Marathousa 2: A New Middle Pleistocene Locality in the Megalopolis Basin (Greece) with Evidence of Hominin Exploitation of Megafauna (*Hippopotamus*)

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ABSTRACT

In this article we present the new open-air Middle Pleistocene locality Marathousa 2, which was discovered during a double intensive and targeted field survey in the lignite mines of the Megalopolis Basin (Greece). The locality is situated just below the Lignite Seam III of the Marathousa Member (Choremi Formation), and its similar stratigraphic position to the chronologically well-constrained locality Marathousa 1 (dated between 500 and 400 ka and correlated to Marine Isotope Stage 12) indicates a comparable age for Marathousa 2. The locality most notably yielded dental and postcranial remains of *Hippopotamus*, with those found at the locality's Area A most likely belonging to a single individual. The dimensions of the dental elements support an attribution to *Hippopotamus antiquus*, a large-sized taxon, almost twice as large as the recent *Hippopotamus amphibius*, and with strong aquatic habits. Cut marks identified on a thoracic vertebra indicate hominin butchering of the carcass. Preliminary paleoenvironmental remarks are based on the mammal and mollusk fauna. The latter is represented solely by freshwater taxa and is dominated by Valvatidae (*Valvata cristata*, *Valvata studeri*) and Bithyniidae (*Bithynia candiota*), but includes also, in lower percentages, Sphaeriidae, Lymnaeidae, Planorbidae and Unionidae. The available paleoenvironmental evidence indicates that hominin activities took place at the margins of or near, a likely cold, freshwater body, but with temperatures that allowed its persistence throughout the year, and perhaps under drier conditions compared to preceding and succeeding periods in the basin. In addition to the exploitation of elephants in Marathousa 1, Marathousa 2 provides further evidence of megafauna exploitation during the Middle Pleistocene in the Megalopolis Basin and one of the few examples of hippopotamus carcass processing during the Lower Paleolithic in Europe. Therefore, it advances our knowledge of the food acquisition strategies and subsistence behavior of Pleistocene *Homo*, and highlights the need for further research in the basin, where megafauna are well recorded.

INTRODUCTION

With a body mass exceeding 1 ton, elephants (*Palaeoloxodon*), mammoths (*Mammuthus*), hippopotamuses (*Hippopotamus*), and rhinoceroses (*Stephanorhinus*, *Coelodonta*) formed the megafauna of the Pleistocene terrestrial ecosystems of Europe and were the largest herbivores that roamed the landscapes of this epoch. Due to their large size, they constituted a unique food package in terms of fat and meat quantity, and therefore they may have represented an attractive target for Paleolithic hominins in order to meet the necessary caloric and nutritional demands of their metabolism (e.g., Ben-Dor et al., 2011, 2021; Reshef and Barkai, 2015). Indeed, meat consumption was a crucial factor in the adaptations and ecology of Pleistocene hominins, and particularly megafauna seem to have affected not only their diet but also several aspects of their subsistence behavior, ecology, and culture (e.g., Domínguez-Rodrigo et al., 2014a; several studies in Konidaris et al., 2021 and references cited therein). However, the enormous body size (big game procurement) and specific aspects of each taxon's ecology and ethology (similar to its recent closest relatives) would require, among others, cooperation and coordinated effort among hominin group members, employment of special obtainment tactics and exploitation techniques, as well as the investment of energy and time (e.g., Agam and Barkai, 2018; Konidaris and Tourloukis, 2021; Linares Matás and Yravedra, 2021). The hominin involvement in the accumulation and modification of megafaunal remains can be deduced from direct (e.g., cut marks, breakages for brain/marrow extraction, megafaunal bone tools) and indirect (e.g., presence of lithic/wooden artifacts at the site, use-wear analysis, human fossils) evidence. Nonetheless, the interpretation is not always clear-cut, because both direct and indirect lines of evidence have their own limitations. Most importantly, cut marks are relatively rarely preserved on megafaunal bones (e.g., due to their thick cartilage and periosteum), while subsequent action of biotic (e.g., carnivores) and abiotic agents (e.g., weathering, water transport) may modify or even eliminate the original, anthropogenic bone surface modifications (e.g., Haynes and Klimowicz, 2015; Pineda et al., 2019). Furthermore, the stratigraphic association of megafaunal and cultural remains does not imply *de facto* the hominin exploitation of the carcasses, and their causal association requires taphonomic analysis (e.g., Giusti, 2021).

In this article, we provide evidence for hippopotamus exploitation by hominins at the new Middle Pleistocene locality Marathousa 2 in the Megalopolis Basin (southern Greece). Our aim is to contribute to the understanding of Middle Pleistocene hominin subsistence behavior, with emphasis on megafauna procurement, as well as to enrich our knowledge on *Homo*–*Hippopotamus* interactions in the Paleolithic, which are still meager in the European record. A preliminary announcement of Marathousa 2 was presented in Konidaris et al. (2019). Here, we provide elaborated and updated data about the locality, stratigraphy, fauna, and taphonomy, and we discuss the paleoenvironmental context of the locality based on the first results from the ongoing study on mollusks from the Megalopolis Basin (Boni, 2022; Boni et al., in prep.).

THE MEGALOPOLIS BASIN AND PREVIOUS RECENT RESEARCH

The Megalopolis area (Arcadia, Peloponnesus, Greece; Figure 1a) is an intramontane basin, which was filled by fluviolacustrine deposits from the late Neogene onwards. Dur-

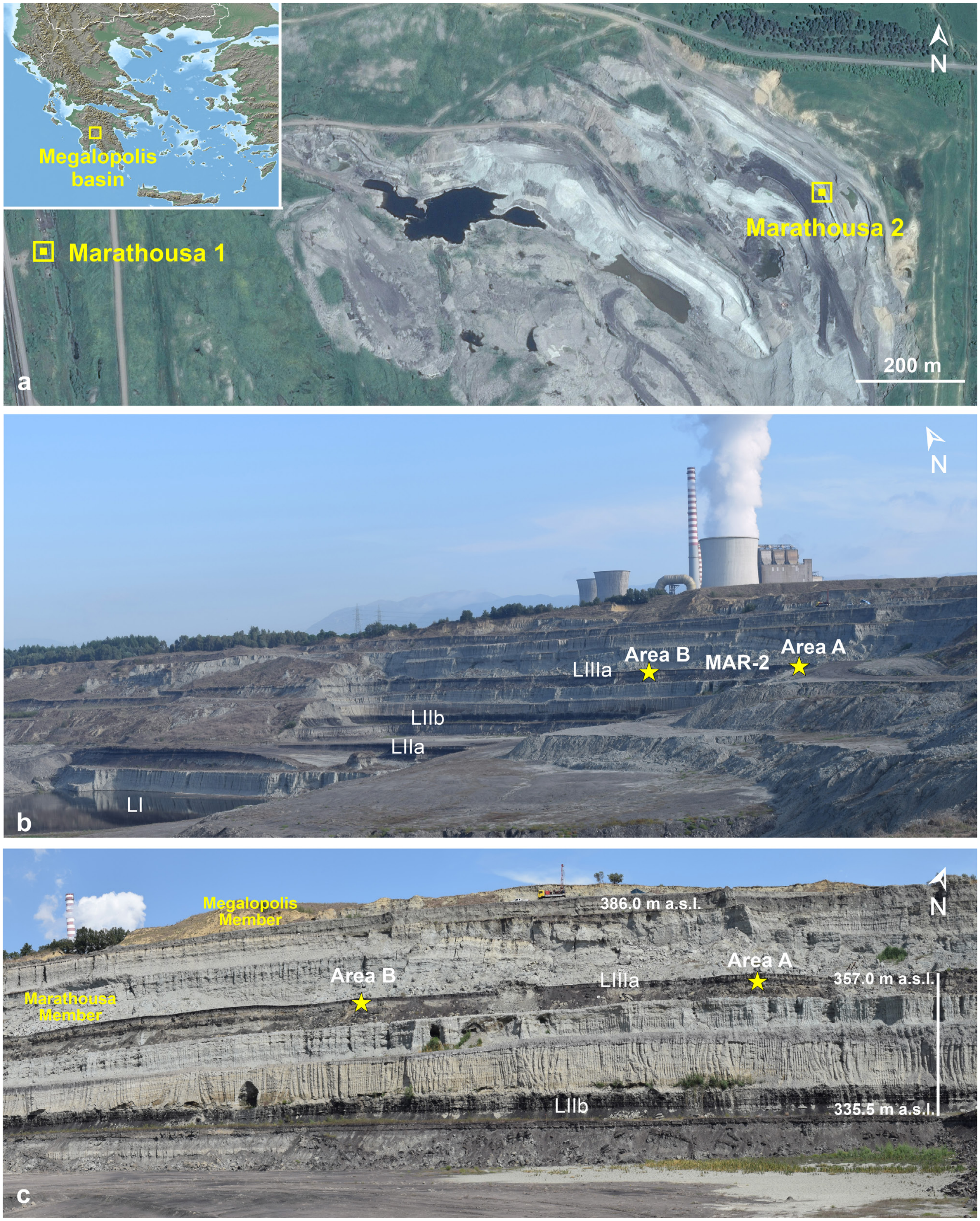


Figure 1. a) Geographic position of the Megalopolis Basin and Marathousa 2 within the Marathousa mine (maps taken from Copernicus Land Monitoring Service, https://land.copernicus.eu/ and Google Earth; lignite mine expansion in 2022); b, c) panoramic views of the eastern quarry of the Marathousa mine, indicating the Marathousa and Megalopolis Members of the Choremi Formation, the lignite seams and the location of MAR-2 (Areas A and B); elevations (m a.s.l.) in c were recorded with the use of a Differential GPS.

ing the late Early Pleistocene and the Middle Pleistocene (ca. 900 to 150 ka), the basin hosted a large and shallow lake, which resulted in a stratigraphic sequence composed mainly of lacustrine sediments intercalated by lignite seams (Tourloukis et al., 2018a; van Vugt et al., 2000; Vinken, 1965). In 1969 an open-cast lignite mine and power plant were established in the basin. As a result of these mining operations, long fossiliferous sections are exposed, offering the unique opportunity to study the stratigraphy and paleobiome of the Pleistocene paleolake. Numerous Pleistocene vertebrate remains from the basin have been identified and collected through the years (the first systematic excavations took place in 1902; Skouphos, 1905), including a hominin molar, a surface find described during the 1970s together with a diverse mammal fauna (Sickenberg, 1975; Appendix by Marinos), whose morphology and size suggest it belonged to the Neanderthal lineage (Röding et al., 2021).

