1. Introduction

The Megalopolis area is an intramontane basin situated in western Arcadia, in the centre of the Peloponnese (Fig. 1a). Geologically it is a graben, formed in the Mesozoic western Arcadia, in the centre of the Peloponnesus (Fig. 1a).

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The good state of preservation of the MAR-1 bones allows the identification of taphonomic modifications. Cut marks on the elephant skeleton, and on other elephant and mammal bones, indicate human exploitation by means of butchering activities, in accordance with the traits of the lithic assemblage and its spatial association with the bones. Carnivore activity is also recorded on some elephant and cervid bones. Marathousa 1 is among the oldest elephant butchering sites in Europe and the only one known in Southeastern Europe.

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The skeleton of a straight-tusked elephant (*Palaeoloxodon antiquus*) and other large mammals from the Middle Pleistocene butchering locality Marathousa 1 (Megalopolis Basin, Greece): preliminary results

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**A B S T R A C T**

In this article, we present the first results on the large mammal fauna from the new open-air Lower Palaeolithic locality Marathousa 1 (MAR-1) (Megalopolis Basin, Peloponnese, Greece). MAR-1 belongs to the Marathousa Member of the Choremi Formation and its large mammal faunal list (collection 2013–2016) includes the castorid *Castor fiber*, the mustelids *Mustela* sp. and *Lutra simplicidens*, the felid *Felis* sp., the canids *Vulpes* sp. and *Canis* sp., the elephantid *Palaeoloxodon antiquus*, the hippopotamid *Hippopotamus antiquus*, the bovid *Bison* sp., and the cervids *Dama* sp. and *Cervus elaphus*. This faunal association is common in the Galerian (Middle Pleistocene) mammal communities of Europe (ca. 0.9–0.4 Ma). The MAR-1 fauna is consistent with a temperate climate and is indicative of a landscape with substantial woodland components with more open areas, close to permanent and large freshwater bodies. Of particular interest are an elephant cranium and numerous postcranial elements, which were found in close anatomical association and are attributed to a single individual of the straight-tusked elephant *Palaeoloxodon antiquus*. The skeleton belonged to a male individual in its late adulthood close to or in its sixties, with live skeletal height around 3.7 m at the shoulder and body mass around 9.0 tonnes. The good state of preservation of the MAR-1 bones allows the identification of taphonomic modifications. Cut marks on the elephant skeleton, and on other elephant and mammal bones, indicate human exploitation by means of butchering activities, in accordance with the traits of the lithic assemblage and its spatial association with the bones. Carnivore activity is also recorded on some elephant and cervid bones. Marathousa 1 is among the oldest elephant butchering sites in Europe and the only one known in Southeastern Europe.

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Megalopolis Basin took place in several localities in 1902 by Professor T. Skouphos (University of Athens) (Bürchner, 1903; Skouphos, 1905; Melentis, 1961), but unfortunately, as with several historical collections, the fossils lack precise stratigraphic information. Therefore, this collection, which was studied in detail by Melentis during the 1960s (Melentis, 1961, 1963a, b, 1965a, b, c, d, e, 1966), does not represent a single stratified fossil accumulation and cannot be used for biochronology. Since then, further palaeontological work in the basin has been conducted, including the collection of Pleistocene fossils and a human molar from the Marathousa Beds by a team of German geologists in the 1960s (Sickenberg, 1975); the study on the magneto- and cyclostratigraphy of the basin, as well as the micro- and macrovertebrate fauna of the Choremiou section (Marathousa Member), conducted by van Vugt and colleagues in the 1990s (van Vugt, 2000); the palaeontological excavations by the University of Athens (Theodorou, 2014) and the study by Athanassiou and colleagues in the Kyparissia mine (Athanassiou et al., this issue). The Pleistocene fossil fauna from Megalopolis is therefore relatively well known. However, most of the collections mentioned above do not represent a single stratified assemblage, which can be used for secure biochronological and palaeoecological interpretations; furthermore, none of this material was found in association with archaeological remains and therefore it cannot provide information about early human activities. Here we report on the first such stratified assemblage associated with palaeolithic cultural remains, recovered from a controlled excavation context at the new open-air Lower Palaeolithic site Marathousa 1. The aim of this article is to provide preliminary results about the large mammal fauna and the biochronology of Marathousa 1, as well as remarks on palaeoecology and taphonomy.

