, with the aim to better investigate the bottom of the sequence [15,70,105]. Five sedimentary units have been identified, including five archeo- and paleosurfaces (G, H, I1, I2, and J). These levels were dated by  $^{40}\text{Ar}/^{39}\text{Ar}$  to between  $690.3 \pm 5.8$  ka and  $695.2 \pm 6.2$  ka, which corresponds to the end of MIS 17. As such, Notarchirico is one of the key sites for better understanding the age of the earliest Acheulean occupations and the impact of climatic changes on mammal paleocommunities between 700 and 600 ka. During 2017–2018 fieldwork activities, three hippopotamus remains were found in levels G and I1, representing an addition to the species previously known at Notarchirico. Although the specimens recovered are of limited taxonomic value, they testified to the presence of hippopotamuses in southern Italy during the end of MIS 17.

Terranera is another locality in the Venosa Basin, though it is lesser known than Notarchirico and Loreto. The toponym Terranera probably indicates an area where several deposits (e.g., Cicoria, Mandorleto, Siniscalchi) were identified, but also systematically excavated ([106] and references therein). Two fieldwork activities were carried out during the first decades of the XX century, coordinated by Quintino Quagliati in 1909 and Ugo Rellini in 1914 ([106] and references therein). The archeological and paleontological materials of Terranera have been dispersed among several Italian institutions since the beginning of the research in the area (National Archeological Museum of Taranto, Museum of Civilizations [Rome], National Archeological Museum of Venosa, Italian Institute of Human Paleontology [Anagni], Museum of Paleontology, Naples University Federico II, Museum of origins, Sapienza University of Rome).



**Figure 2.** Cranial remains of *H. antiquus* from Vallinfreda (52a and 52; (A)) and *H. amphibius* from Cava Nera Molinario (IsIPU-CNM10, IsIPU-CNM11, IsIPU-CNM14, IsIPU-CNM15, IsIPU-CNM43; B,C). Fossil in dorsal (B) and occlusal (A,C) views.



**Figure 3.** Hemimandibles remains from the Italian Peninsula: *H. antiquus* from Vallinfreda (SN180FS; (1A,B)), Terranera (SN 1936; (2A,B)), and Campo di Merlo (24; (3A,B)); *H. amphibius* from Monte Antenne (128; (4A,B)) and Tor di Quinto (SN16; (5A,B)). Fossils in labial (A) and occlusal (B) views. Scale bar 10 cm.

Following the modern geological mapping of the Venosa Basin, three units are recognized in the area of Terranera: Monte San Marco Formation (Early Pleistocene), Foggianello Synthem (early Middle Pleistocene, ca. between 740 and 687 ka), and Barile Synthem (early Middle Pleistocene, ca. between 670 and 610 ka) [107]. The first formation, however, is related to marine deposition [107]. According to [108], fossils and artifacts were collected from a sand bed with the presence of volcanic material (number 3 in the deposit, ca. 1.2–1.5 m thick) in a succession characterized by the alternation of fluvio-lacustrine and volcanic levels [108], which, more generally, suggests continental deposition.

The fauna from Terranera was never described, except for a fragment of an antler attributed to *Megaceros* (= *Praemegaceros*) *solilhacus* by [66]. This species is also indicative

of an early Middle Pleistocene age, being its earliest occurrence in Isernia La Pineta (ca. 600 ka; [72]).

Among the fossils collected between 1928 and 1940 belonging to the Briscese collection and stored at Museo Archeologico Nazionale “Mario Torelli”, a nearly complete mandible and other remains of hippopotamuses are preserved (Figure 3). The mandible is long and slender and displays a concave basal profile of the mandibular corpus in lateral view. The isolated lower canines (not preserved in the mandible) have parallel grooves on the external surface. These features align with the morphology of *H. antiquus* [22,24,26].

Trentangioli (or Trentangeli) is another site located in the Venosa Basin, where mammal remains were collected during geo-paleontological surveys between 1928 and 1940 ([84] and references therein). The fossil material is currently stored at the National Archeological Museum “Mario Torelli” of Venosa, part of the Briscese collection. In the other deposits of the Venosa Basin, fossils were found in fluvio-lacustrine levels with abundant volcanic material and, therefore, attributed to the Middle Pleistocene. The sample consists of several dental remains, among which are two fragmentary lower canines. These display convergent grooves on the external surfaces, a feature shared with *H. amphibius* [22,24,26].

#### 4.3. Isernia La Pineta

The open-air archeological and paleontological site of Isernia La Pineta is considered a reference for studies of human evolution in Europe ([109] and references therein). The site was discovered during work for the Napoli–Vasto highway in 1978, in the proximity of the Isernia–Roma railway line. Decades of systematic excavations have been carried out, coordinated by one of the authors (CP) with the permission of Soprintendenza Archeologia Belle Arti e Paesaggio of the Molise Region, the “Direzione Regionale Musei Molise”, and the support of Ferrara University. The site yielded hundreds of fossil remains and artifacts, among which was a deciduous tooth attributed to *Homo cf. heidelbergensis* ([109] and references therein).

The age of archeological and paleontological levels of Isernia La Pineta was initially considered close to 700 ka and later dated at ca. 610 ka with the  $^{40}\text{Ar}/^{39}\text{Ar}$  method [65]. In 2015, the age was revised again, attributing Unit 4 (a tephra level) to  $586 \pm 1$  ka [109]. The authors also dated reworked volcanic material from levels 3coll, 3s10, and 3s6 (just above the main archeosurface, 3a), yielding an age of  $586 \pm 2$  ka,  $583 \pm 3$  ka, and  $587 \pm 2$  ka, respectively. The upper part of Unit 1 (U1) was dated with the  $^{40}\text{Ar}/^{39}\text{Ar}$  method at  $499 \pm 13$  ka [65].

The mammal assemblage is considered characteristic of the Galerian Mammal Age [73,110,111], giving the name to a Faunal Unit of the Italian biochronological scheme (see [1]). Hippopotamus remains were ascribed to *Hippopotamus cf. antiquus* [26,73]. The sample includes several dental remains, among which is a lower canine that displays parallel grooves on the external surface, as typically observed in *H. antiquus* [22,24,42].

#### 4.4. Bussi

The paleontological deposit of Bussi was never fully described but only mentioned in several geological works [57]. The locality is part of the Tirino valley, an intermontane basin of the Abruzzi Apennines [57]. *Hippopotamus antiquus* remains, associated with other fossils of *Elephas (=Palaeoloxodon) antiquus*, were found in a whitish silt level resulting from lacustrine deposition, identified as the Convento dei Cappuccini Unit by [57]. The mentioned unit was chronologically attributed to the early part of the Middle Pleistocene [57]. The hippopotamus remains from Bussi consist of several isolated dental remains and a fragment of a hemimandible. These specimens probably belong to the same skull and were likely disarticulated during the excavation. The lower canine, the only element useful for taxonomical purposes, displays parallel grooves on the external surface, a trait commonly observed in *H. antiquus* [22,24,42].