A joint team of the Ephorate of Palaeoanthropology–Speleology (Hellenic Ministry of Culture and Sports) and the University of Tübingen (Germany), conducted in 2012–2013 under the auspices of the Ephorate of Palaeoanthropology–Speleology and in the framework of the ERC Starting project 'Paleoanthropology at the Gates of Europe' [PaGE; Harvati and Tourloukis, 2013), a double intensive and targeted field survey in the basin's Pleistocene sediments (Thompson et al., 2018). This survey resulted in the discovery of the new open-air Middle Pleistocene (Lower Paleolithic) site Marathousa 1 (MAR-1; see Figure 1a) in 2013, which was subsequently systematically excavated until 2019 (Panagopoulou et al., 2015, 2018; Harvati et al., 2018). MAR-1 is radiometrically, magnetostratigraphically, and biochronologically dated to 500–400 ka, and is correlated to the glacial Marine Isotope Stage (MIS) 12 (Blackwell et al., 2018; Doukas et al., 2018; Jacobs et al., 2018; Konidaris et al., 2018; Tourloukis et al., 2018a). The locality is situated between two lignite seams (Lignite Seams IIb and IIIa) in what was once a lake shore (Karkanas et al., 2018). It has yielded a stratified and exceptionally well-preserved archaeological and paleontological assemblage, including lithic and bone artifacts, micro- and macrofauna (insects, ostracods, mollusks, fishes, amphibians, reptiles, birds, mammals), and micro- and macroflora (Doukas et al., 2018; Field et al., 2018; Konidaris et al., 2018, 2022; Michailidis et al., 2018; Tourloukis et al., 2018b; Bludau et al., 2021; Boni, 2022; ongoing studies). Additionally it preserves evidence of hominin butchering of elephant and other large mammal carcasses, documented also in a use-wear analysis of lithics from the site, providing insights into hominin subsistence stategies and megafauna exploitation in particular (Konidaris et al., 2018; Guibert-Cardin et al., 2022).

A new, 5-year field survey (Megalopolis Paleoenvironmental Project; MegaPal) was initiated in 2018 under the auspices of the Ephorate of Palaeoanthropology and Speleology (Hellenic Ministry of Culture and Sports) and the American School of Classical Studies at Athens, in the framework of the ERC Consolidator Project 'Human Evolution at the Crossroads' (CROSSROADS). This work conducted further systematic, targeted investigations in the lignite mines and river terraces of the basin, with the goal of reconstructing the paleoenvironment and its evolution through the Pleistocene, as well as to potentially identify new localities with evidence of human activity.

Thus, overall, recent and current research in the Megalopolis Basin provides a detailed glimpse into the Middle Pleistocene ecosystems of the region, testifying to the early human presence in Greece, while highlighting the significant potential of the basin for research on hominin evolution, dispersals, and adaptations, and emphasizing the need for systematic, multidisciplinary, and high-resolution paleoenvironmental investigations throughout the basin's Pleistocene stratigraphic sequence.

THE NEW LOCALITY MARATHOUSA 2

In 2018, the MegaPal survey led to the discovery of the new open-air locality, Marathousa 2 (MAR-2), where stratified fossils were identified in an exposed profile of one of the artificial terraces in the Marathousa mine (Figure 1b, c). MAR-2 is located ~1.5km east of MAR-1 and within a clastic sedimentary sequence of the Marathousa Member (Choremi Formation; Vinken, 1965), above Lignite Seam IIb and directly below Lignite Seam IIIa (see Figure 1) as defined by Löhnert and Nowak (1965) (for further details on the geology and stratigraphy of the Megalopolis Basin see Karkanas et al. [2018] and Tourloukis et al. [2018a]). Two areas of interest were designated, both yielding mainly hippopotamus fossils—Area A (GPS coordinates: N 37° 24´ 35.0´´, E 22° 06´ 29.8´´; WGS84 datum) with vertebrae and ribs most likely belonging to a single hippopotamus individual, as well as a lithic artifact; and, Area B (N 37° 24´ 36.9´´, E 22° 06´ 27.1´´; WGS84 datum), about 90m NW of Area A, with some isolated hippopotamus teeth and ribs. All MAR-2 fossils were collected from the exposed artificial profiles, without the means of a systematic excavation.

STRATIGRAPHY

The sedimentary sequence in both areas is similar and the only differences occur in its uppermost part (Figure 2). The lowermost stratigraphic units (UA1, UB1; in Area A and Area B, respectively) consist of bluish grey, massive sandy muds, representing deposition in a swampy, relative shallow permanent water body. Above them, a thin organic- and shell-rich sandy layer (UA2, UB2) indicates a location closer to the shoreline of this lake environment. The upper units (UA3, UB3) consist of blackish, bedded lignitic clay with patches of sand, pointing to deposition in a marshy environment. The sequence continues with a relatively thin layer of bluish grey, massive sandy muds (UA4, UB4) indicating also in this layer the existence of permanent, shallow swamps. The overlying units (UA5, UB5) are characterized by finely bedded to laminated silts and sands, implying a higher-energy environment in proximity to fluvial inputs. At the upper part of this unit, a slightly cemented erosional exposure surface distinguishes the lower from the upper part of the sedimentary sequence in both areas. This upper part begins with the *Hippopotamus*-bearing sedimentary units UA6 and UB6, which are correlated and represent

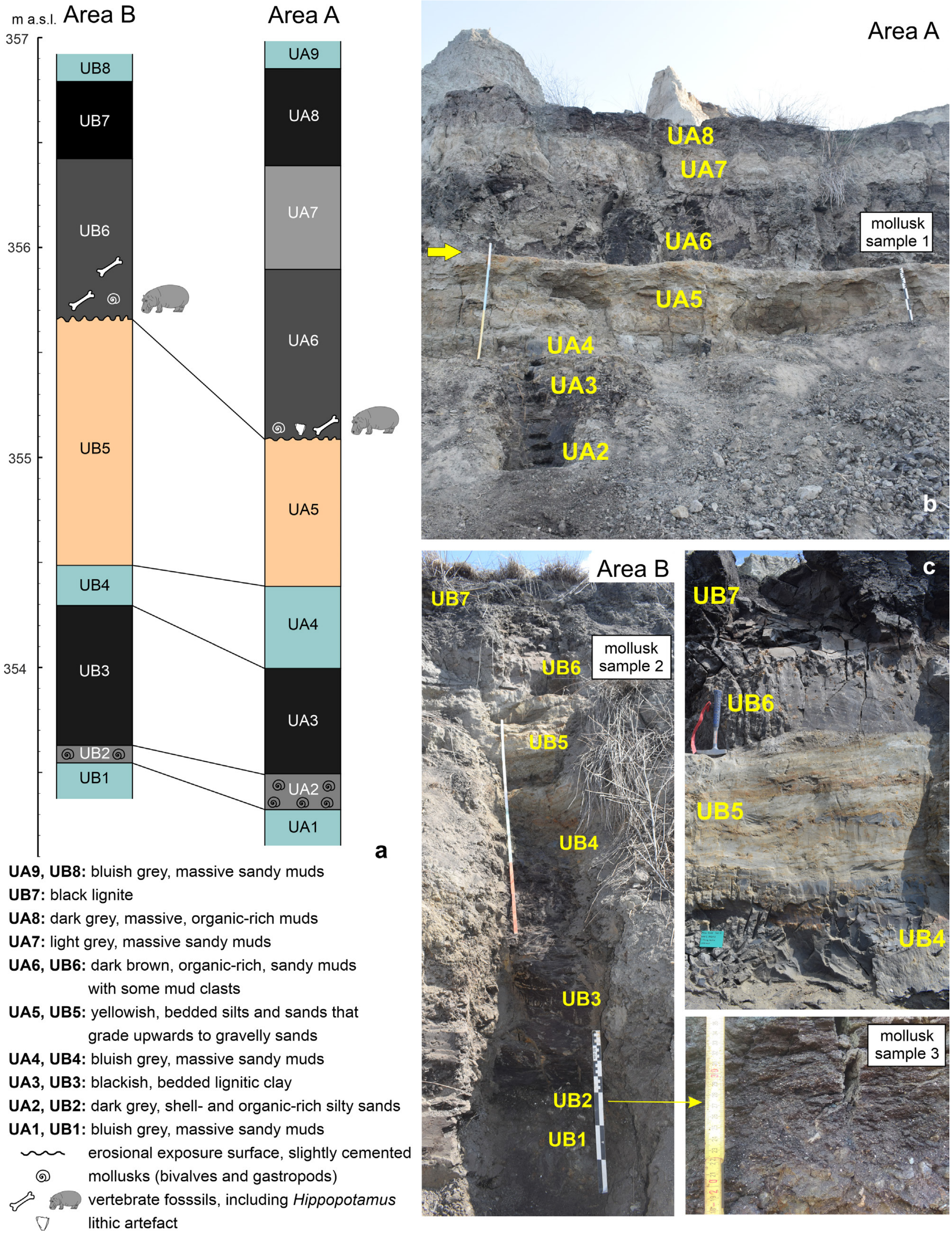


Figure 2. a) Schematic stratigraphic columns of Area A and Area B of Marathousa 2 showing the stratigraphic units (contacts between the units were recorded with a Differential GPS) and the correlations between the two areas; b) part of the section of Area A, showing the stratigraphic units (the arrow marks the major erosional contact between UA5 and UA6; meter stick on the left is 1m, scale on the right is 50cm) and the location of mollusk sample 1; c) views of the section of Area B, showing the stratigraphic units and the location of mollusk samples 2 and 3.