2. Locality, materials and methods

Marathousa 1 was discovered during systematic survey by a joint team of the Ephorate of Palaeoanthropology-Speleology of the Greek Ministry of Culture and the Palaeoanthropology department of the University of Tübingen in the framework of the ERC project PaGE —Palaeoanthropology at the Gates of Europe: human evolution in the southern Balkans— (Harvati and Tourloukis, 2013). The survey was conducted in 2012 and 2013, with the goal of locating sites with archaeological/palaeoanthropological interest (see Thompson et al., this issue). The new locality Marathousa 1 (MAR-1) was discovered in 2013, when stratified bones and lithic artefacts were identified in a profile of the Marathousa Member (Choremi Formation) (Panagopoulou et al., 2015). The find-bearing layers occur between two lignite seams (Fig. 1b) and are composed mainly of silty sands. Two excavation areas were defined: Area A and Area B, both yielding lithics (see Panagopoulou et al., this issue and Tourtikis et al., this issue a), micro- and macro-fauna (fishes, amphibians, reptiles, birds, mammals; see also Doukas et al., this issue and Michailidis et al., this issue), as well as micro- and macro-flora (Field et al., this issue). Area A represents a dense accumulation of elephant bones, belonging to a single individual of the straight-tusked elephant *Palaeoloxodon antiquus*, associated with lithic artefacts and other faunal remains. Area B, which lies ca. 60 m to the south of Area A, is generally characterized by the presence of relatively abundant lithic artefacts in association with faunal remains. Lithological and stratigraphic correlations between the excavated sequences (Fig. 1b; Karkanias et al., this issue), along with spatial patterns (Giusti et al., this issue), archaeological (Panagopoulou et al., this issue; Tourloukis et al., this issue a) and palaeoontological/zooarchaeological evidence (this study) altogether indicate that the find-bearing units in the two excavation areas are correlated and belong to the same depositional event. Consequently, notwithstanding the fact that the archaeological signature of the two excavation Areas may represent different episodes and/or human activity areas (Panagopoulou et al., this issue; Tourloukis et al., this issue a), the palaeontological material is treated here as a single faunal assemblage. The preliminary faunal lists for Area A and Area B are presented in Table 1. More information on the locality and the stratigraphy can be found in Panagopoulou et al. (this issue), Karkanias et al. (this issue) and Tourloukis et al. (this issue b).

The studied material includes all the large mammal specimens collected from Marathousa 1 during the field seasons 2013—2016. All specimens are stored at the Ephorate of Palaeoanthropology-Speleology in Athens (Greece). Measurements were taken with digital calipers or, in the case of very large specimens, with a measuring tape.

Cut mark analysis: We inspected every bone with a stereomicroscope (Leica MZ95, 10× eyepiece, 0.63–6× zoom objective lens) or in the case of very large specimens with hand lenses under strong direct light. Specimens with marks were molded using high-resolution silicone (polyvinyl siloxane; Regular Body Mircosystem, Coltene President). Each cast was subsequently poured with epoxy resin (Epo-tek 301 Parts A and B) in order to produce replicas. Data were acquired with the use of a Sensofar Pli Nex confocal imaging profiler with 10× objective lens with a vertical resolution of <50 nm, a lateral sampling interval of 1.66 μm, and an aperture of 0.30. Three dimensional representations and profiles of the striations were obtained with the SensoMAP 7.0 software using the default settings without application of filters, apart from removing outliers, while all data were first leveled. Profiles between 30% and 70% of the marks’ length were studied for the cross-sectional analysis (Mate González et al., 2015).

Table 1

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Area A</th>
<th>Area B</th>
<th>Section between Areas A and B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rodentia</td>
<td>Castoridae</td>
<td>Castor</td>
<td>fiber</td>
<td>UA2, UA3, UA3/UA4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Mustelidae</td>
<td>Mustela</td>
<td>sp. (large-sized)</td>
<td></td>
<td>UA3</td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Mustelidae</td>
<td>Lutra</td>
<td>simplicident</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Felidae</td>
<td>Felis</td>
<td>sp.</td>
<td></td>
<td>UA4</td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Canidae</td>
<td>Vulpes</td>
<td>sp.</td>
<td></td>
<td>UA4</td>
<td></td>
</tr>
<tr>
<td>Carnivora</td>
<td>Canidae</td>
<td>Canis</td>
<td>sp.</td>
<td></td>
<td>UB4</td>
<td></td>
</tr>
<tr>
<td>Proboscidea</td>
<td>Elephantidae</td>
<td>Palaeoloxodon</td>
<td>antiquus</td>
<td>UA3/UA4</td>
<td>UB4, UB5</td>
<td></td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>Hippopotamidae</td>
<td>Hippopotamus</td>
<td>antiquus</td>
<td>UA2, UA3</td>
<td>UB4</td>
<td></td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>Bovidae</td>
<td>Bovis</td>
<td>sp.</td>
<td></td>
<td>UB4</td>
<td></td>
</tr>
<tr>
<td>Artiodactyla</td>
<td>Cervidae</td>
<td>Cervus</td>
<td>elaphus</td>
<td>UA3, UA3/UA4</td>
<td>UB4, UB5</td>
<td></td>
</tr>
</tbody>
</table>

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3. Palaeontology

3.1. The Marathousa 1 elephant skeleton

The MAR-1 excavation is in progress, but important skeletal elements of the elephant have been already unearthed in Area A, including the cranium (MAR-1-942/676-6; pending final preparation), which bears the pair of upper third molars and the proximal part of the right tusk (Fig. 2a). The morphology of the cranium with widely laterally divergent (flaring) premolar tusk alveoli, accompanied with dental features such as the relatively narrow crown, the intensively folded enamel of the lamellae and the presence of pointed midline sinuses (Saegusa and Gilbert, 2008; Lister et al., 2012), support the attribution to *Palaeoloxodon*. The combination of the above features excludes an attribution to *Mammuthus*, the other candidate elephantid genus of the European Pleistocene (which is characterized by tusk alveoli that are sub-parallel and situated close to one another, relatively wide molars with weakly folded enamel and absence of pointed midline sinuses; Lister and Stuart (2010), Lister et al. (2012)), and are shared with the European straight-tusked elephant *Palaeoloxodon antiquus*. The final preparation and study of the cranium will likely reveal additional relevant morphological features.