#### 4.5. Rignano Flaminio

A fluvial–lacustrine deposit exposed at Rignano Flaminio (north of Rome) was recently described by [71]. The base of the succession was represented by the Tufo Rosso a Scorie Nere, a deposit dated at approximately  $449 \pm 2$  ka [112]. The fossil-bearing level was attributed to MIS 11 (between 430 and 405 ka; [71]). The analysis of a radius/ulna attributed to *Hippopotamus cf. amphibius* revealed that this bone was intentionally fractured and retouched by humans [71]. The sample from Rignano Flaminio is preserved at the MUST. After examining the material, we suggest an open attribution to *Hippopotamus* sp. due to the lack of morphological features diagnostic at the species level.

#### 4.6. Serbaro di Romagnano

This locality is a karst-infilling deposit near the village of Romagnano. The vertebrate assemblages found in the cavities of the area were biochronologically dated based on the micromammal content [113]. However, no microvertebrate remains were identified at Serbaro di Romagnano [113]. According to [82,83], the mammal assemblage can be attributed to the Fontana Ranuccio FU (sites whose faunas are associated with this FU date to ca. 500–400 ka). Pasa [81] attributed two dental remains to *H. amphibius*: an upper third molar and a lower third molar. The latter tooth is in an advanced stage of wear, group XVIII, according to the scheme of [14], which should correspond to an age of 38 years. The measurements of this tooth are excluded from the biometric comparison. The limited taxonomical value of these remains prevents a specific attribution.

#### 4.7. Grotta Romanelli

Grotta Romanelli was immediately considered a key site for paleontological and archeological research on the Mediterranean Quaternary [114–117]. Its importance in the European context originates from the coupling of the extraordinary number of findings and the robust chronostratigraphic setting described by [118,119]. The author interpreted the basal conglomerate level as a Thyrrenian beach deposit (early Late Pleistocene), constraining the whole succession to approximately the last 128 ka. This schematic model was corroborated by radiometric datings performed at the end of the 1960s [120–122].

After more than 40 years of inactivity in the cave, a new project was started in Grotta Romanelli in 2015, coordinated by the Sapienza University of Rome under the direction of one of us (RS) and with the authorization of the Soprintendenza ai Beni Archeologici della Puglia (now Soprintendenza Archeologia Belle Arti e Paesaggio di Brindisi e Lecce). One of the main results of the new project was the review of the chronostratigraphic setting of the cave [85]. New geomorphological and geological data, in addition to new radiometric datings, revealed that the basal levels of the cave have to be ascribed to the late Middle Pleistocene (levels K and I *sensu* [118,119]; ISU1 and ISU2 *sensu* [85]).

Fossils from the lower levels stored at ISIPU were studied by [26] and attributed to *H. antiquus*. Other remains of hippopotamuses from the lower levels of Grotta Romanelli are preserved at MUCIV. The entire sample consists of isolated postcranial bones, generally of juvenile individuals (long bones show disarticulated epiphyses), and two deciduous teeth. These specimens are of limited taxonomic value, limiting the attribution to the genus *Hippopotamus*.

#### 4.8. Rome Area

The territory of Rome, including the urban area of the city and its surroundings, is generally known in the literature as Campagna Romana (Roman Campaign). This area has yielded an impressive archeological and paleontological record, collected in dozens of sites. The historical deposits of Rome were generally destroyed by the urban growth of the XX century or otherwise buried by roads, places, houses, train stations, etc., and are located in what today is the urban area of the city [123,124]. Since the Quaternary, the area of Rome was shaped by the action of the Tiber and Aniene Rivers, combined with the volcanic activity of the Alban Hills and the Sabatini Mounts. This could be schematized

as follows: the rivers hollowed out the fluvial valleys and coastal plain incisions during a glacial stage, filled with deposits, which often included pyroclastic products, during the following phases (e.g., [124–126]). The presence of volcanic materials (pumice, tephra, as primary deposition or reworked) in alluvial–deltaic sediments allows a reliable age to be obtained for many of these localities (obtained by radiometric dating or through correlations with previously dated deposits).

The Rome basin, however, can be divided into several areas where fossiliferous deposits show, more or less, a similar age.

#### 4.9. Cava Alibrandi, Cava Arnolfi, Campo di Merlo, and Cava di Breccia di Casal Selce

These four fossiliferous sites are located in the Ponte Galeria area, in the surroundings of Rome (at ca. 15 km from the center of the city). In this area, several quarries have been opened for the extraction of gravels used for construction works since the 1960s, exposing long geological successions studied by many authors ([55,127] and references therein). Fossils in this area, collected from the gravel and sand levels from many quarries, are commonly dated to the early Middle Pleistocene. The richness and completeness of the fossils collected in this area led paleontologists to identify Ponte Galeria as the first Faunal Unit of the Middle Pleistocene (ca. 700 ka).

Bonadonna [128] reported the presence of mammal remains at Cava Arnolfi (11 Km of Portuense Road), identifying a lower canine as *H. amphibius* (later considered *H. antiquus* by [36,129]). The lower canine displays parallel grooves on the external surfaces of the canines, features commonly detected in *H. antiquus* [22,24,42].

Capasso Barbato and Petronio [61] described remains collected at Cava Alibrandi (13.5 Km of Aurelia Statal Road). A rib was ascribed to *Hippopotamus* sp. by the authors, an attribution confirmed in this work.

Petronio [129] described a mandibular fragment found at Campo di Merlo (a quarry located in the proximity of the crossroad between the Magliana Road and Portuense Road; Figure 3). The fragment was attributed to *H. antiquus* based on a concave profile of the mandibular corpus in lateral view [129]. However, the material from Campo di Merlo, currently stored at the MUST, was probably recovered during the XX century and acquired by the museum during the early 1900s. In addition to the mandibular fragment, at Campa di Merlo, a lower canine was found, which displays parallel grooves on the external surfaces of the canines, a morphology shared with *H. antiquus* [22,24,42]. Following this, the attribution to *H. antiquus* proposed by [129] can be confirmed.

Additional mammal remains from Ponte Galeria were listed in [130], but the author mentioned a number of localities without providing information about the exact toponym of the provenance of the hippopotamus material. As aforementioned, the ages of these fossiliferous deposits are quite close, all attributed to the Ponte Galeria FU. Three dental remains, two fragments of a canine and a deciduous tooth, and other postcranial bones preserved at the MUST show only a general indication of Ponte Galeria. The canine, in particular, shows parallel grooves on the external surfaces of the canines, a trait generally observed in *H. antiquus* [22,24,42].

Cava di Breccia of Casal Selce is located along the Castel di Guido Road, near the Aurelia Statal Road in the proximity of the highway exit of Castel di Guido. The deposit preserves a long sedimentary succession, with two different fossiliferous levels (e.g., [2,55,72]). Abundant mammal remains were collected from the salmon sand level, which was correlated to the Santa Cecilia Formation [131], while [55] dated the pumice falls intercalating with this deposit at  $611 \pm 6$  ka. The hippopotamus sample includes several fragments of dental remains and a fragment of a femur attributed to *H. antiquus* in previous work (e.g., [2,55]). For taxonomical purposes, a fragmentary lower canine displays fairly parallel enamel ridges and grooves along the external surface. This feature is generally observed in *H. antiquus* [22,24,42].