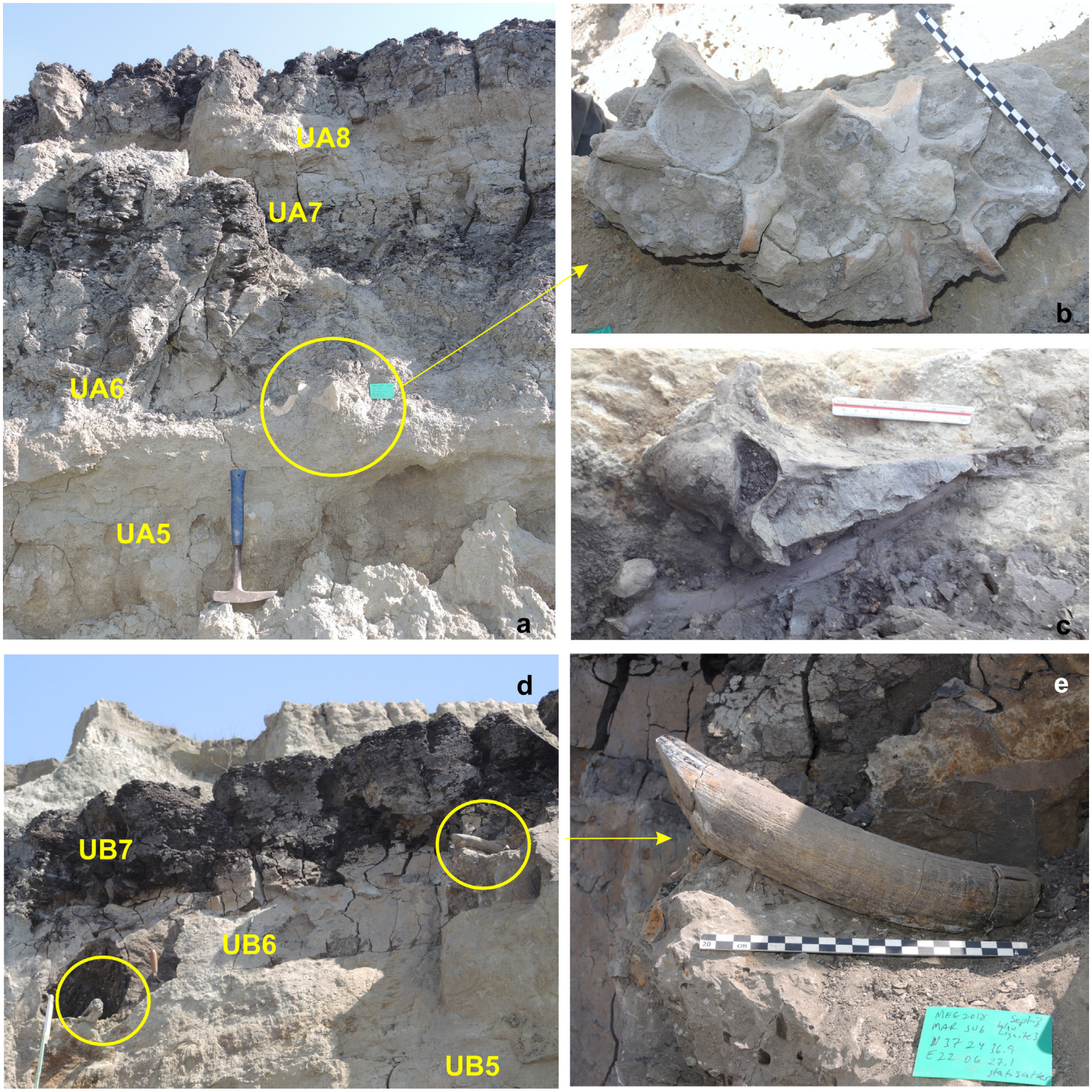


Figure 3. a) Close-up view of Area A, marking stratified Hippopotamus *cervical vertebrae; b) two cervical vertebrae of* Hippopotamus in situ *in Area A; c) thoracic vertebra and rib of* Hippopotamus in situ *in Area A; d) part of the section of Area B marking stratified* Hippopotamus *dental remains e) detail with the upper canine of* Hippopotamus in situ.

the same depositional event. These units consist of dark brown, organic-rich, sandy muds with some mud clasts (see Figure 2; Figure 3), interpreted to have been formed during a terrestrially generated sedimentary process, such as a mudflow deposited at the former lake margin. In Area B, the hippopotamus fossils have a rather wide vertical distribution within this unit (see Figure 3d), while in Area A the hippopotamus bones (and the lithic artifact) occur at the bottom of this deposit, near the erosional contact with the sandy sediments of the underlying unit (see Figure 3a–c; Figure 4). In Area A, UA6 is overlain by light grey, massive sandy muds (UA7) followed by dark grey, massive and organic-rich muds (UA8), while in Area B UB6 is overlain by a black lignite (UB7), which represents Lignite Seam IIIa of the basin. In both areas, the sequence ends at the top with bluish grey, massive sandy muds (UA9, UB8).

METHODS

MOLLUSK SAMPLING AND ANALYSIS

Three sediment bulk samples were collected from MAR-2 (see Figure 2)—sample 1 (Area A; UA6, layer with *Hippopotamus* fossils), sample 2 (Area B; UB6, layer with *Hippopotamus* fossils), and sample 3 (Area B; UB2, ~2m below sample

Figure 4. a) Grey flint flake in situ in Area A, at the base of stratigraphic unit UA6 near the erosional contact with UA5; b), the flake, in b1, dorsal; b2, right lateral; b3, ventral; b4, left lateral; and, b5, proximal views; the striking platform is visible in b5.

2). Each sediment sample (~3kg) was air-dried and then soaked in 10l containers, half-filled with water and ~50ml of 30% concentration H_2O_2. Samples were water-screened in 0.5mm-sized mesh, left to air-dry, and subsequently were dry-screened in 5.00mm, 3.16mm, and 1.60mm mesh screens. Examination of the samples was conducted under a stereoscopic microscope equipped with objective lenses of 0.63×, 1.00×, 1.6×, and 2.5× magnification, and 10× ocular lenses. Complete or partly fragmented recognizable mollusk shells were collected and identified to the lowest taxonomic level possible, based mainly on the study of Schütt et al. (1985) on the Pleistocene mollusks from the Megalopolis Basin. All recognizable shells were counted, and their percentages were calculated.

SKELETAL PART REPRESENTATION AND BONE SURFACE MODIFICATIONS ANALYSIS

Standard taphonomic counting units and methods were used for the recording of the mammal fauna (Table 1)—number of identified specimens (NISP; each distinct anatomical element is tallied as 1, following Stiner [1994: 69], and Lyman [2008: 34–35]), minimum number of elements (MNE), and minimum number of individuals (MNI). However, it should be noted that the available sample size is small. Bone surfaces were examined for traces of weathering, abrasion, trampling, carnivore tooth marks, and anthropogenic modifications, following criteria described in Behrensmeyer (1978), Binford (1981), Pobiner (2008), Domínguez-Rodrigo et al. (2009, 2010), and Fernández-Jalvo and Andrews (2016). In order to study the micromor-

TABLE 1. NUMBER OF IDENTIFIED SPECIMENS (NISP), MINIMUM NUMBER OF ELEMENTS (MNE), AND MINIMUM NUMBER OF INDIVIDUALS (MNI) FOR THE MAMMAL FAUNA FROM MARATHOUSA 2.

		Area A			Area B			Both Areas	
Taxon		**NISP**	**MNE**	**MNI**	**NISP**	**MNE**	**MNI**	**NISP**	**MNI**
Castor fiber	Femur	1	1	-	-	-	-	-	-
	Total	**1**		**1**				**1**	**1**
Hippopotamus antiquus	Teeth	-	-	-	5	-	-	-	-
	Vertebrae	5	5	-	-	-	-	-	-
	Ribs	7	3	-	2	2	-	-	-
	Total	**12**		**1**	**7**		**1**	**19**	**2**
Dama sp.	Teeth	3	-	-	-	-	-	-	-
	Mandible	1	1	-	-	-	-	-	-
	Radius	1	1	-	-	-	-	-	-
	Metacarpal	1	1	-	-	-	-	-	-
	Total	**6**		**1**				**6**	**1**
Cervus elaphus	Phalanx	1	1	-	-	-	-	-	-
	Total	**1**		**1**				**1**	**1**

phological features and obtain high-resolution quantitative data on the observed anthropogenic cut marks, 3D data were acquired with the use of a Sensofar Plμ Neox confocal imaging profiler with a 10× objective lens, a vertical resolution of <50nm, a lateral sampling interval of 1.66μm and an aperture of 0.30. 3D representations were constructed and analyzed with the SensoMAP 8.2 following the methodology of Pante et al. (2017). Cut mark morphology and dimensions may vary, among others, by bone portion, carcass size, lithic raw material, tool type, and cutting-edge angle (see discussion and references in Maté-González et al. [2019]), and thus any comparison requires a large dataset and the inclusion of several critical parameters. Therefore, the present 3D study can be regarded as the first step in the ongoing study of the Megalopolis cut marks.