The proximate spatial accumulation of several elephant bones, the lack of duplication, and the consistency in size and ontogenetic age indicate the presence of a single elephant individual (Fig. 1c). There is no anatomical connection between the bones; despite this, however, the skeleton is not largely dissociated so that several originally articulated bones occur in approximate anatomical association (Fig. 1c). To date, numerous skeletal elements have been recovered in addition to the cranium, such as vertebrae (including atlas, axis and sacrum), ribs, the left humerus (pending preparation), the right ulna, the pelvis, the right femur, the left tibia and several carpals, tarsals, metapodials and phalanges, for a total of 77 teeth and bones recorded so far (Fig. 3).

The available skeletal elements of the MAR-1 elephant provide metric data for the approximate estimation of its shoulder height and body mass. For the estimation of shoulder height from isolated limb bones, we used the regression equations of Lister and Stuart (2010), which have been developed on the basis of mounted skeletons of mammoths, and we obtained a live shoulder height (including flesh) of approximately 3.7 m for the MAR-1 elephant (Table 2). The ulna is considered problematic for the estimation of the shoulder height (Lister and Stuart, 2010) and therefore is not included. The body mass of the elephant can be estimated using the prediction equations of Christiansen (2004), which are based on samples of recent *Loxodonta africana* and *Elephas maximus*. Using the best predictors proposed by Christiansen for the available MAR-1 bones (Table 3), body mass estimates range significantly from ~6.7 to 11.0 tonnes with an average of 8.8 tonnes. Among the possible measurements, ulna length and ulna least circumference of the diaphysis are the most reliable estimators, given their lowest standard error of the estimation (SEE) and prediction error (PE) percentages. These provide a mass of ~9.0 tonnes for the MAR-1 elephant. Another method for the body mass estimation uses prediction equations of body mass against shoulder height for recent elephants (Roth, 1990 and references cited therein). Given the estimated live shoulder height of 3.7 m for the MAR-1 elephant, an average body mass of ~9.1 tonnes is obtained. The results of the best osteological predictor (ulna) and of the mass estimate based on the shoulder height are in very good agreement, and therefore a body mass of 9.0 tonnes is proposed for the MAR-1 elephant (Table 3).

Age at death can be estimated by the dental-wear-based age criteria for the extant African elephant *Loxodonta africana* provided by Laws (1966). That author used the lower teeth, but a similar wear pattern can be assumed for the upper teeth. The anterior parts of the M3s are not well preserved so the exact number of plates is difficult to reconstruct (at least pending final preparation of the cranium). Nevertheless, it appears that the teeth likely fall within Laws’ group XXVII, which corresponds to the average age of 53 in African Equivalent Years (AEY). Recent revisions on Laws’ age assignments propose that this age group corresponds to an upper limit of 60–66 AEY with 70+ longevity for the African elephant (Stansfield, 2015; Haynes, 2017). *Palaeoloxodon antiquus* had a significantly larger body size than extant African elephants, and due to the general positive scaling of longevity to body size across mammals, also probably had a longer total lifespan (Eisenberg, 1990; Maiorana, 1990); therefore, a slightly older true age is expected for the MAR-1 elephant. When the formula of Blueweiss et al. (1978) (longevity in days proportional to body mass in grams0.17) is applied, assuming a longevity of 70 years and a body mass of 6.0 tonnes for males of *L. africana*, and a body mass of 9.0 tonnes for the MAR-1 elephant, a longevity of approximately 75 years can be hypothesized for the latter. Consequently, the estimated upper limit of the ontogenetic age for the MAR-1 elephant is 60 to (66) × 75/70 = 64–71 years. Therefore, it is reasonable to assume that the MAR-1 elephant was in its late adulthood (but not senile) close to or in its sixties. This age is in agreement with the extent of epiphyseal fusion of the skeletal elements. Elephants have a prolonged period of growth and the fusion of their long bones extends into their middle age or even further, and males complete their epiphyseal fusion sequence well after females (Haynes, 1991, 2017). Considering that the MAR-1 elephant is male (see below), and following the fusion sequence in recent male elephants and mammoths provided by Roth (1984), Lister (1999) and Haynes (2017), the last epiphyses to fuse are the proximal femur, and then the distal radius and ulna. Assuming similar fusion series for the MAR-1 elephant, the not completely fused distal ulna and the fused proximal femur (Fig. 2d, f), support the advanced age for the MAR-1 elephant.