#### 4.10. Cava Nera Molinario, Monte Antenne, Ponte Molle, and Tor di Quinto

The area of Tor di Quinto is located on the right bank of the Tiber River. Several quarries were opened for the extraction of gravels for building during the XIX and early XX centuries ([70] and references therein). The names of most of these deposits commonly correspond to those of the quarries (Cava means quarry in Italian), for example, Cava Nera Molinario or Cava Montanari. In the Tor di Quinto area, the fossil remains were collected by gravel and sand deposits quarried for the extraction of building materials [40,125]. The most important toponyms are Cava Montanari (described in Section 2), Cava Nera Molinario, Monte Antenne, Ponte Molle, and Tor di Quinto; all of these yielded hippopotamus remains.

The sedimentary succession of Cava Nera Molinario was carefully described by [132]. This is one of the few still-existing deposits in the urban area of Rome described during the XX century, which was revised by [133]. The authors recognized the presence of three volcanic deposits: Tufo del Palatino ( $533 \pm 2$  ka), Tufo Giallo di Prima Porta ( $516 \pm 1$  ka), and Tufo Rosso a Scorie Nere ( $452 \pm 2$ – $447 \pm 7$  ka). Fossils have been attributed to the Valle Giulia Formation (MIS 13, [55,133]). Material from Cava Nera Molinario was attributed to *Hippopotamus* sp. [55], but without a formal description. Five specimens, the left and right fragmentary maxillaries, the right and left fragmentary occipital–parietal portions, and a fragment of parietal–frontal bone, could belong to the same cranium (Figure 2). The studied sample, however, is of poor taxonomic value and, therefore, is ascribed herein to *Hippopotamus* sp.

In general, the Tor di Quinto area was first described by [134], who explored several quarries opened at that time in this district but also observed several successions exposed during the construction of some main roads, for example, the Cassia and Flaminia roads. One of the sites described by [134] was Tor di Quinto (or Torretta di Quinto). The geological setting of this area was recently revised by [70], where a number of boreholes were integrated with the data published during the XX century and collected in still-existing deposits in this district. The results demonstrated that the majority of the fluvial deposits with gravels and sands and rich in volcanic material can be ascribed to the Valle Giulia Formation [70]. A similar age was also proposed by [56], who attributed the fossils from Tor di Quinto to the Valle Giulia Formation.

The hippopotamus material from Tor di Quinto includes two fragments of a hemimandible, isolated teeth, a fragmentary tibia, and a vertebra (Figure 3). Unfortunately, one of the two hemimandibles preserved only the portion of the first and second molars, while the second consists of the portion between the third premolar and the third molar, but the mandibular corpus is damaged, and the basal profile cannot be observed. Two lower canines show convergent grooves on the external surface, a trait commonly observed in *H. amphibius* [22,24,42].

The stratigraphical succession of Monte Antenne was described by [69], who reported the presence of sands at the base of the deposit with several volcanic levels above.

The remains of hippopotamuses were collected from the sandy levels, where a complete skull was identified during the first geo-paleontological survey. The author stated that, after its discovery, the skull was left in its original position in the outcrop, to be recovered the next day. Unfortunately, the skull was significantly damaged, and only a fragment of the left hemimandible and several isolated teeth were found [69]. These were ascribed to *H. amphibius* [69]. The sedimentary succession of Monte Antenne was attributed to the Valle Giulia Formation by [55]. According to [69], the hippopotamus material from Monte Antenne belonged to a single individual. The hemimandible consists of a fragment of the portion between the fourth premolar and the third molar. Considering its fragmentary status, the morphology of the lateral profile (concave or convex) cannot be recognized. The two lower canines show convergent grooves on the external surface. This feature would confirm the attribution proposed by [69] to *H. amphibius*.

Ponte Molle is another historical locality of Tor di Quinto, well known in the literature thanks to the richness and completeness of the fossil specimens [70]. The chronostratigraphic setting of the site was recently redefined, and the whole deposit was attributed to

the Middle Pleistocene [70]. In particular, the fossiliferous level, gravel with a sandy matrix and volcanic materials, was constrained to between 540 ka and 460 ka [70]. The faunal assemblage identified at the site suggested an interglacial period (MIS 13). The authors of [70] discussed the problematic taxonomical attribution of Quaternary hippopotamuses. The authors ascribed the fossils from Ponte Molle to *H. ex gr. antiquus*, exclusively based on the medium size of the remains. This attribution can be revised following the work of [22].

The sample from Ponte Molle includes two fragments of mandibles, several isolated teeth, and postcranial bones. The morphological analysis revealed that the corpora of the two hemimandibles were damaged, and the lateral profile could not be observed. Three lower canines from Ponte Molle show convergent grooves on the external surface, whereas only one possesses a parallel arrangement. Ponte Molle yielded one of the most impressive vertebrate records of Quaternary mammals, with thousands of remains dispersed among several Italian institutions since the early stages of research. Fossils were mainly found at the end of 1800 and in the early decades of 1900 in several quarries opened in the Tor di Quinto area or in long, extensive sedimentary succession exposed by construction works on the two main roads of this district (Flaminia and Cassia roads; [70]). As discussed by [70], the putative presence of fossils recovered from older deposits outcropping in the area of Tor di Quinto cannot be excluded. Another possibility is that some fossils could have been removed from older deposits due to the activity of the Tiber River and been deposited in the fluvial levels of Ponte Molle, resulting in reworked elements.

The overall features of the fossils from Ponte Molle fall within the variability of extant hippopotamuses, but considering the variation in lower canine morphologies, the sample is attributed to *H. cf. amphibius* [22,24,42].

#### 4.11. Collina Barbattini—Via Aurelia Km 18.0–19.3

A number of Middle Pleistocene localities were discovered during the XX century along the Aurelia Statal Road. Several of these take their name from the kilometer of the Statal Road in the proximity of the deposits.

Two main areas can be identified: the first is the hill located between 18.0 km and 19.3 km of the Aurelia Statal Road toward the city of Rome, called Collina Barbattini; the second is at about 18.9 Km of the Aurelia Statal Road toward the city of Civitavecchia [76,77].

Paleontological findings in this area were initially collected by Ernesto Longo and later donated to the MUST. This sample, in addition to other mammal fossils found in the same area, was described by [77]. Additional remains were found between 18 and 20 km during work on the motorway junction of Castel Guido [76]. These sites are geographically really close to each other, and fossils were recovered from a fluvial–lacustrine level correlated to the San Paolo Formation (MIS 11) by [75].

At Collina Barbattini, [77] reported the presence of four dental remains of juvenile individuals (Longo collection) attributed to *Hippopotamus* sp. and three other fossils, including a fragment of a canine, a tibia, and a second metacarpal, ascribed to *Hippopotamus* cfr. *antiquus*. For the tibia and metacarpal, we previously mentioned that the putative postcranial characters proposed by [26] for specific attribution need to be confirmed. At the moment, a taxonomic attribution based on size repartition is avoided. The canine has only its apical portion, and it would seem to belong to a juvenile individual (as for the other teeth of the Longo collection). Even these three fossils are ascribed to *Hippopotamus* sp. here.