RESULTS

LITHIC ARTIFACT

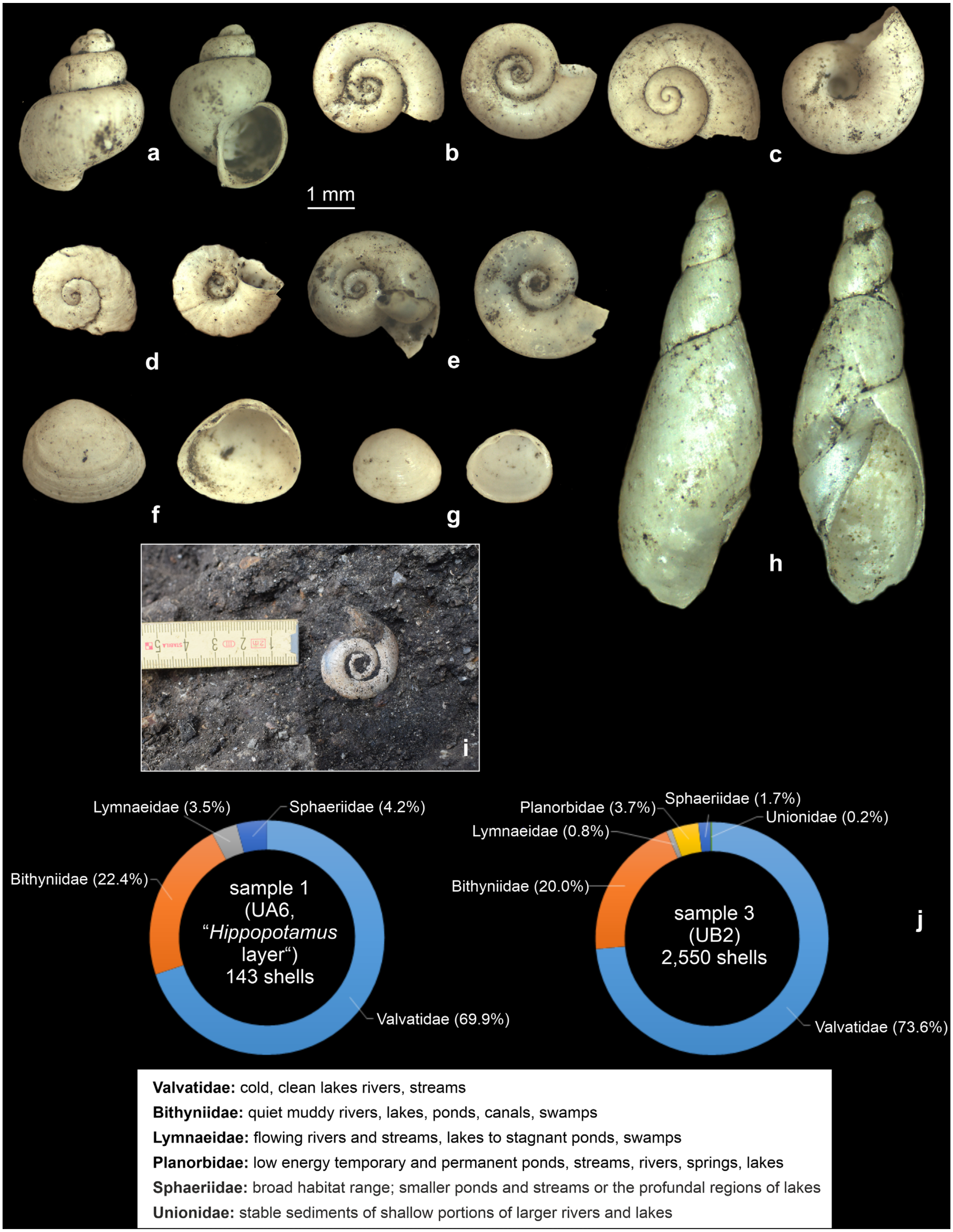
During the cleaning and subsequent sampling of the section profile at Area A, a lithic was recovered in spatial and stratigraphic association with the *Hippopotamus* bones, at the base of the mudflow (UA6) near the erosional contact with the underlying sands (see Figures 2a, 4a). It is a broken flake (length: 25mm; width: 24mm; thickness: 6mm) made of grey, grainy flint, which exhibits a distal step termination and a Siret fracture on the left lateral side (see Figure 4b). Although the artifact is fragmented and typo-technologically non-diagnostic, it must be noted that artifacts of similar dimensions and of the same raw material have been found at the nearby site of MAR-1 (Tourloukis et al., 2018b), as well as at other sites in the basin (unpublished data). It is also notable that, similar to the aforementioned traits of the MAR-2 specimen, the MAR-1 lithic assemblage includes several examples of artifacts bearing knapping accidents, such as siret fractures or distal abrupt breaks (hinged distal or step fractures), which result from variation in the propagation speed of the fracture front (e.g., Inizan et al., 1999), owing to the mechanical properties of the raw material and/or to anthropogenically-controlled parameters (e.g., excess knapping force, or mistakes by novice knappers). Examination of the artifact with high-power magnification failed to identify clear evidence of use-wear traces. Nevertheless, the lithic artifact is especially significant, not only because it provides further evidence for human activity at the site, but also because it further supports the evidence of cut marks that are identified on the faunal remains (see below).

MOLLUSKS

Representative specimens of the mollusk fauna and its composition are shown in Figure 5. Below are the total number of shells and gastropod opercula collected from each sample, the taxa identified per sample, as well as and the percentages of the most abundant species.

Sample 1 (UA6): This sample was not very rich in mollusks, and included 143 shells and ~100 gastropod opercula, belonging to at least six taxa. The most common species was *Valvata cristata* (44.1%), followed by *Valvata studeri* (25.9%) and *Bithynia candiota* (23.4%). Sphaeriids (Sphaeriidae indet.) and lymnaeids (*Lymnaea stagnalis*, *Galba truncatula*) were also present in much lower percentages, while some unidentified large gastropod shell fragments belong probably to *Planorbarius corneus*. Indeed, a complete shell of *Planorbarius* was found *in situ* at the site (see Figure 5i).

Sample 2 (UB6): This sample was very poor in mollusks, with only 10 *Valvata cristata* and 2 *Bithynia candiota* shells, and 30 gastropod opercula observed.



Valvatidae: cold, clean lakes rivers, streams
Bithyniidae: quiet muddy rivers, lakes, ponds, canals, swamps
Lymnaeidae: flowing rivers and streams, lakes to stagnant ponds, swamps
Planorbidae: low energy temporary and permanent ponds, streams, rivers, springs, lakes
Sphaeriidae: broad habitat range; smaller ponds and streams or the profundal regions of lakes
Unionidae: stable sediments of shallow portions of larger rivers and lakes

Figure 5. Mollusks from Marathousa 2; a) Bithynia candiota*; b)* Valvata cristata*; c)* Valvata studeri*; d)* Gyraulus crista*; e)* Planorbis planorbis*; f)* Sphaeriidae *indet. 1; g)* Sphaeriidae *indet. 2; h)* Lymnaea stagnalis*; i) a shell of* Planorbarius in situ *within the stratigraphic unit UA6 of Area A, close to the contact with the underlying UA5; j) family composition of the mollusk fauna in samples 1 and 3, and habitat distribution at family level of gastropods (Strong et al. 2018) and bivalves (McMahon and Bogan 2001).*

Sample 3 (UB2): This was the richest and most diverse sample, comprising 2,550 shells and ~2,000 opercula, from at least 12 taxa; numerous shell fragments were present. The most common species was *Valvata cristata* (60.9%), followed by *Bithynia candiota* (20.0%) and *Valvata studeri* (12.7%). Planorbids (*Gyraulus crista*, *Gyraulus* cf. *acronicus*, *Segmentina nitida*, *Planorbis planorbis*), sphaeriids (Sphaeriidae indet.), lymnaeids (shells that most likely belong to juvenile and/or fragmented specimens of *Galba truncatula*, *Lymnaea stagnalis* and *Stagnicola palustris*), and unionids (*Unio* cf. *pictorum*, and some large shell fragments) were also present.

HIPPOPOTAMUS

In Area A, two cervical vertebrae (identified as the fourth, MAR-2A-1a, and the sixth cervical vertebrae, MAR-2A-1b), a thoracic vertebra (MAR-2A-6; the exact anatomical position unknown, but belonging to the cranial part of the thoracic series), another one tentatively identified as the last thoracic vertebra (because of the absence of clear articular facets for ribs; MAR-2A-14), a spine of thoracic vertebra (MAR-2A-4), and several rib fragments (MAR-2A-2, 3, 7, 11, 13, 15, 16) were found (Figure 6a–e; see Table 1; Table 2). The vertebrae present a morphology consistent with an attribution to *Hippopotamus* (e.g., Reynolds, 1922). The cervical vertebrae and the last thoracic vertebra (MAR-2A-14) are missing the cranial articular plates and have caudal ones that are not completely fused, while the other thoracic vertebra (MAR-2A-6) preserves an unfused cranial plate and lacks the caudal one. This condition points to a similar ontogenetic age and indicates that the bones likely belonged to the same skeletally immature individual. The proximate spatial distribution of the vertebrae and the ribs (see Figure 3b, c), and the similarity in their size, also strongly suggest the presence of a single *Hippopotamus* individual at Area A.

In Area B, a lower first incisor (MAR-2B-1), an upper canine (MAR-2B-2), a third and a fourth upper premolar (MAR-2B-6 and 7), a heavily worn cheek tooth (MAR-2B-3), and rib fragments (MAR-2B-4 and 5) were found (Figure 6f–i; see Tables 1 and 2). Although the remains were found isolated and dispersed inside UB6, an attribution to a single late prime adult individual is quite probable, as the upper canine and the cheek teeth all correspond to advanced dental wear stages. The morphology of the teeth is compatible with both continental Pleistocene hippopotami species of Europe, *H. antiquus* (Early Pleistocene–early Middle Pleistocene) and *H. amphibius* (late Middle Pleistocene–Late Pleistocene). We therefore focus our comparisons on the crown dimension of the more informative upper canine. In the biplot for the upper canine (Figure 7), MAR-2B-2 is distinct from both fossil and recent *H. amphibius* due to its large dimensions and plots well within the sample of *H. antiquus* (data from Mazza, 1995). The MAR-2 canine is also clearly larger than the specimens from the Middle Pleistocene sites Mosbach and Jockgrim (Germany), attributed to H. *tiberinus* (= *H.* ex gr. *antiquus*).

The taxonomy of European *Hippopotamus* is not yet clarified. The main open question is whether two species were present (*H. antiquus* and *H. amphibius*), or whether only one species with two subspecies (*H. amphibius amphibius* and *H. amphibius antiquus*) existed. Furthermore, the validity of the proposed species *H. tiberinus* and *H. incognitus* is debated (see Athanassiou, 2022 and references therein). Here we provisionally follow the two-species taxonomic approach of Petronio (1995) and consider *H. tiberinus* as part of *H. antiquus*. Based on its large dental dimensions, we attribute the MAR-2 *Hippopotamus* to the large-sized *H. antiquus*.

OTHER VERTEBRATE FAUNA

Two chelonian shells, one from Area A (MAR-2A-19) and the other from Area B (MAR-2B-8), belong to a freshwater turtle, well represented in the Megalopolis Basin by *Emys* and *Mauremys* (Vlachos and Delfino, 2016; Athanassiou et al., 2018). A diaphysis of a femur from Area A, partially preserving the third and lesser trochanters, shows morphology and dimensions compatible with an attribution to *Castor fiber* (e.g., Fischer, 1991), a species already known in the basin from several sites (Athanassiou, 2018; Konidaris et al., 2018, and unpublished field data).