Elephants, both recent and extinct, are characterized by pronounced sexual dimorphism, particularly with regard to body size—males being considerably larger than females (Haynes, 1991; Sukumar, 2003). Several observations on the MAR-1 elephant indicate that it was male: a) Based on the Neumark-Nord (Germany) *P. antiquus* (Palombo et al., 2010, fig. 22), female individuals are not expected to significantly surpass a shoulder height of 3.0 m; the estimated shoulder height of 3.7 m for the MAR-1 elephant exceeds this limit considerably. b) The dimensions of the postcranial elements help to distinguish the sex of extinct elephantids based on the larger size observed in males (e.g., Kroll, 1991; Averianov, 1996; Tsoukala and Lister, 1998; Palombo and Villa, 2003). The large size of several bones, such as the atlas (W max: 491 mm), axis (H max: 333 mm), ulna (L max: 1035 mm), femur (L max: 1330 mm), tibia (L max: 792 mm) and calcaneus (D max: 274 mm), fit within the ranges of corresponding bones belonging to presumed male individuals of *P. antiquus* (Kroll, 1991). c) The developed dorsal and ventral tubercles and the marked muscle scars on the cranial articular surfaces of the atlas, which contrast with the presumed female atlas from Crumstadt, Germany (Kroll, 1991, p. 14), as well as the robust odontoid process (dens) of the axis (Fig. 2b and c), point to a male (Averianov, 1996; Marano and Palombo, 2013). d) The morphology and the ratios between measurements of the pelvic girdle are essential to the sex determination of proboscideaes (Lister, 1996a; Palombo and Villa, 2003). The MAR-1 pelvis is still under preparation and the two inommates were found separated almost at the pubic symphysis. Therefore, the ratio between the pelvic aperture width and the ilium shaft width, a major criterion for sex determination, is not available at the
Fig. 2. a–f. *Palaeoloxodon antiquus* remains from the Marathousa 1 (Area A) skeleton; a, cranium in situ (MAR-1-942/676-6) and detail of the left and right upper third molars; b, atlas, MAR-1-940/674-39, cranial view; c, axis, MAR-1-940/675-41, lateral view; d, right ulna, MAR-1-940/677-21, medial view; e, right half of the pelvic girdle, MAR-1-938/674-37, caudal view; f, right femur, MAR-1-940/675-50, cranial view; g, ratio between pelvic aperture height and ilium shaft width (measurements are shown in ‘e’); circles: males, squares: females; data from Lister (1996a), Göhlich (2000) and Lister et al. (2012).
Fig. 3. Schematic drawing of a *Palaeoloxodon antiquus* skeleton (by K. Schauer/C. Beauval available at www.archeozoo.org) showing the identified anatomical parts (in parentheses the side or the number of specimens; R: right, L: left) belonging to the Marathousa 1 (Area A) skeleton (collection 2013–2016).

Table 2
Estimation of the shoulder height of the Marathousa 1 (Area A) elephant from femur and tibia lengths, based on linear regression equations (SH = aX + b; SH: shoulder height, X: the bone length in mm, a, b: slope and intercept of regression equation) given by Lister and Stuart (2010).

<table>
<thead>
<tr>
<th>Element/measure</th>
<th>MAR-1 measure (mm)</th>
<th>a</th>
<th>b</th>
<th>R-square</th>
<th>MAR-1 skeletal SH estimate ± 95% confidence/prediction interval (mm)</th>
<th>MAR-1 live SH (mm) ±6% for flesh</th>
</tr>
</thead>
<tbody>
<tr>
<td>femur length ('best')</td>
<td>1330</td>
<td>3.0438</td>
<td>–549.104</td>
<td>0.8901</td>
<td>3449 ± 112/349</td>
<td>3656</td>
</tr>
<tr>
<td>tibia length ('best')</td>
<td>792</td>
<td>3.8455</td>
<td>462.384</td>
<td>0.7219</td>
<td>3508 ± 225/593</td>
<td>3718</td>
</tr>
<tr>
<td>Average SH</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3687</td>
</tr>
</tbody>
</table>

Table 3
Estimation of the body mass of the Marathousa 1 (Area A) elephant based on predictive equations of modern elephants, a, from bone lengths (Christiansen, 2004); SEE: standard error of the estimation and PE: prediction error percentages, and b, from shoulder height (Roth, 1990 and references cited therein); BM: body mass, SH: shoulder height.

<table>
<thead>
<tr>
<th>a. Element</th>
<th>Equation</th>
<th>MAR-1 measure (mm)</th>
<th>a</th>
<th>b</th>
<th>% SEE</th>
<th>% PE</th>
<th>Estimated BM (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ulna length</td>
<td>log (BM) = a + b (logX)</td>
<td>1035</td>
<td>–4.135</td>
<td>2.674</td>
<td>8.41</td>
<td>5.34</td>
<td>8452</td>
</tr>
<tr>
<td>ulna least circumference</td>
<td>where X is the bone</td>
<td>430</td>
<td>–1.349</td>
<td>2.022</td>
<td>5.78</td>
<td>4.42</td>
<td>9460</td>
</tr>
<tr>
<td>femur length</td>
<td>variable (mm)</td>
<td>1330</td>
<td>–5.658</td>
<td>3.036</td>
<td>14.54</td>
<td>6.15</td>
<td>8242</td>
</tr>
<tr>
<td>tibia length</td>
<td></td>
<td>792</td>
<td>–3.084</td>
<td>2.378</td>
<td>12.47</td>
<td>6.93</td>
<td>6748</td>
</tr>
<tr>
<td>tibia least circumference</td>
<td></td>
<td>360</td>
<td>–2.724</td>
<td>2.647</td>
<td>10.72</td>
<td>6.57</td>
<td>11,029</td>
</tr>
<tr>
<td>Average (all bones)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8786</td>
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<tr>
<td>Average (ulna)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8956</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>b. Source population</th>
<th>Equation (SH in cm)</th>
<th>MAR-1 SH (cm)</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Estimated BM (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. africana</em> (males)</td>
<td>BM = 5.07 × 10^{-4} × SH^{2.003}</td>
<td>370</td>
<td></td>
<td></td>
<td></td>
<td>8011</td>
<td></td>
</tr>
<tr>
<td><em>L. africana</em> (males)</td>
<td>BM = 3.06 × 10^{-4} × SH^{2.000}</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8088</td>
<td></td>
</tr>
<tr>
<td><em>L. africana</em> (males)</td>
<td>BM = 1.81 × 10^{-4} × SH^{2.007}</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>7678</td>
<td></td>
</tr>
<tr>
<td><em>E. maximus</em> (males and females)</td>
<td>BM = 4.68 × 10^{-4} × SH^{2.003}</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11,228</td>
<td></td>
</tr>
<tr>
<td><em>E. maximus</em> (males, captive)</td>
<td>log (BM) = –3.436 + 2.906 log (SH)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10,646</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
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<td>9130</td>
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<td>Average (both methods)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9043</td>
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</tbody>
</table>