The fossils listed by [76] from Collina Barbattini were also attributed to *Hippopotamus* sp. The sample consists of a IV metatarsal, a fragment of a humerus, and four fragmentary dental remains. These fossils are of limited taxonomic value, and therefore, the attribution proposed by [76] is confirmed here.

#### 4.12. Batteria Nomentana, Sedia del Diavolo, Vigne Torte, and Villa Chigi

These deposits are located in the proximity of the Aniene River, just outside the old Roman wall that encloses the center of Rome. A number of quarries were opened for

the extraction of building materials and commonly show the “Tufo litoide” as the basal level (e.g., [84,135,136]). As aforementioned, the volcanic deposit historically called “Tufo litoide” is today known as Tufo Lionato, a pyroclastic-flow deposit erupted from the Colli Albani volcanic district dated to approximately 367 ka, representing an important chronostratigraphic marker in the area of Rome [137].

Sedia del Diavolo is undoubtedly one of the most famous sites in this part of Rome for its paleontological content and the great number of papers that described the site and its stratigraphic succession. Important Italian scientists wrote about Sedia del Diavolo, such as Alberto Carlo Blanc, Alessandro Portis, Enrico Clerici, Giuseppe Ponzi, Guglielmo Terrigi, and Romollo Meli ([138] and references therein). The deposit can be divided into three main units, listed from bottom to top, as follows: the Tufo Lionato deposit, the fluvial gravel levels, and the pumiceous ash flow deposit. The third-listed deposit was dated at approximately 284 ka by [139]. Caloi and coauthors [138] attributed the fragmentary dental remains to *Hippopotamus* cf. *amphibius*, since the lower canines show convergent grooves on the external surface. These fossils are stored at the MUST, and our review confirms this morphology, generally observed in extant *H. amphibius* [22,24,42]. However, a nearly complete mandible is currently displayed in the exhibition called “Animals, Plants, Rocks and Minerals: The ISPRA Collections” in the Museum of Civilization. Considering its important taxonomic value, the study of this fossil can help in the classification of hippopotamuses from Sedia del Diavolo.

The stratigraphic succession of Batteria Nomentana, located near the crossroad between the homonymous road (Batteria Nomentana) and Nomentana road, was discovered by [84]. When Meli described the deposit, he highlighted a strong resemblance to that exposed in the well-known site of Sedia del Diavolo (only 500 m from Batteria Nomentana). The fossiliferous levels of Batteria Nomentana were constrained from 367 to 287 ka by [56]. Three fragmentary lower canines and a second lower incisor were collected at the site. The canines possess convergent grooves on the external surface, a typical trait of extant *H. amphibius* [22,24,42].

Fossils from Vigne Torte were initially mentioned by [136] when the author described the bovine cranial material preserved in the “Museo geologico universitario di Roma” (most of the collections today are part of the MUST). The name Vigne Torte indicated a number of quarries opened along the Salaria Road for the extraction of gravels from 1894 to 1896 [136]. As for the other sites in this district, the lower deposit of these quarries was the Tufo Lionato [136]. The deposition of the fossils collected from the fluvial gravel levels of Vigne Torte was constrained to approximately between 367 and 287 ka [56]. Remains of hippopotamuses were attributed to *Hippopotamus* sp. by [72] but were never described. The sample consists of several isolated dental remains and one astragalus. These specimens are of poor taxonomic value and are generically attributed to *Hippopotamus*.

The last deposit in this area is Villa Chigi, which was never described in the literature. The authors of [72] only listed the mammal remains found at Villa Chigi and housed in the MUST. By analyzing the original specimen labels, it is possible to note that the fossils were collected from the gravel levels of the Aniene River from a quarry opened near the Villa Chigi (“Nelle ghiaie dell’Aniene (quaternarie) alla cava di breccia presso la Villa Chigi fuori porta Salaria”). The deposit is not far from the Vigne Torte quarries always opening for the extraction of gravels for building materials. Also, considering the geological context of this area, where a number of fossils were found in fluvial–lacustrine deposits attributed to the Aurelia Formation, it could be assumed that the age of the fluvial gravel deposit of Villa Chigi is similar to that of other localities known in this geographic area (Monte delle Gioie, Prati Fiscali, and others described here). One fragment of a maxillary and three isolated teeth were found at Villa Chigi. Considering the limited taxonomic value of these remains, the sample is attributed to *Hippopotamus* sp.

## 5. Discussion

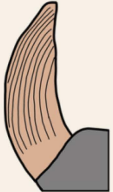

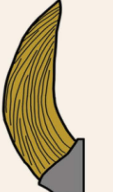
### 5.1. Taxonomic Attribution

The taxonomic attribution of Pleistocene hippopotamuses is mainly based on cranial morphologies [22,24,26]. Diagnostic features in the postcranial bones were proposed by [26], but these were adopted in only a few works. When skulls are unavailable, taxonomic identification is often based on chronological grounds or limited to the genus level (Table 1). Several examples come from the Italian sites of Slivia [51], Monte delle Picche [56], Pagliare di Sassa [46], and Borgonuovo [63], whose remains are attributed to *Hippopotamus* sp.

One operational strategy for the identification of postcranial bones considered the dimensions of the remains, with large-sized specimens attributed to *Hippopotamus antiquus* [24,36]. Conversely, the large sample from Cava Redicicoli highlighted that Pleistocene hippopotamuses display huge variations and, more generally, that the size of the bones can also be affected by sex and age [22]. The oversimplified model involving the attribution of large-sized bones to *H. antiquus* and medium- and small-sized bones to *H. amphibius* cannot be confirmed. The differences presented by [26] should be tested on other Pleistocene samples so that they could virtually represent another tool for the specific identification of fossil hippopotamuses. Keeping these considerations in mind, it is understandable why this work is based on cranial and dental materials.