A right mandibular fragment (MAR-2A-8) of a deer preserving the M_1–M_3 (see Figure 6j; see Table 2) was found at Area A. The morphology and dimensions of the molars are similar to the those of the fallow deer from MAR-1 (Konidaris et al., 2018), and therefore it is attributed to *Dama* sp. Additionally, a complete radius (MAR-2A-18; see Figure 6k) presents morphological features similar to those of *Dama* (Lister, 1996), and its dimensions (see Table 2) distinguish it from the larger *Cervus* (Konidaris et al., 2018: Table 4); a cervid metacarpal fragment (MAR-2A-5) has dimensions that also permit its attribution to fallow deer. A cervid medial phalanx (MAR-2A-12) from the same area has dimensions consistent with those of the red deer *Cervus elaphus* (Stefaniak, 2015: Table 71).

TAPHONOMY

The good state of preservation of the MAR-2 mammal bone surfaces (almost fresh with only minor weathering) promotes the identification of taphonomic surface modifications. Of particular importance is the *Hippopotamus* thoracic vertebra MAR-2A-6 (belonging to the partial skeleton), which shows two striations at the preserved middle part of the lateral side of the spinous process, oblique relative to the axis of the bone (Figure 8a). In order to study their micromorphological features and acquire quantitative data, the marks were 3D scanned and processed (Figure 8b-g; see Methods). The values of the parameters are given in Table 3. The two marks, of which the ventral one (mark 1) is longer than the dorsal one (mark 2), are almost parallel (at a maximum distance of ~2.5mm to each other), almost straight, have V-shaped cross-sections (see Figure 8c-g), and preserve internal microstriations. These characteristics are observed with high frequency in anthropogenic cut marks (e.g., Domínguez-Rodrigo et al., 2009; Fernández-Jalvo and Andrews, 2016), including those inflicted on hippopotamus bones (e.g., Domínguez-Rodrigo et al., 2014b; Yravedra et al., 2019). In contrast, abrasional modifications (including trampling) create mostly multiple, randomly

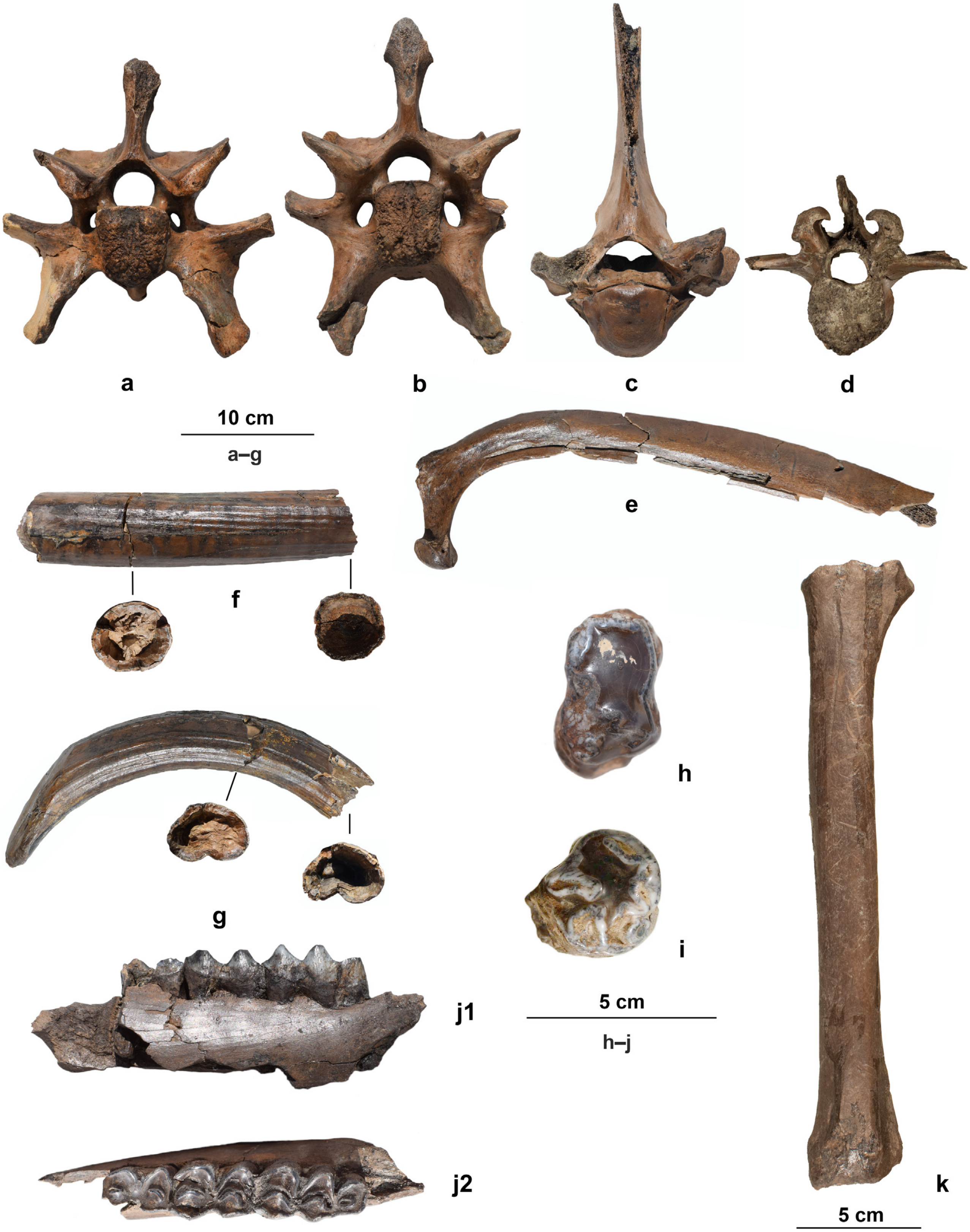


Figure 6. Large mammals remains from Marathousa 2; a–i) Hippopotamus antiquus; *j–k)* Dama *sp. from Marathousa 2; a) fourth (MAR-2A-1a) cervical vertebra, cranial view; b) sixth cervical vertebra (MAR-2A-1b), cranial view; c) thoracic vertebra (MAR-2A-6), cranial view; d) thoracic vertebra (MAR-2A-14), cranial view; e) rib fragment (MAR-2A-2), cranial view; f) lower first incisor (MAR-2B-1), labial view, with cross-sections; g) right upper canine (MAR-2B-2), mesial view, with cross-sections; h) left third upper premolar (MAR-2B-6), occlusal view; i) left upper fourth premolar (MAR-2B-7), occlusal view; j) right mandibular fragment preserving the M_1–M_3 (MAR-2A-8), in medial (j1), and dorsal (j2) views; k) left radius (MAR-2A-18), cranial view.*

TABLE 2. DENTAL AND POSTCRANIAL MEASUREMENTS (in mm) OF THE *HIPPOPOTAMUS*, *DAMA*, AND *CERVUS* REMAINS FROM MARATHOUSA 2.

	Hippopotamus antiquus				*Dama* sp.
	i1	C	P3	P4	m1-m3
	MAR-2B-1	MAR-2B-2	MAR-2B-6	MAR-2B-7	MAR-2A-8
L	(255)	(292)	39.2	41.1	-
W max	-	-	26.3	34.3	-
DMD	52.0	58.5	-	-	-
DAP	-	42.7	-	-	-
DLL	56.6	-	-	-	-
L molars	-	-	-	-	64.6
L × W m1	-	-	-	-	16.8 × 11.7
L × W m2	-	-	-	-	19.9 × 14.8
L × W m3	-	-	-	-	26.1 × 14.7

	Hippopotamus antiquus			
	MAR-2A-1a	MAR-2A-1b	MAR-2A-6	MAR-2A-14
	cervical vertebra	cervical vertebra	thoracic vertebra	thoracic vertebra
L corpus	90	74	67	70.5
W max	(204)	(155)	-	-
H	(199)	226	(168)	(142)
W cranial extremity	48	43	60	55
H cranial extremity	59	61	66	57
W caudal extremity	66	67	88	67
H caudal extremity	71	72	60	63

	Dama sp.		*Cervus elaphus*
	radius	MtIII+IV	PhII
	MAR-2A-18	MAR-2A-5	MAR-2A-12
L	258.5	-	46.6
DT proximal	48.1	34.4	21.9
DAP proximal	23.4	-	(27.1)
DT diaphysis	26.1	-	-
DAP diaphysis	13.8	-	-
DT distal	39.1	-	-
DAP distal	26.2	-	-

Measurements in parentheses represent the greatest measurable value of the parameter, due to incomplete preservation. Abbreviations: **DMD**, mesio-distal diameter; **DAP**, antero-posterior diameter; **DLL**, linguo-labial diameter; **H**, height; **L**, length; **W**, width.

distributed and intersecting striations, with usually sinuous trajectories, and flat- and broad-based grooves in cross-section (Domínguez-Rodrigo et al. [2009, 2010]; see, for example, the rounded fallow deer radius MAR-2A-18 [see Figure 6k], which shows different preservation status/modifications than the *Hippopotamus* bones of the partial skeleton [see Figure 6a-e]). Carnivore tooth scores usually have U-shaped cross-sections (e.g., Pobiner, 2008), while carnivore gnawing was not observed on any of the preserved hippopotamus bones of Area A. Importantly, the preparation of the bones was carried out with wooden tools, so the possibility that these marks have a recent origin is exclud-