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moment. However, the ratio between pelvic aperture height and ilium shaft width, an alternative sex indicator (Lister, 1996a) can be calculated for the MAR-1 specimen. The value for this ratio (2.19) places the MAR-1 elephant among the male individuals of *P. antiquus*, as well as those of *Mammuthus* (Fig. 2e, g), again supporting male sex. e) As was mentioned above, the fused proximal femur and the not completely fused distal ulna, combined with the advanced ontogenetic age, is consistent with a male sex.

3.2. Other large mammals from Marathousa 1

The presence of a beaver in the MAR-1 fauna is recognized by incisors, cheek teeth and postcrania elements. The lower incisors with straight anterior margin, smooth enamel on the outer side and triangular cross-section, the high-crowned cheek teeth with long and deep striae/striids, and the humerus with a wide caput humeri attached to the tuberculum majus (Fig. 4g, Table 4), are some morphological features distinct from *Trogontherium cuyeri*, and similar to *Castor fiber* (Guenther, 1965; Kretzoi, 1969; Fischer, 1991; Postowicz-Frel, 2008).

The carnivores are represented by two mustelids, two canids and one felid. The first mustelid is known by a mandibular fragment, showing typical *Lutro*-like pars anceps (MAR-1-939/675-35; Fig. 4k; Willemsen, 1992; Sotnikova and Titov, 2009). Features on the m1, such as the trigonid that is broader than the talonid (Table 5), the shallow talonid basin, the large metacoonid, and the absent hypoconulid, all distinguish the MAR-1 otter from *L. lutra* and resemble *L. simplicidentes* (Willemsen, 1992). The studied specimen’s m1 is very similar in its dimensions to known lower molars of *L. simplicidentes* from various European localities (Willemsen, 1992; Sotnikova and Titov, 2009; Cherin and Rook, 2014). Sotnikova and Titov (2009) erected the new subspecies *L. s. tamanesis*, based on the morphology of a lower carnassial from Chumbur Kosa (Sea of Azov, Russia), whose talonid width is equal to that of the trigonid, the metacoonid is slightly enlarged, the talonid blade bears a complete number of well-developed cusps and the distal occlusal outline is relatively pointed. Apart from the latter feature, the simplified talonid morphology and the overall proportions of the MAR-1 m1 are distinct from *L. s. tamanesis*, and similar to *L. s. simplicidentes* from Hundsheim (Austria, holotype), Voigststedt, Mosbach-2 (Germany), East Runton and West Runton (England) (Thenius, 1965; Willemsen, 1992). If this subspecific distinction is corroborated in the future by additional samples, then the MAR-1 mandibular specimen could be referred to the nominal subspecies.

The other mustelid is represented by a tibia (MAR-1-939/637-2; Fig. 4h). Its size (Table 4) is smaller than recent *Meles* and *Martes*, but larger than *Mustela erminea* and *M. nivalis*, and falls within the size variation of *M. putorius*, *M. eversmanni* and *M. lutreola* (Archaeozoology collection-University of Tübingen; Galik, 1997). Because taxonomic identification based on a single tibia is very difficult (Ziegler, 1996; Galik, 1997), the range of variation of Pleistocene specimens is unknown and cranial or dental remains have not been recovered to date for this taxon from the site, we refer to this mustelid as *Mustela sp.* (large-sized).

A lower carnassial (MAR-1-932/595-69) belongs to a small canid, and presents morphology and dimensions similar to *Vulpes*. The m1 is characterized by a rather strong and distinct metacoonid, which is higher than the entoconid and lower than the paraconid; bicuspid talonid with stronger hypoconid; a weak entoconid; and, a low hypoconulid (Fig. 4d–f). The dimensions of the tooth (L × W: 14.2 × 5.8 mm) are larger than *V. alpeceoides*, e.g., from Dafnero-1 (Greece: L: 12.8–13.2, W: 5.3–5.6 mm; Koufos and Kostopoulos, 1997), but at the upper limit of *V. praeglacialis*, e.g., from L’Escale (France: L: 13.2–14.3, W: 4.9–5.7 mm; Bonifay, 1971), and are almost exact to PEC 1600 of *V. praeglacialis* from Petralona (Greece; L × W: 14.2 × 5.7 mm; Baryshnikov and Tsoukal, 2010). They are smaller than *V. vulpes* from L’Escale (L: 15.0–16.9, W: 5.0–6.2 mm; Bonifay, 1971), as well as from Ágos Georgios Cave (Greece; L × W: 15.5 × 6.2 mm; Tsoukal, 1992), but within the range of variation of Late Pleistocene and recent red foxes (e.g., Ballesio, 1980; Petronio et al., 2006). Although an attribution to *V. praeglacialis* is possible, taking into account the large size variability in foxes (e.g., Kurten, 1965; Davis, 1977) we attribute the MAR-1 fox to *Vulpes* sp.