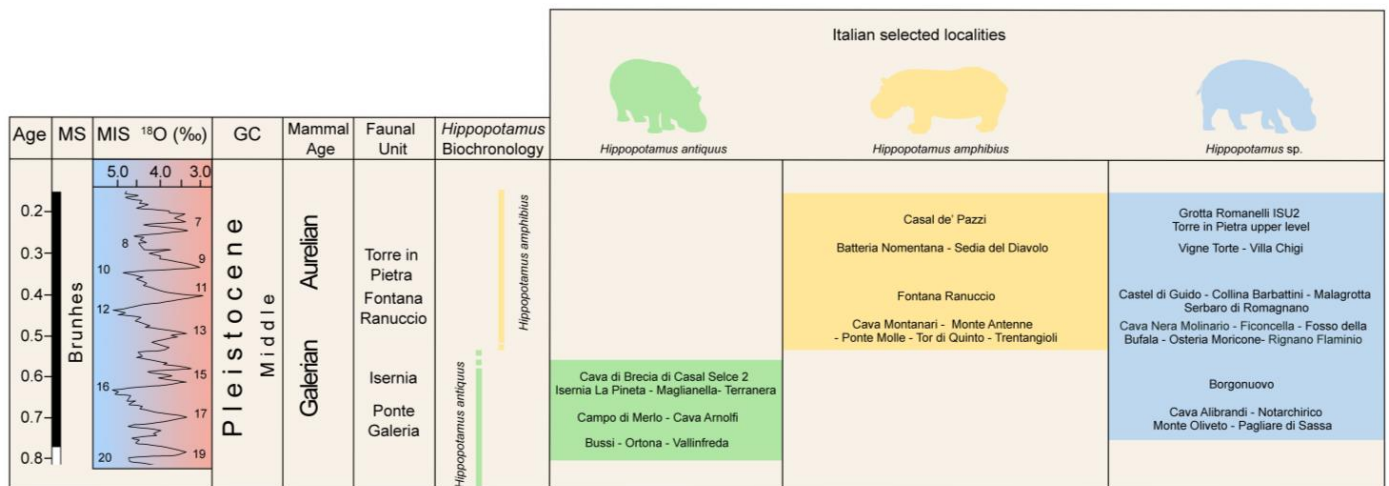
Mandibular remains were found in several of the studied sites, but only those from Terrenera and Vallinfreda display useful features for specific identification. The two fossils possess a concave profile of the mandibular corpus in lateral view, a feature typically observed in *H. antiquus* [22,24,26]. For the identification of other fossil samples, the only character that can be analyzed is the arrangement of the enamel ridges and grooves on the external tooth surfaces of the lower canines. Initially, this feature was considered diagnostic by [42], who analyzed the sample from Valdarno Superiore (Upper Valdarno). The authors stated that parallel enamel ridges and grooves on the external tooth surfaces of lower canines were observed in 15 out of 16 remains. Subsequently, [24] confirmed the validity of this feature for specific identification, but only if concurrently observed together with other diagnostic characters on the same specimens. The author of [26] argued that convergent enamel ridges are rather frequent in *H. amphibius* (extant and fossils), while both morphotypes are observed in *H. antiquus*. It should be considered that [26] set the dispersal of *H. amphibius* only during the early Late Pleistocene, attributing the entire Middle Pleistocene to *H. antiquus* (= *H. tiberinus*). Another aspect is that the author reported no detailed information on the distribution of these morphotypes in the *H. antiquus* record. Recent results published by [40] reinforced the view that *H. amphibius* dispersed in Europe during the Middle Pleistocene (ca. 500 ka), dismantling the hypothesis of [26]. The parallel arrangement of the enamel ridges and grooves on the external surfaces of the lower canines, in addition to the Valdarno Superiore, was identified in specimens of *H. antiquus* from the Italian sites of Cava Redicicoli [22], Cava Santarelli [45], Chiusi [41], Colle Curti [26,43], Ortona [34], and Saticula [48]. Other European remains of *H. antiquus* show this feature, as, for example, documented at Incarcal [27] and Untermassfeld [30]. A parallel arrangement is also found in several samples analyzed in this work, such as Terranera and Vallinfreda, attributed to *H. antiquus* (Table 2). A convergent arrangement of the enamel ridges and grooves on the external surfaces of the lower canines was observed in the skull of Cava Montanari [40] and in the sample from Barrington [26], attributed to *H. amphibius*. In the studied material, a convergent arrangement was observed in several samples attributed to the mid-to-late Middle Pleistocene (Table 2).

**Table 2.** Morphology of hippopotamus canines. Light pink—Epivillafranchian specimens of *H. antiquus*; green—Middle Pleistocene specimens of *H. antiquus*; light orange—Middle Pleistocene specimens of *H. amphibius*. Canines drawn from [26]: *H. antiquus* from Valdarno Superiore—National History Museum of Paris (3866); *H. amphibius* from Barrington—Sedgwick Museum of Cambridge (D 3980); extant *H. amphibius* from Zoo—Comparative Anatomy Laboratory of Paris (1917–249).

			Grooves on the external surface of canines		
			Parallel	Convergent	
					
Sites	Species	References	Fossil <i>H. antiquus</i>	Fossil <i>H. amphibius</i>	Extant <i>H. amphibius</i>
Cava Santarelli	<i>Hippopotamus antiquus</i>	[45]	X		
Colle Curti	<i>Hippopotamus antiquus</i>	[26,43]	X		
Saticula	<i>Hippopotamus antiquus</i>	[48], this work	X		
Cava Redicicoli	<i>Hippopotamus cf. antiquus</i>	[40], this work	X		
Bussi	<i>Hippopotamus antiquus</i>	This work	1 specimen		
Ortona	<i>Hippopotamus antiquus</i>	[34,58]	X		
Vallinfreda	<i>Hippopotamus antiquus</i>	This work	1 specimen		
Cava Arnolfi	<i>Hippopotamus antiquus</i>	This work	1 specimen		
Campo di Merlo	<i>Hippopotamus antiquus</i>	This work	1 specimen		
Cava di Breccia—Casal Selce 2	<i>Hippopotamus antiquus</i>	This work	1 specimen		
Isernia La Pineta	<i>Hippopotamus antiquus</i>	This work	3 specimens		
Terranera	<i>Hippopotamus antiquus</i>	This work	5 specimens		
Cava Montanari	<i>Hippopotamus amphibius</i>	[22]			1 specimen
Monte Antenne	<i>Hippopotamus amphibius</i>	This work			2 specimens
Ponte Molle	<i>Hippopotamus cf. amphibius</i>	This work			3 specimens
Tor di Quinto	<i>Hippopotamus amphibius</i>	This work		1 specimen	3 specimens
Trentangioli	<i>Hippopotamus amphibius</i>	This work			2 specimens
Batteria Nomentana	<i>Hippopotamus amphibius</i>	This work			3 specimens
Sedia del Diavolo	<i>Hippopotamus amphibius</i>	This work			6 specimens

Considering the lack of diagnostic features in the teeth, which represent the majority of hippopotamus remains known from the Quaternary in Europe, we reiterate the importance of the morphology of the lower canines for the specific distinction between *H. antiquus* and *H. amphibius*. This feature might be somewhat variable, as exemplified by the presence of 1 specimen (out of 16) from the Valdarno Superiore that does not show a parallel arrangement of the canines [42]. Nonetheless, there is an almost complete chronological separation between canines with parallel (prior to ca. 500 ka) and convergent (since ca. 500 ka) arrangements from the Middle Pleistocene in Italy, which coincides with the earliest appearance of *H. amphibius* in the European fossil record. The only exception to this sharp separation is a “parallel” canine from Ponte Molle, whereas the other three specimens from the site show a “convergent” morphology. This might indicate intraspecific variability, as in the case of the Valdarno Superiore; it could also indicate that both *H. antiquus* and *H. amphibius* were present at Ponte Molle, and indeed, a short chronological overlap between the two species in Europe would be supported by the last occurrence of *H. antiquus* (ca. 450 ka) in the Iberian Peninsula [140] or that the “parallel” canine is one of the few spurious older remains collected at Ponte Molle (see [70] for discussion).

In any case, our review confirms that the *H. antiquus*–*H. amphibius* transition occurred during the Middle Pleistocene (MIS 13, Figure 4).



**Figure 4.** Biochronological scheme on quaternary time scale with selected Italian localities mentioned in the text. Abbreviations: MS—Magnetostatigraphy; GC—Geochronology; MIS—Marine Isotope Stage(s).