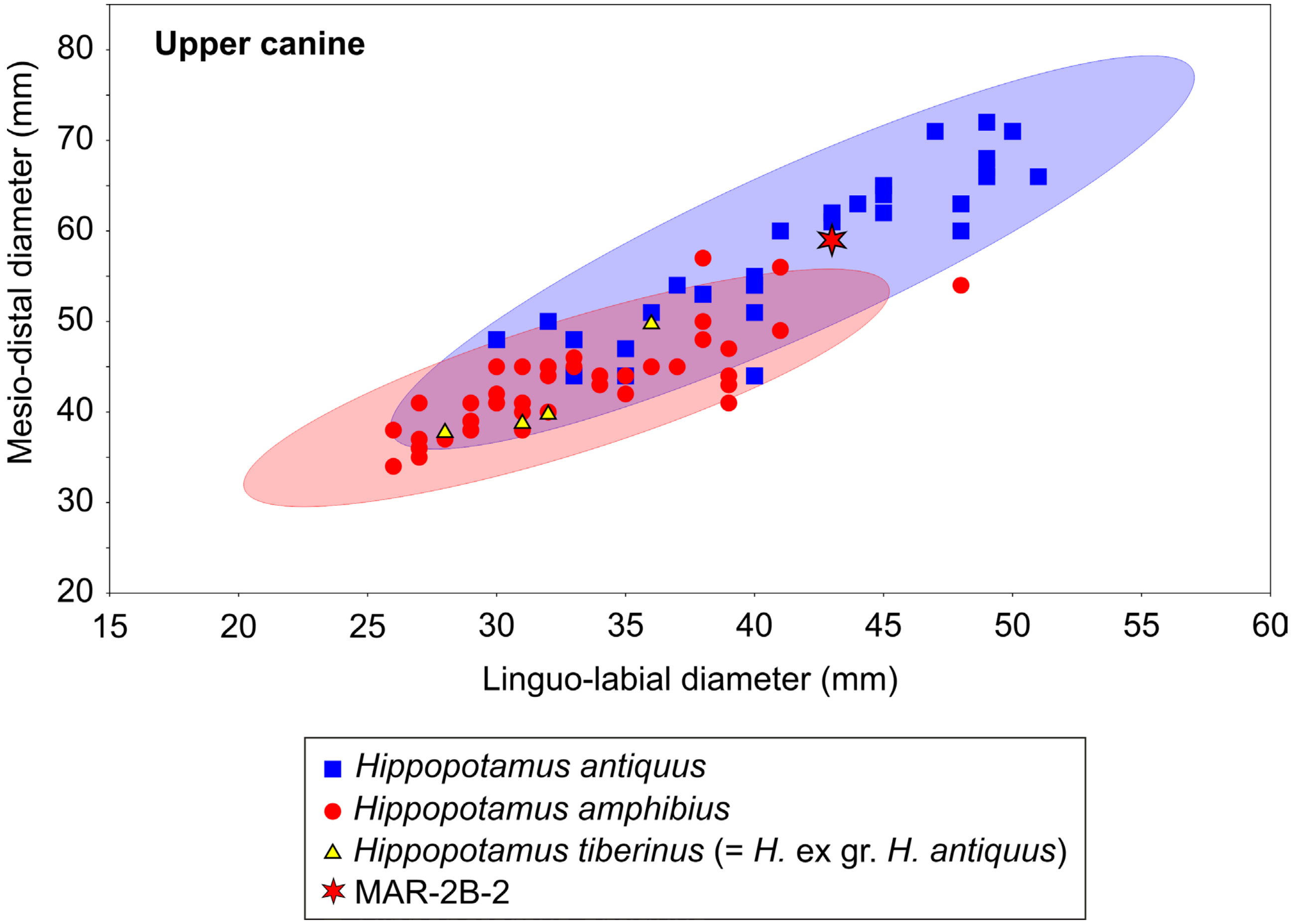


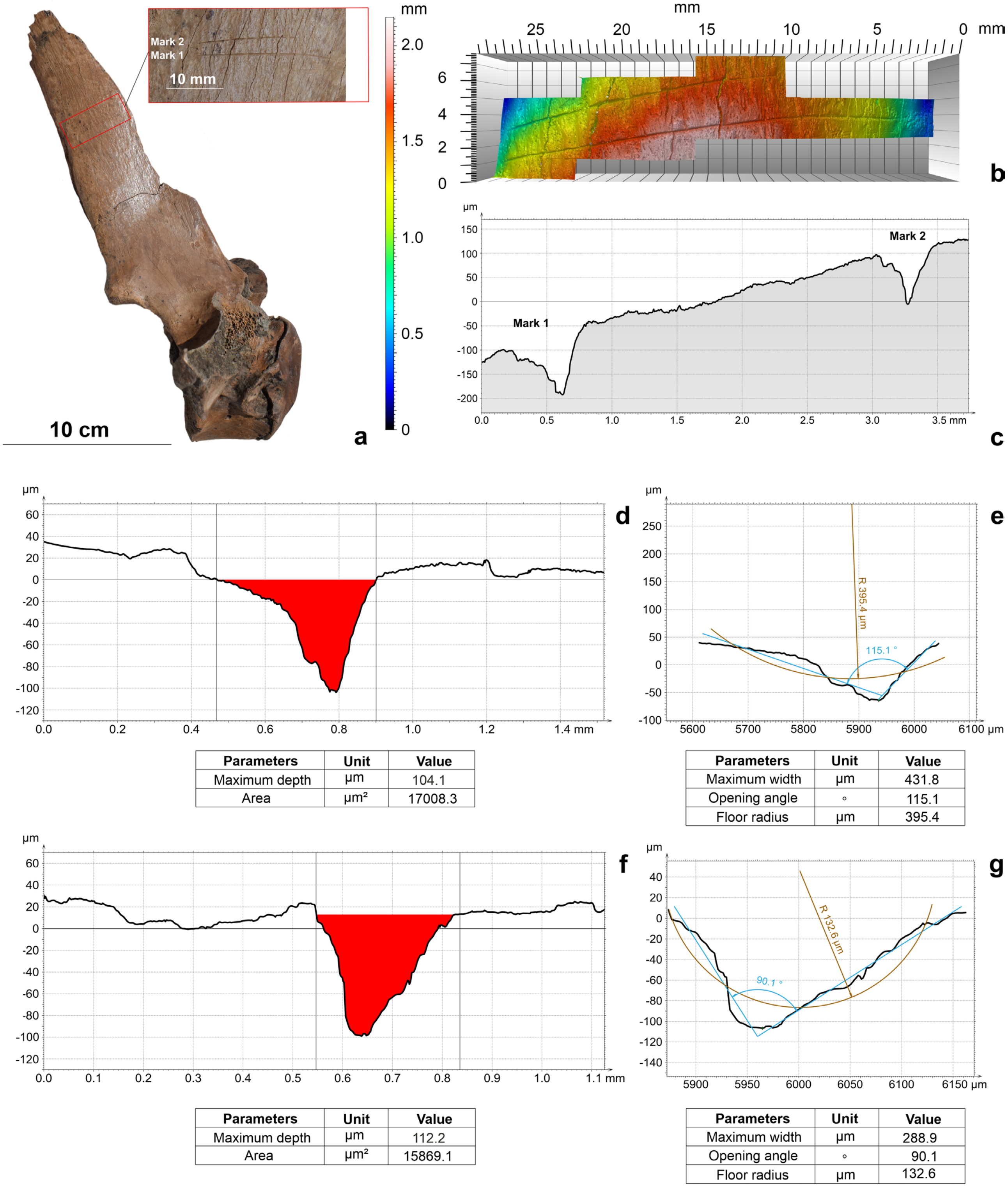
Figure 7. Biplot comparing Hippopotamus *upper canines from various localities with 95% confidence ellipses for* H. antiquus *and* H. amphibius *(data from Mazza 1995); performed with the software package PAST v. 4.04 (Hammer et al. 2001).*

ed. The anatomical position of the MAR-2 striations further supports their identification as cut marks, as vertebrae of hippopotami (as well as of other large mammals including other megaherbivores) frequently preserve evidence of human induced marks (e.g., Crader, 1983; Pobiner et al., 2008; see also Voormolen, 2008: Figure 2.7.2 for a cut-marked spinous process of a *Bos/Bison* thoracic vertebra, and Lupo and O'Connell, 2002 for 40% cut-marked thoracic vertebrae from actualistic butchering of medium- to large-sized mammals). In particular, the location of the MAR-2 cut marks at the preserved middle part of the thoracic spine is indicative of filleting (Voormolen, 2008; Rodríguez-Hidalgo et al., 2017). There are no data for hippopotamus bone utility values, but based on data for other large mammals, thoracic vertebrae are ranked high in terms of utility value and energy return (Marean and Cleghorn, 2003; Morin and Ready, 2013). Additionally, the MAR-2 marks are similar to the cut marks inflicted on elephant bones at MAR-1 (see for instance Konidaris et al., 2018: Figure 9b–d), a geographically nearby and geochronologically similar site, with a rich small-sized lithic assemblage, whose preliminary traceological analysis further confirms that stone tools were used in butchering activities (Tourloukis et al., 2018b; Guibert-Cardin et al., 2022). Besides the morphological match with known cut marks on megafauna from the region, the MAR-2 cut-marked vertebra is spatially and stratigraphically associated with a lithic artifact, thus providing a link between faunal and cultural remains.

DISCUSSION

AGE OF MARATHOUSA 2 – PALEOECOLOGICAL REMARKS

Hippopotamus antiquus was present in Europe during the Early Pleistocene–early Middle Pleistocene, and although its last occurrences are not certain, it seems that it was replaced by *H. amphibius* during the second half of the Middle Pleistocene (Pandolfi and Petronio, 2015; Martino and Pandolfi, 2022). Based on the Italian record, the last occurrence of *Hippopotamus* ex gr. *antiquus* is possibly documented at Castel di Guido, whose dating has been recently revised to 0.412±2 ka and correlated to MIS 11 (Mazza and Bertini, 2013; Marra et al., 2018; Martino and Pandolfi, 2022). *Hippopotamus antiquus* is a frequent faunal element in the Megalopolis Basin, as part of assemblages from different stratigraphic levels (Melentis 1965; Athanassiou et al., 2018; Konidaris et al., 2018; unpublished field data). The similar stratigraphic position of MAR-2 with MAR-1 (between Lignite Seams II and III) suggests a comparable age (500–400 ka) for the locality. Considering its position in the sedimen-



Parameters	Unit	Value
Maximum depth	µm	104.1
Area	µm²	17008.3

Parameters	Unit	Value
Maximum width	µm	431.8
Opening angle	°	115.1
Floor radius	µm	395.4

Parameters	Unit	Value
Maximum depth	µm	112.2
Area	µm²	15869.1

Parameters	Unit	Value
Maximum width	µm	288.9
Opening angle	°	90.1
Floor radius	µm	132.6

Figure 8. a) Cut marks on the Hippopotamus *thoracic vertebra (MAR-2A-6), right lateral view, in rectangle the area with the cut marks; b) 3D topographic representation of the cut marks; c) profile of the cut marks at approximately 50% of the length of Mark 1; d) area of a hole extracted from the central profile of Mark 1; e) contour analysis showing opening angle and floor radius from the portion of the central profile as shown in d; f) area of a hole from the central profile of Mark 2; g) contour analysis from the portion of the central profile as shown in f.*

TABLE 3. MEASUREMENTS OF THE CUT MARK VARIABLES FROM THE *HIPPOPOTAMUS* VERTEBRA.