A carnivore axis (MAR-1-933/594-77) and a fifth metatarsal (MAR-1-932/596-79) resemble in morphology those of canids and correspond to the size of a wolf. The reduced ventral keel and the caudally bent articular facets for the atlas, which are only slightly dorsoventrally extended (Fig. 4j), are different from *Cuon priscus* from Hundsheim and resemble *Canis* (Thenius, 1954). Its dimensions (LcDe: 50.6, LApA: 50.2, BFcR: 30.9, H: 39.0; according to von den Driesch (1976); articular facets for atlas: 17.2 × 11.5; all in mm) are similar to *Canis mosbachensis* from Untermählfeld (Germany) and *C. lupus lunellensis* from Lunel-Viel (France) (Sotnikova, 2001; Boudadi-Maigne, 2010). The morphology and the dimensions of the metatarsal also match those of *Canis* (Fig. 4i, Table 4). The metatarsal is of the smaller than that of *C. lupus* (L: 85.7–90.9, DT diaphysis: 70.8–82.2, DT distal: 11.4–12.9; all in mm), and is more similar in size to that of *C. lupus lunellensis* (L: 70.6–77.2, DT diaphysis: 5.5–8.9, DT distal: 8.8–10.1; all in mm); it fits best with the *C. mosbachensis* specimens from L’Escale (France; L: 66.7–75.7, DT diaphysis: 4.7–5.5, DT distal: 8.4–9.9; all in mm) (Boudadi-Maigne, 2010). Although an attribution to the latter species seems plausible, we attribute both specimens to *Canis* sp., because of a certain degree of overlap between *C. mosbachensis* and *C. lupus lunellensis*, and especially due to the lack of more diagnostic specimens.

An isolated upper carnassial (MAR-1-933/596-19) belongs to a small feld. The protocone is broken; the relatively strong parastyle is slightly labially situated and a lower but distinct ectoparastyle is located at the mesiolabial side. The paracoon is prominent and the metastyle becomes rounded at its distal end (Fig. 4a–c). The dimensions of the tooth (L × W: (11.0) × 5.4 mm) are clearly smaller than those reported for *Lynx* (15.9–19.1 × 6.6–9.1 mm) and they fall comfortably within the range of variation of the extant European wildcat Felis silvestris silvestris (9.6–12.1 × 4.5–6.7 mm), close to the *Felis* specimens from West Runton (11.3 × 6.1 mm) and Lunel-Viel (12.2 × 6.1 mm) (Bonifay, 1971; Ballesio, 1980; Lewis et al., 2010; Ghezzo et al., 2015; Boscaini et al., 2016). Candidate Felis species for the Pleistocene of Europe are *F. lunennis* and *F. silvestris*. Upper dentition that could be referred with certainty to the former species is so far unknown, while additionally its taxonomy is in question, mainly due to the scarcity of findings, with some researchers considering *F. lunennis* as a subspecies of *F. silvestris*. In the absence of additional relevant comparative material, we attribute the MAR-1 wildcat to *Felis* sp.

In addition to the *Palaeoloxodon antiquus* skeleton in Area A, isolated elephant bones were excavated in Area B, as well as recovered from the section between the two areas. These include several tusk, vertebra, rib and tibia fragments. The lack of diagnostic specimens does not permit a taxonomical attribution; however, given that they originate from the same geological layer as the skeleton, they are tentatively attributed also to *P. antiquus*.