### 5.2. Size Variability and Climatic Impact on Hippopotamuses

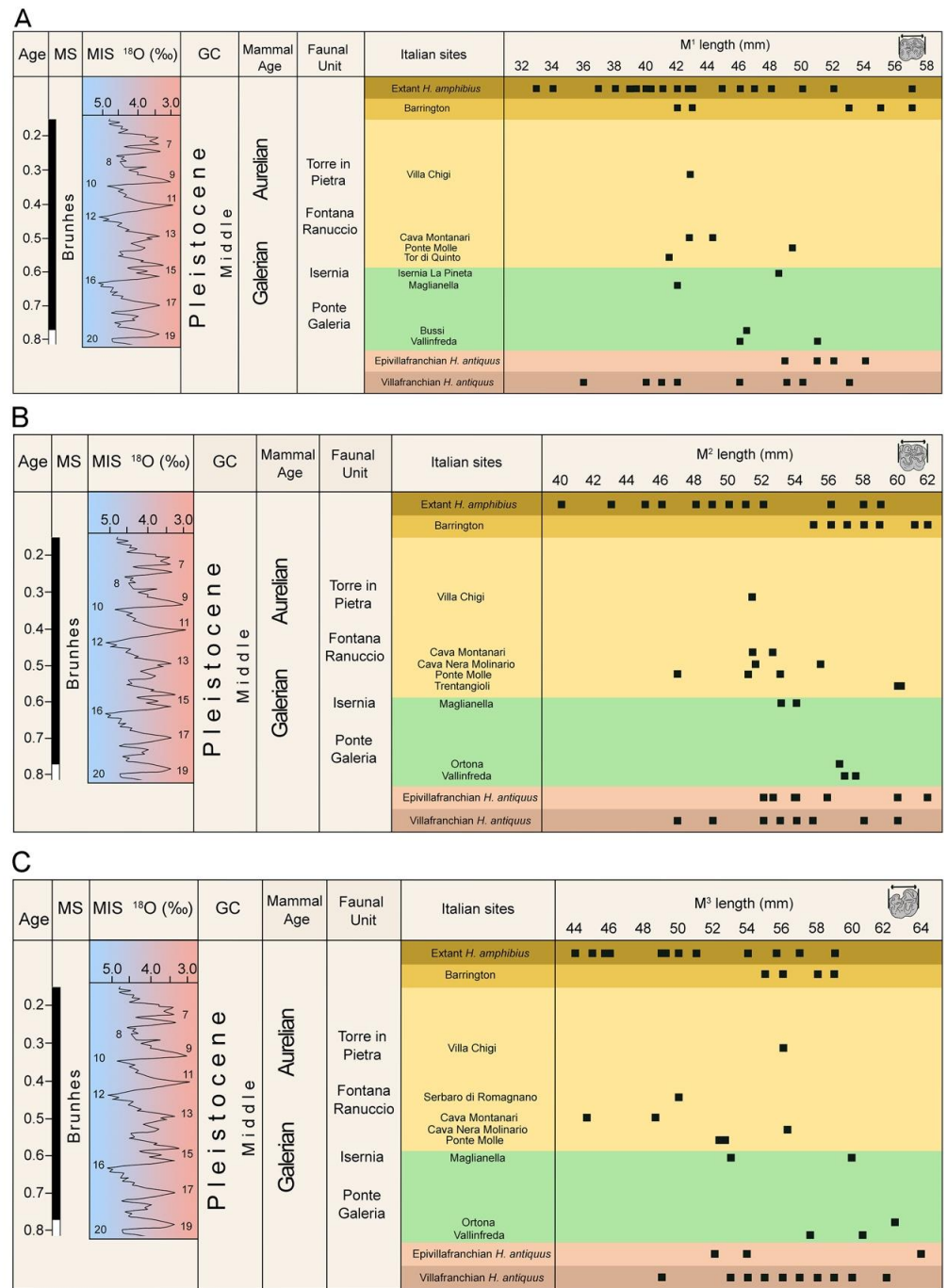
Size variation in fossil mammals and its relationship with climate oscillations have been investigated in several species, for example, *Crocota crocuta* [141], *Bos primigenius* [142,143], *Canis lupus* [144,145], and *Sus scrofa* [146]. In the majority of these studies, the size variation was regarded as linked to climatic changes, in agreement with the ecogeographical rule proposed by [147] that predicts larger sizes in colder climates. The opposite situation was observed in an *S. scrofa* fossil from the Late Pleistocene of Apulia, with smaller individuals occurring during glacial stages, a pattern interpreted as resulting from the decrease in available trophic resources [146]. Hippopotamuses have a peculiar ecology, which similarly suggests a complex response to fluctuations in climate and resources. Indeed, they are strongly dependent on the presence of water, to the extent that they are considered indicators of humid conditions and mild winters [29,34,48,148]. Although it is generally believed that *H. antiquus* was larger than *H. amphibius*, size variations in Pleistocene fossil hippopotamuses of Europe have been poorly investigated [24,26,149–151]. Mazza and Bertini [34] suggested that size fluctuations observed in Quaternary hippopotamuses reflect changes in resources, which, in turn, are dependent on temperature and precipitation, silt levels also allowing for the recognition of a chronological subdivision: large-sized

specimens during the Early Pleistocene; small-sized specimens during the Middle Pleistocene (with sharper climatic oscillations); and large-sized specimens during the early Late Pleistocene (in warm and humid environments). Recently, [22] studied the large sample from Cava Redicicoli, highlighting two important aspects: the large dimensional variability of postcranial bones (also affected by sex and age) not connected with climatic changes and the general size similarity between Middle and Late Pleistocene specimens and extant *H. amphibius*, confirming the large size for Early Pleistocene remains of *H. antiquus*.