	Surface area (µm²)	Volume (µm³)	Maximum depth (µm)	Mean depth (µm)	Maximum length (mm)	Maximum width (mm)
Mark 1	4372089	2.29E+08	169.3	52.4	25.7	0.5
Mark 2	2682591	1.41E+08	162.5	52.5	17.5	0.4

Data collected with the use of a confocal profilometer and analyzed with the SensoMAP software.

tary sequence, MAR-2 is placed at the transition from a glacial (with drier and colder conditions) to an interglacial (humid and warmer conditions) stage, similar to MAR-1 but most likely closer to the glacial termination (Karkanas et al., 2018).

Hippopotamus antiquus was a large-sized hippopotamid, probably highly dependent on water and aquatic vegetation (Palmqvist et al., 2003; Martínez-Navarro, 2010; Madurell-Malapeira, 2012); therefore, its presence indicates the existence of permanent freshwater bodies, which agrees well with the occurrence of the—also semiaquatic—beaver and of a freshwater turtle. Such a coexistence is recorded also at MAR-1, where the predominantly fish-foraging otter "*Lutra*" *simplicidens* is also documented (Konidaris et al., 2018). In central and northern European localities, the presence of *Hippopotamus* is generally considered an indicator of temperate climate; however, it is the presence and amount of water (linked to precipitation), rather than temperature, that are of vital importance in the habitat of this genus (Mazza and Bertini, 2013). Therefore, the capacity of the Megalopolis Basin to retain freshwater bodies throughout the year, even during the colder periods of the Middle Pleistocene (most likely including also the glacial maxima: see e.g., Bludau et al., 2021), may have rendered this basin a refugium region for the European hippopotamus populations in the alternating climatic conditions of this epoch. Stable isotope studies on Megalopolis Basin hippopotami, including those from MAR-2, are currently in progress (Roditi et al., in prep.) and are expected to provide additional paleoecological information. Furthermore, the presence of *Dama* sp. at MAR-2 also suggests relatively mild climatic conditions, as the fallow deer in Northern and Central Europe is generally limited to interglacial stages, being less tolerant to open and cold conditions, and preferring more temperate climates (Lister, 1984). Interestingly, the association between *Hippopotamus* and *Dama* is common in the Megalopolis Basin (Athanassiou, 2018; Konidaris et al., 2018; unpublished field data).

Important paleoenvironmental indications are also provided by the preliminary results from the study of the mollusk fauna. Generally, the low number of shells in sample 1 (UA6) and particularly sample 2 (UB6) point to rather stressful conditions for mollusks. The high number of shells in sample 3 (UB2), close to the base of the stratigraphic section, on the other hand, indicates a favorable habitat that allowed them to thrive and develop large populations. Based on the ecological group classification of Ložek (1964), the MAR-2 mollusk fauna consists solely of aquatic (freshwater) taxa. The three dominant species, *Valvata cristata*, *Valvata studeri*, and *Bithynia candiota* indicate high oxygen content and are found in areas rich in aquatic vegetation (Schütt et al., 1985; Davies, 2008; Welter-Schultes, 2009). *Valvata cristata* and *Valvata studeri* live mostly in muddy substrates and indicate more permanent water bodies, as the former is rarely found in temporary waters, and the latter does not tolerate drought (Welter-Schultes, 2009). *Bithynia candiota* and *V. studeri* are found in shallow water, while *V. cristata* prefers standing or slow running water (Glöer and Meier-Brook, 1998). The great dominance of Valvatidae (69.9% in sample 1; 73.6% in sample 3; sample 2 is very poor, but still Valvatidae are dominant) may be an indication of cold, clean freshwater bodies (see Figure 5j; Strong et al., 2008). Furthermore, although in low percentages, the slight increase of lymnaeids in sample 1 (see Figure 5) and, in particular, the occurrence of *Galba truncatula* (1.4% in sample 1, and perhaps in sample 3) are also informative. This is a semiterrestrial freshwater gastropod and its presence implies the existence of pools on a floodplain (White et al., 2008); as member of the 'slum group' of Sparks (1961), it prefers small water bodies that have been subjected to stagnation, drying, and substantial temperature variations.

Overall, based on the current mammal and mollusk evidence, the hippopotamus-bearing layer at MAR-2 was formed at the margins of, or near, a freshwater body, which was likely cold, but with temperatures that allowed it to persist in non-freezing conditions throughout the year. However, the low number of shells indicates a relatively small water body and perhaps relatively dry conditions. On the other hand, the rich and diverse mollusk assemblage from the lower level suggests a larger water body. Therefore, water fluctuations/variable conditions can be assumed along the MAR-2 sequence as also suggested by the sedimentary characteristics of the deposits. Ongoing studies on ostracods, pollen, biomarkers, and stable isotopes will provide further insights for the detailed paleoenvironmental reconstruction of MAR-2.

REMARKS ON *HIPPOPOTAMUS* BUTCHERING WITHIN THE CONTEXT OF MEGAFAUNA EXPLOITATION

With an average body mass of ~1300–1400kg, the modern *Hippopotamus amphibius* is a highly prized prey for contemporary hunter-gatherers (Speth, 2010). This is due to its high meat yield (800kg), the substantial quantity of fat palatable to humans (5% of its liveweight) and large number of calories (>900,000 in total) that can be acquired from a single carcass (Speth, 2010; Ben-Dor et al., 2011; Linares Matás and Yravedra, 2021). Considering the even larger body weight of some of the Pleistocene species (see below), hippopotami may have represented one of the highest-ranked targets also for Paleolithic hominins. However, in contrast to the rather well-recorded exploitation of the significantly larger proboscideans (elephants and mammoths), direct evidence of exploitation (in the form of cut marks) of hippopotami (as well as rhinoceroses) during the European Lower and Middle Pleistocene has been relatively limited. Yet, hippopotami are often found in sites where proboscidean or other large mammal butchering is reported (Konidaris and Tourloukis, 2021). Therefore, the scarcity of cut marks on hippopotami remains cannot be solely attributed to preservation limitations or other biasing factors, such as: a) the presence of a thick cartilage and periosteum that impedes the penetration and contact of stone tools with bones of megafauna; b) meat stripping as the primary goal of butchering rather than bone fracturing for flaking or marrow exploitation, which requires cleaning and scraping of bones; c) the butchering by experienced individuals without producing modifications; or, d) the obliteration of marks due to weathering and other abiotic or biotic processes (see e.g., Haynes and Klimowicz, 2015; Gingerich and Stanford, 2018; Pineda et al., 2019). Out of a sample of 35 western Eurasian open-air localities of the Lower and Middle Pleistocene, 12 have yielded proboscidean bones bearing cut marks, while 22 sites have yielded proboscidean remains preserving all types of direct anthropogenic evidence (e.g., cut marks, breakages for brain/marrow extraction, proboscidean bone artifacts; Konidaris and Tourloukis, 2021). In contrast, cut marks on hippopotamus bones are reported only from five open-air sites and one cave site, which are limited to the peri-Mediterranean region (Figure 9, Table 4)—Barranco León (~1.4 Ma; Spain), Fuente Nueva 3 (~1.3 Ma; Spain), Vallparadís (~1.0 Ma; Spain), Bolomor Cave (~120 ka; Spain), Gesher Benot Ya'aqov (~780 ka; Israel), in addition to Marathousa 2 (besides Bolomor Cave and Gesher Benot Ya'aqov with *H. amphibius*, all other sites have yielded *H. antiquus*; however, Bar-Yosef and Belmaker [2011] list *H. antiquus* in Gesher Benot Ya'aqov). Even if we add to these sites El Kherda and Ain Hanech (Algeria; Sahnouni et al. [2013] with *Hippopotamus gorgops*) at the African peri-Mediterranean region (see Figure 9), still the record remains rather scarce. This could be attributed to differences in ethology and preferred habitats between elephants and hippopotami (Konidaris and Tourloukis, 2021 and references therein); or the non-overlapping foraging activity patterns of hominins (diurnal) and hippopotami (nocturnal; spending the day mostly submerged in water). As previously mentioned, *H. antiquus*, which persists throughout the Lower Paleolithic, is thought to have been characterized by even stronger aquatic life habits than the modern common hippopotamus. This Pleistocene taxon is believed to have ventured only sporadically out of water bodies and to have fed mainly on aquatic vegetation (Palmqvist et al., 2003; Martínez-Navarro, 2010). Occasional nocturnal feeding activity on land, similar to *H. amphibius*, cannot be excluded. However, even so, tracking down and hunting hippos in the dark would be particularly difficult and challenging for hominins, especially considering the territorial, gregarious, and overall dangerous nature of these animals, which currently are responsible for numerous human deaths annually (Eltringham, 2004; MacDonald, 2009). Moreover, the very large size of *H. antiquus*, almost twice as big as *H. amphibius* (*H. antiquus* mean body mass: ~3.0 tons; *H. amphibius* mean body mass: ~1.5 tons; Martínez-Navarro, 2010; Martínez-Navarro et al., 2015) would pose an additional deterring factor. Interestingly, the African record (perhaps more extensively investigated) of hippopotamus exploitation during the Lower and early Middle Pleistocene is more abundant and quite balanced between hippopotami and proboscideans (Linares Matás and Yravedra, 2021). This difference between records underlines the need to further explore hippopotamus exploitation from a multidisciplinary perspective, including hominin behavior, trophic dynamics, technological developments, taphonomy of the hippopotamus-bearing sites, Pleistocene hippopotamus paleoecology, recent hippopotamus ethology, and ethnography.

Based on the available data, it is not possible to ascertain the mode of acquisition (scavenging or hunting) of the MAR-2 hippopotamus carcass, nor is it possible to state whether hominins had primary or secondary access to the carcass. Nevertheless, some preliminary conclusions can be drawn. Axial elements are commonly ravaged during the first stages of consumption by large carnivorans, and thoracic vertebrae are usually among the most affected elements (Marean et al., 1992; Domínguez-Rodrigo, 1999; Arriaza et al., 2016). The distal part of the spinous process, which is often affected by carnivore furrowing, also in very large-sized mammals (Domínguez-Rodrigo, 1999; Haynes and Hutson, 2020; see also Konidaris et al., 2018: Figure 4o), is lacking due to the bad preservation of this bone portion (see Figures 3c, 6c). Nonetheless, carnivore tooth-marks are absent in all preserved hippopotamus bones from Area A. On the other hand, the presence of filleting cut marks indicates access of hominins to a fleshed or at least only moderately defleshed hippo carcass (see Gidna et al., 2014). Considering that vertebrae are elements of high-processing cost, the marks on the spinous process may indicate a more intensive exploitation of the carcass (Marean and Cleghorn, 2003; Rodríguez-Hidalgo et al., 2017).