The artiodactyls are represented by a hippopotamid, a bovid and two cervids. The presence of the hipposidont is documented by a dp2. (MAR-1-939/676-6) and a third metacarpal (MAR-1-1). The dp2 is long and narrow (L: 27.5, W: 4.5, H: 15.1; all in mm). It is formed by one conical main cusp, whose distal wall bears a conjunct low cusplet; distolabially there is an additional, relatively
Fig. 4. a–c, Felis sp., right P4, MAR-1-933/596-19; a, labial; b, lingual; c, occlusal view; d–f, Vulpes sp., left m1, MAR-1-932/595-69; d, labial; e, lingual; f, occlusal; g, Castor fiber, left humerus, MAR-1-941/567-54; caudal view; h, Mustela sp., right tibia, MAR-1-939/637-2, dorsal view; i, Canis sp., left fifth metatarsal, MAR-1-932/596-79, dorsal view; j, Canis sp., axis, MAR-1-933/594-77, lateral view; k, Lutra simplicidens, left mandibular fragment with p3–m1, MAR-1-939/675-35, lingual view; l, Cervus elaphus, right third and fourth metacarpal, MAR-1-939/637-1, dorsal view; m–n, Dama sp., right mandibular fragment with p2–m3 showing carnivore gnawing, MAR-1-934/594-71 and MAR-1-932/598-51 (refitted specimens); m, labial; n, lingual view; o, Palaeoloxodon antiquus, spinous process of a vertebra showing carnivore gnawing, MAR-1-935/602-83, lateral view.
strong and more isolated cusplet (Fig. 5a–c). The dp2s of the two species commonly occurring in Middle Pleistocene European localities, *Hippopotamus antiquus* and *H. amphibius*, show morphological variability. MAR-1-939/676-6 is morphologically similar to that of *H. amphibius* figured by Hooijer (1942, pl. 10) and to some specimens of *H. antiquus* from Untermaßfeld (Kahlke, 1997). The comparative material is rather limited, but MAR-1-939/676-6 is longer than those of *H. amphibius* [L: 21.0–22.0 mm (n = 2); Faure (1985)] and falls at the upper limit of *H. antiquus* from Untermaßfeld [L: 20.5–27.5 mm (n = 4); Kahlke, 1997)]. The third metacarpal is more robust than those of *H. amphibius* and fits comfortably within the range of variation of *H. antiquus* (Fig. 5d–f, Table 4). The taxonomy of the Middle Pleistocene hippopotamuses from Europe is under debate, but following the two species/groups concept of Petronio (1995), Palombo and Valli (2003, appendix) and Pandolfi and Petronio (2015), both specimens can be referred to the large-sized *H. antiquus*.

A large-sized bovid is represented by an intermediate phalanx of the hindlimb (MAR-1-934/609-23) presenting *Bison*-like features (Fig. 6a–d, Table 4; Sala, 1986; Balkwill and Cumbaa, 1992). Its metacarpal is more robust than those of *B. primigenius* and *B. priscus*, being closer to *B. schoetensacki* (Fig. 6f and g). Although an allocation to the latter species could be considered, a single phalanx does not allow for a secure specific attribution. We therefore prefer to refer the MAR-1 large bovid to *Bison* sp. for the time being.

The cervids belong to two size-groups. A small- to medium-sized cervid is recognized by a mandibular fragment bearing the p2–m3 (MAR-1-934/594-71 refit with MAR-1-932/598/51; Fig. 4m–n, Table 5). Morphological features of the mandible and the teeth, such as the small labial foramen below the distal edge of the p2, the shorter mandibular diastema than the molar tooth row, the separated paraconid and parastylid on the p3, the stronger ectostylid on the m1 relative to the m2, the antero-posteriorly separated protoconid and hypoconid on the molars, and the overlap of the anterior entoconid and the posterior metaconid wings on the m3, are common *Dama* characters (Lister, 1996b; Breda and Lister, 2013; Breda, 2015). The MAR-1 teeth present some morphological similarities with the type series of the newly erected species *D. roberti* from Pakefield (England) and Soleilhac (France) [p3: paraconid and parastylid are not well-separated; p4: metaconid and entoconid form a closed lingual wall ("molarised"); m3: absence of an additional stylid between hypoconid and talonid, lack of a clear step between the lingual walls of second and third lobes] (Breda and Lister, 2013). However, they also present some features

The high values of the DAP/DT proximal (1.15) and DAP/DT distal (1.25) indices of MAR-1-934/609-23 are different from those of *B. primigenius* and *B. priscus*, being closer to *B. schoetensacki* (Fig. 6f and g). Although an allocation to the latter species could be considered, a single phalanx does not allow for a secure specific attribution. We therefore prefer to refer the MAR-1 large bovid to *Bison* sp. for the time being.

The high values of the DAP/DT proximal (1.15) and DAP/DT distal (1.25) indices of MAR-1-934/609-23 are different from those of *B. primigenius* and *B. priscus*, being closer to *B. schoetensacki* (Fig. 6f and g). Although an allocation to the latter species could be considered, a single phalanx does not allow for a secure specific attribution. We therefore prefer to refer the MAR-1 large bovid to *Bison* sp. for the time being.

The cedroids belong to two size-groups. A small- to medium-sized cervid is recognized by a mandibular fragment bearing the p2–m3 (MAR-1-934/594-71 refit with MAR-1-932/598/51; Fig. 4m–n, Table 5). Morphological features of the mandible and the teeth, such as the small labial foramen below the distal edge of the p2, the shorter mandibular diastema than the molar tooth row, the separated paraconid and parastylid on the p3, the stronger ectostylid on the m1 relative to the m2, the antero-posteriorly separated protoconid and hypoconid on the molars, and the overlap of the anterior entoconid and the posterior metaconid wings on the m3, are common *Dama* characters (Lister, 1996b; Breda and Lister, 2013; Breda, 2015). The MAR-1 teeth present some morphological similarities with the type series of the newly erected species *D. roberti* from Pakefield (England) and Soleilhac (France) [p3: paraconid and parastylid are not well-separated; p4: metaconid and entoconid form a closed lingual wall ("molarised"); m3: absence of an additional stylid between hypoconid and talonid, lack of a clear step between the lingual walls of second and third lobes] (Breda and Lister, 2013). However, they also present some features