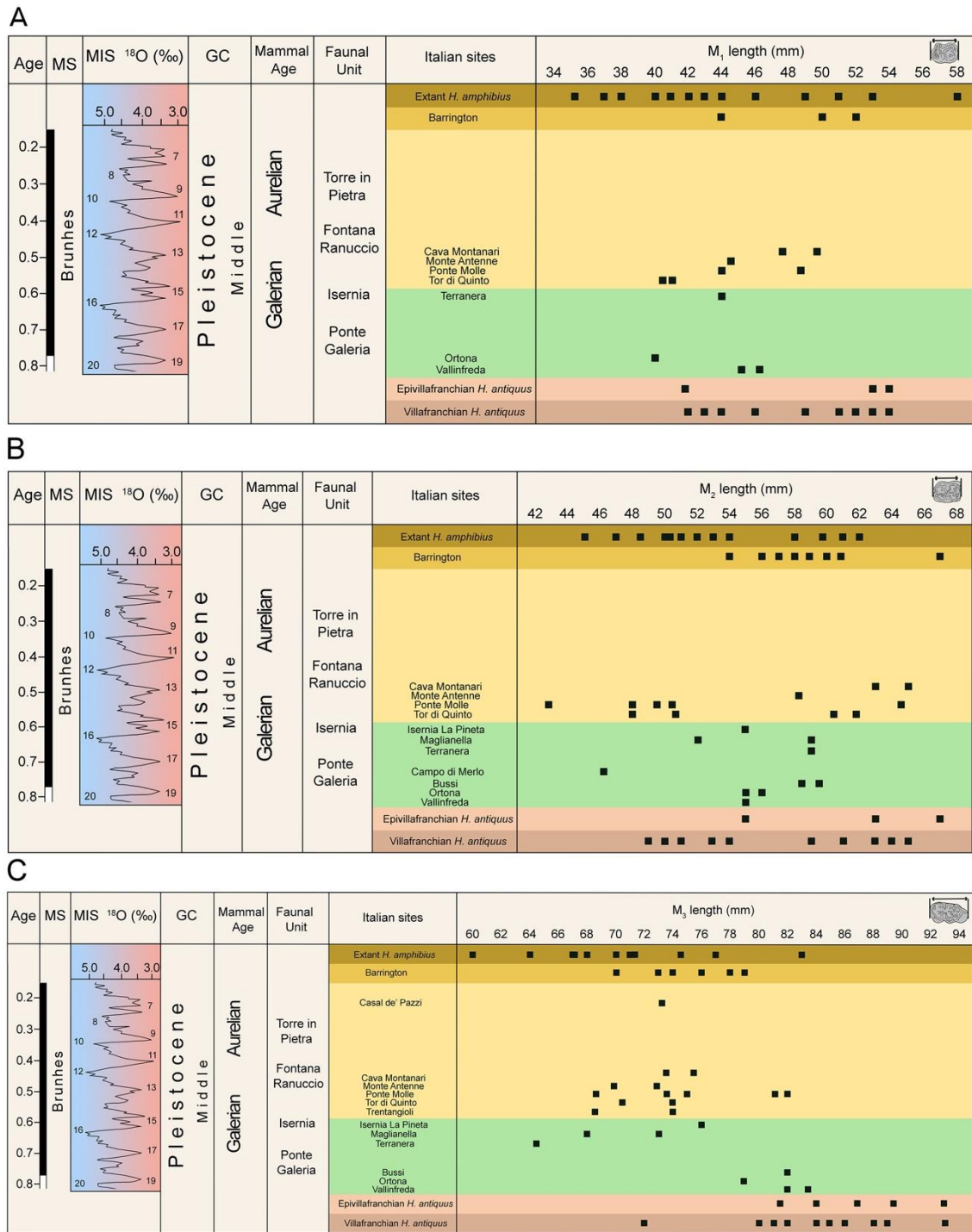
In this work, a considerable number of fossils were considered by integrating the data present in the literature.

Investigating the tooth length in upper and lower molars reveals a similar pattern for most tooth positions, with Early Pleistocene (Villafranchian and Epivillafranchian) *H. antiquus* being larger (on average) than extant *H. amphibius*, but with a wide overlap (Figures 5 and 6). The range of extant *H. amphibius* encompasses that of most fossil hippopotamuses, both *H. antiquus* and *H. amphibius*. There is, in general, no clear-cut dimensional separation between *H. antiquus* and *H. amphibius* from the Middle Pleistocene in Italy. Rather, a decrease in size seems to have occurred within *H. antiquus* after or during MIS 16, with smaller specimens documented, for instance, at Isernia La Pineta and Terranera. Marked size differences are mainly observed in M<sub>3</sub> L (Figure 6C). Therefore, in order to better explore the dimensional variability of M<sub>3</sub>, two bivariate plots were generated (Figures 7 and 8). The first (Figure 7), depicting the length vs. breadth of the tooth, shows two distinct groups (Villafranchian and Epivillafranchian *H. antiquus*, and fossil *H. amphibius* from Barrington and extant specimens). For Middle Pleistocene specimens, Terranera and Maglianella display a small size compared to other *H. antiquus*, whereas Cava Montanari and Ponte Molle possess a larger size than the *H. amphibius* variability. The second plot (Figure 8), the M<sub>2</sub> length vs. the M<sub>3</sub> length, shows clear differences between groups, with *H. antiquus* being larger than *H. amphibius*. The only exception is the sample from Maglianella, which falls in the range of extant *H. amphibius*. This would seem to confirm that *H. antiquus* has a larger size if compared with *H. amphibius*, but these differences are more evident when more biometric measurements are considered.

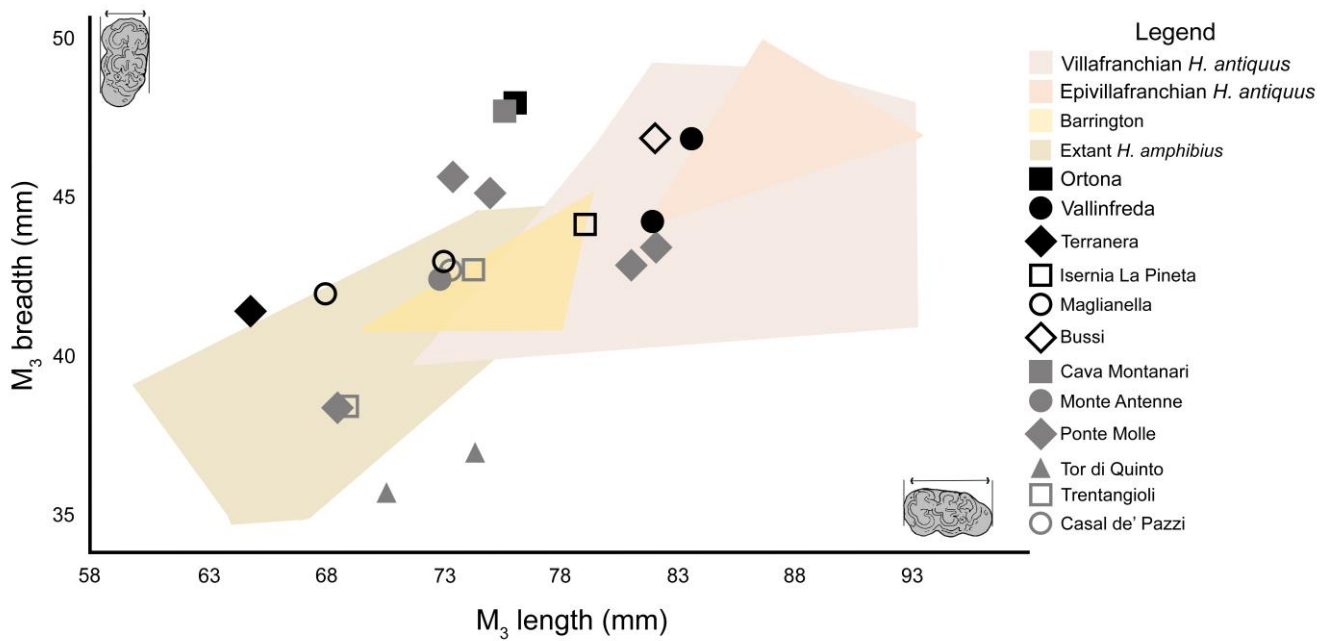
Our results suggest that multiple factors should be considered when discussing size fluctuations in Quaternary hippopotamuses, in agreement with previous studies [34]. *Hippopotamus antiquus* was larger, on average, than extant *H. amphibius*, but the huge size variation in the latter indicates the need to exercise caution in the attribution of isolated remains. This is especially true for the Middle Pleistocene around 500 ka, where both species might be present, although no dimensional sorting is clear. A decrease in size occurred instead during the early Middle Pleistocene and within *H. antiquus*, probably triggered by the severe glacial conditions known to have characterized MIS 16, which indeed allows an effective separation between large- (Bussi, Ortona, Vallinfreda) and small-sized (Isernia La Pineta, Maglianella, Terranera) samples. A few specimens do not adhere to this pattern, perhaps indicating peculiar local conditions or merely due to individual variability. Indeed, the availability of fossil material is still rather limited to consider this interpretation conclusive, but our overview of the Italian Middle Pleistocene provides important new data.