Although the systematic and targeted hunting of healthy prime hippopotamus individuals does not appear viable (in the sense of a habitual/regular basis) in light of what was mentioned above (semiaquatic lifestyle, different foraging activity patterns, very large size, gregarious, territorial and dangerous), hunting of the juvenile MAR-2 individual cannot be excluded. Hippopotamus hunting might have preferably involved more vulnerable (e.g., juveniles or old adults) and/or weakened (e.g., due to diseases, injuries, malnutrition) individuals. On the other hand, if

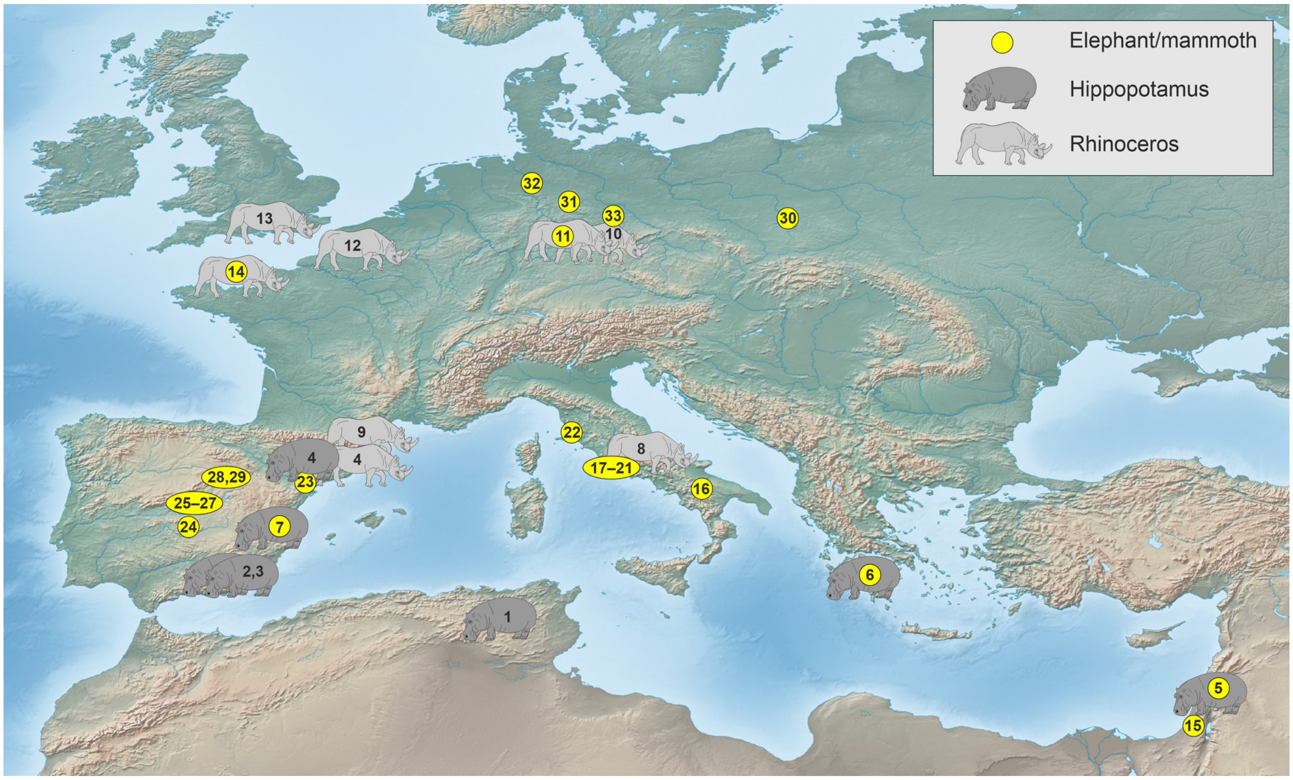


Figure 9. Map showing the location of Lower–Middle Pleistocene sites of western Eurasia and the northern peri-Mediterranean Africa where (possible) direct evidence of megafauna (hippopotami, rhinoceroses, and proboscideans) exploitation by hominins is reported (made with Natural Earth, naturalearthdata.com). 1) El Kherda, Ain Hanech, Algeria; 2) Barranco León, Spain; 3) Fuente Nueva-3, Spain; 4) Vallparadís, Spain; 5) Gesher Benot Ya'aqov, Israel; 6) Marathousa localities (MAR-1 and MAR-2), Greece; 7) Bolomor Cave, Spain; 8) Guado San Nicola, Italy; 9) Caune de l'Arago, France; 10) Taubach, Germany; 11) Bilzingsleben, Germany; 12) Biache-Saint-Vaast, France; 13) Boxgrove, England; 14) La Cotte de St Brelade, England; 15) Revadim, Israel; 16) Notarchirico, Italy; 17) Fontana Ranuccio, Italy; 18) La Polledrara, Italy; 19) Castel di Guido, Italy; 20) Malagrotta, Italy; 21) Casal de' Pazzi, Italy; 22) Poggetti Vecchi, Italy; 23) Barranc de la Boella, Spain; 24) Áridos 2, Spain; 25) EDAR Culebro 1, Spain; 26) PRERESA, Spain; 27) Arriaga, Spain; 28) Ambrona, Spain; 29) Torralba, Spain; 30) Bełchatów, Poland; 31) Schöningen, Germany; 32) Lehringen, Germany; 33) Neumark-Nord 1, Germany. For chronology and selected references on the western Eurasian sites see Table 3 and Konidaris and Tourloukis (2021). Hippo and rhino drawings (not to scale) were redrawn and modified from https://www.drawingtutorials101.com/.

TABLE 4. LOWER–MIDDLE PLEISTOCENE SITES OF WESTERN EURASIA AND NORTH AFRICA WITH REPORTED CUT MARKS ON HIPPOPOTAMI.

	Locality	Country	Age	Species	Skeletal element	Purpose	Other modifications
1	El Kherda, Ain Hanech	Algeria	~1,8 Ma	*Hippopotamus gorgops*	rib (diaphysis, ventral)	evisceration	
2	Barranco León	Spain	~1.4 Ma	*Hippopotamus antiquus*	humerus (diaphysis)	defleshing	
3	Fuente Nueva 3	Spain	~1.3 Ma	*Hippopotamus antiquus*	femur (diaphysis)	defleshing	
4	Vallparadís?	Spain	~1.0 Ma	*Hippopotamus antiquus*	femur	defleshing	
5	Gesher Benot Ya'aqov	Israel	~780 ka	*Hippopotamus ?amphibius*	long bone diaphyses, rib (proximal)	defleshing	percussion marks (marrow exploitation)
6	Marathousa-2	Greece	500–400 ka	*Hippopotamus antiquus*	vertebra	filleting	
7	Bolomor Cave, level IV	Spain	~120 ka	*Hippopotamus amphibius*	three cut-marked bones		burning

Numbering corresponds to the map of Figure 9. References: 1) Sahnouni et al. 2013; 2) Espigares et al., 2019; 3) Yravedra et al., 2021; 4) Martínez et al., 2010, but see Madurell-Malapeira et al., 2012; 5) Rabinovich et al., 2012; 6) this study; 7) Blasco and Fernández Peris, 2012, 2021.

hippopotamus scavenging was carried out, it would likely involve individuals killed either by large carnivorans or during lethal combats between mating male individuals, or those that died due to natural (or pathological) causes. We could not observe evidence of any of the latter on the MAR-2 individual, although it must be noted that the preserved material is limited, hindering more definitive conclusions.

MAR-2 adds to the meager record of hominin-hippopotamus interactions in western Eurasia and is part of the marked increase of sites documenting hominin procurement of megafauna carcasses from the Lower Pleistocene and more regularly from the Middle Pleistocene onwards, as evidenced at a regional (MAR-1 and 2) and European scale (Yravedra et al., 2010; Konidaris and Tourloukis, 2021; Palombo and Cerilli, 2021; Rosell and Blasco, 2021). This marked increase reflects a more regular engaging in megafaunal consumption and further reveals that megafauna (among others, as an animal resource with a high yield) was an important component of hominin subsistence strategies (see e.g., Ben-Dor and Barkai, 2021). Beyond nutritional purposes, megafauna exploitation involved the manufacturing of bone artifacts (e.g., Tourloukis et al., 2018b; see also Zutovski and Barkai [2016] for elephant bone handaxes, as well as Sano et al. [2020] for a biface made from a hippopotamus bone), providing hominins with an additional source of raw material. This overall increase in the record of megafauna exploitation is chronologically correlated, and perhaps associated with, changes in the large carnivoran guild composition (see also Konidaris, 2022), an increase in hominin body size and encephalization, the establishment of a more continuous human presence in Europe, and a set of biocultural changes that affected hominin foraging efficacy, including an increase in group size, cooperative foraging employing ambush tactics, and habitual use of fire (Konidaris and Tourloukis, 2021 and references therein).

CONCLUSIONS

The new locality of Marathousa 2 offers important insights into the Middle Pleistocene ecosystem of the Megalopolis Basin and hominin adaptations in the region. The MAR-2 hippopotamus belongs to the species *Hippopotamus antiquus*, a large-sized taxon almost twice as large as the recent *H. amphibius*, and with strongly aquatic habits. The presence of cut marks on one of the vertebrae of the MAR-2 juvenile hippopotamus individual (Area A) indicates butchering activities by hominins at the margins of a rather cold, but perennial freshwater body, perhaps under relatively drier conditions compared to preceding and succeeding periods of the basin.

Overall, in addition to the exploitation of straight-tusked elephants (*Palaeoloxodon antiquus*) at MAR-1, MAR-2 provides further evidence of megafauna butchering during the Middle Pleistocene in the Megalopolis Basin, the first record of continental hippopotamus exploitation in eastern Europe, and one of the very few examples from the Pleistocene of western Eurasia. As such, it contributes to improving our knowledge of food acquisition strategies and subsistence behaviors of Pleistocene hominins, while further emphasizing the need for continued research in the Megalopolis Basin, where megafauna are well recorded.

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DATA STATEMENT

All data of this study are available within the article.

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