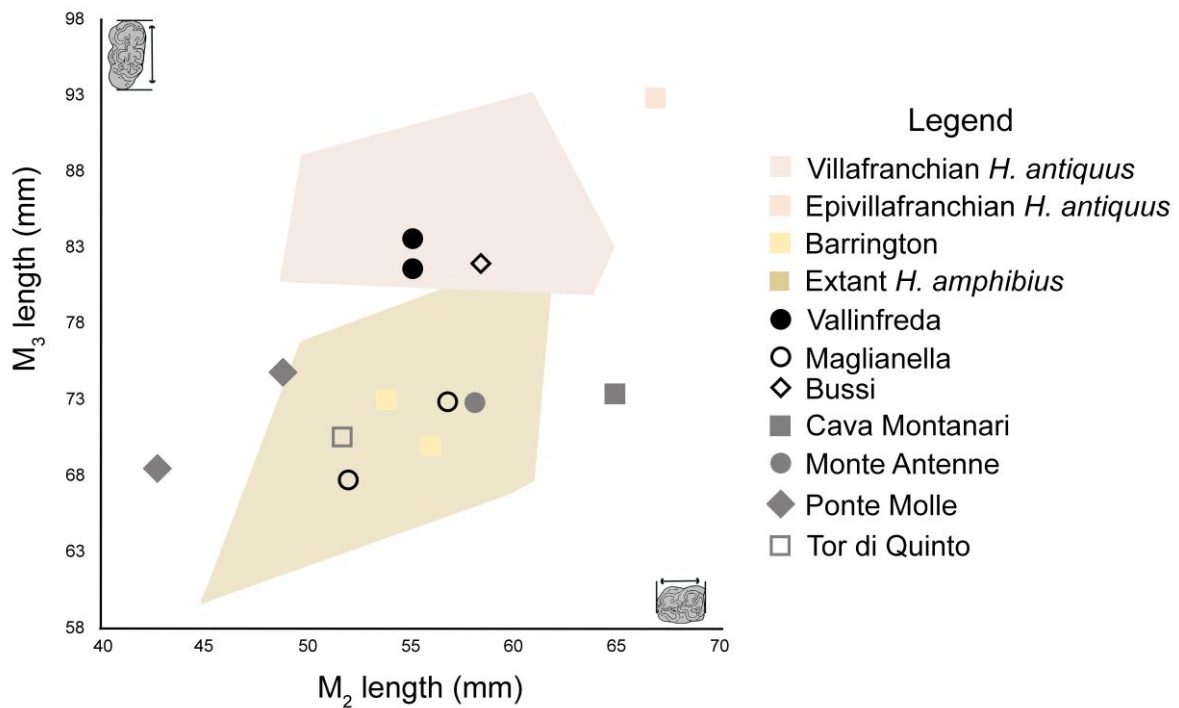
**Figure 5.** The variation in the size of *Hippopotamus*, as indicated by the length of the upper first (M<sup>1</sup>, (A)), second (M<sup>2</sup>, (B)), and third (M<sup>3</sup>, (C)) molars. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after [152]) are on the left, followed by the fossiliferous sites and their suggested ages. Dark pink—Villafranchian specimens of *H. antiquus*; light pink—Epivillafranchian specimens of *H. antiquus*; green—chronological range of Middle Pleistocene *H. antiquus*; light orange—chronological range of Middle Pleistocene *H. amphibius*; dark orange—fossil specimens of *H. amphibius* from Barrington; brown—extant specimens of *H. amphibius*.



**Figure 6.** The variation in the size of *Hippopotamus*, as indicated by the length of the lower first (M<sub>1</sub>, (A)), second (M<sub>2</sub>, (B)), and third (M<sub>3</sub>, (C)) molars. Age in millions of years (vertical axis) and oxygen isotope curves (horizontal axis; after [152]) are on the left, followed by the fossiliferous sites and their suggested ages. Dark pink—Villafranchian specimens of *H. antiquus*; light pink—Epivillafranchian specimens of *H. antiquus*; green—chronological range of Middle Pleistocene *H. antiquus*; light orange—chronological range of Middle Pleistocene *H. amphibius*; dark orange—fossil specimens of *H. amphibius* from Barrington; brown—extant specimens of *H. amphibius*.



**Figure 7.** Standard bivariate plots of the breadth vs. length of the lower third molars ( $M_3$ ) of hippopotamuses. Dark pink—Villafranchian specimens of *H. antiquus*; light pink—Epivillafranchian specimens of *H. antiquus*; orange—fossil specimens of *H. amphibius* from Barrington; brown—extant specimens of *H. amphibius*; black—Middle Pleistocene specimens of *H. antiquus*; gray—Middle Pleistocene specimens of *H. amphibius*.



**Figure 8.** Standard bivariate plots of length of third molar ( $M_3$ ) vs. length of lower second molar ( $M_2$ ) of hippopotamuses. Dark pink—Villafranchian specimens of *H. antiquus*; light pink—Epivillafranchian specimens of *H. antiquus*; orange—fossil specimens of *H. amphibius* from Barrington; brown—extant specimens of *H. amphibius*; black—Middle Pleistocene specimens of *H. antiquus*; gray—Middle Pleistocene specimens of *H. amphibius*.

## 6. Conclusions

This work offers an important overview of the Middle Pleistocene hippopotamuses of the Italian Peninsula, a territory that, for a long time, has been considered key for the evolution of this group in Europe.

Our results confirm that the *Hippopotamus antiquus*–*Hippopotamus amphibius* transition occurred during the Middle Pleistocene, probably during MIS 13. The analysis of a large sample also reinforced the idea that, in the absence of cranial remains, taxonomic attributions of Quaternary hippopotamuses are quite difficult. The only feature useful for specific identification is the arrangement of the enamel ridges on the external surfaces of the lower canines. Our results demonstrated that a parallel arrangement was observed in remains dated prior to ca. 500 ka, whereas a convergent arrangement was generally detected in fossils dated after ca. 500 ka. This would confirm the validity of this feature for taxonomical purposes.

Finally, biometric comparisons show that *H. antiquus* was larger, on average, than extant *H. amphibius*, in agreement with previous studies. Nevertheless, *H. antiquus* specimens dated to ca. 600 ka display a smaller size when compared to older samples of the same species, suggesting that severe glacial conditions recognized to have occurred during MIS 16 could have triggered a decrease in size.

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