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### Table 4

Postcranial measurements (in mm) of the large mammals from Marathousa 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Castor fiber</th>
<th>Mustela sp.</th>
<th>Canis sp.</th>
<th>Hippopotamus antiquus</th>
<th>Bison sp.</th>
<th>Dama sp.</th>
<th>Cervus elaphus</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Specimen</strong></td>
<td>humerus</td>
<td>tibia</td>
<td>m1V</td>
<td>MclII</td>
<td>Phil (hindlimb)</td>
<td>radius</td>
<td>McIII</td>
</tr>
<tr>
<td><strong>Inventory number</strong></td>
<td>MAR-1</td>
<td>941/676-54</td>
<td>939/637-2</td>
<td>932/596-79</td>
<td>1</td>
<td>934/609-23</td>
<td>393/601-6</td>
</tr>
<tr>
<td><strong>Length</strong></td>
<td>85.1</td>
<td>55.5</td>
<td>68.4</td>
<td>172.2</td>
<td>50.8</td>
<td>281.8</td>
<td>270.2</td>
</tr>
<tr>
<td><strong>DT proximal</strong></td>
<td>24.5</td>
<td>10.3</td>
<td>11.9</td>
<td>61.7</td>
<td>35.9</td>
<td>55.8</td>
<td>45.4</td>
</tr>
<tr>
<td><strong>DAP proximal</strong></td>
<td>20.4</td>
<td>8.6</td>
<td>8.7</td>
<td>60.4</td>
<td>41.2</td>
<td>30.2</td>
<td>31.1</td>
</tr>
<tr>
<td><strong>DT diaphysis</strong></td>
<td>9.5</td>
<td>3.5</td>
<td>5.2</td>
<td>49.5</td>
<td>27.4</td>
<td>34.5</td>
<td>26.6</td>
</tr>
<tr>
<td><strong>DAP diaphysis</strong></td>
<td>10.6</td>
<td>4.0</td>
<td>6.8</td>
<td>30.0</td>
<td>28.4</td>
<td>19.7</td>
<td>25.0</td>
</tr>
<tr>
<td><strong>DT distal</strong></td>
<td>30.3</td>
<td>8.0</td>
<td>8.6</td>
<td>60.0</td>
<td>28.7</td>
<td>47.4</td>
<td>45.9</td>
</tr>
<tr>
<td><strong>DAP distal</strong></td>
<td>10.7</td>
<td>6.3</td>
<td>9.8</td>
<td>47.5</td>
<td>35.9</td>
<td>36.0</td>
<td>30.7</td>
</tr>
</tbody>
</table>

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### Table 5

Dental measurements (in mm) of the large mammals from Marathousa 1. Measurements in parentheses represent the greatest measurable value of the parameter. Superscripts indicate in which lobe of the tooth the greatest width was measured.

<table>
<thead>
<tr>
<th>Species</th>
<th>Lutra simplicidens</th>
<th>Felis sp.</th>
<th>Vulpes sp.</th>
<th>Hippopotamus antiquus</th>
<th>Dama sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inventory number</strong></td>
<td>MAR-1</td>
<td>939/675-35</td>
<td>933/596-19</td>
<td>932/595-69</td>
<td>939/676-6</td>
</tr>
<tr>
<td><strong>L premolars</strong></td>
<td>39.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L molars</strong></td>
<td>62.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L dp2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W dp2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L p2</strong></td>
<td>10.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W p2</strong></td>
<td>7.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L p3</strong></td>
<td>13.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W p3</strong></td>
<td>8.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L p4</strong></td>
<td>13.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W p4</strong></td>
<td>9.6 (2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L m1</strong></td>
<td>14.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L m1 trigonid</strong></td>
<td>10.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W m1</strong></td>
<td>5.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W m1 trigonid</strong></td>
<td>5.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W m1 talonid</strong></td>
<td>5.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L m2</strong></td>
<td>18.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W m2</strong></td>
<td>12.7 (2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L m3</strong></td>
<td>27.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W m3</strong></td>
<td>12.7 (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>L P4</strong></td>
<td>(11.0)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>W P4</strong></td>
<td>(5.4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
which are absent from that species but common in *D. dama*,
including *D. d. clactoniana* [p4: presence of an anterior hypoconic
wing; molars: not very strongly developed ectostyldids]. The sig-
nificant inter- and intraspecific dental morphological variability
among *Dama* species/subspecies, and especially the absence of
antlers in MAR-1, do not allow for a definite specific determination.
Therefore, we attribute the MAR-1 fallow deer to *Dama* ssp. Addi-
tionally, a distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
smaller *Capreolus* and the larger *Cervus*.

The second cervid is of medium to large size and its presence
was confirmed by some dental and postcraniaal specimens,
including a radius (MAR-1-933/596-82), a metacarpal (MAR-1-939/
637-1) and a calcaneus (MAR-1-939/635-1). The metacarpal is not
preserved (Fig. 4l); however, the clear space between the
distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
smaller *Capreolus* and the larger *Cervus*.

Although crania or antlers are absent to date from MAR-1, the di-
ination, a distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
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The second cervid is of medium to large size and its presence
was confirmed by some dental and postcraniaal specimens,
including a radius (MAR-1-933/596-82), a metacarpal (MAR-1-939/
637-1) and a calcaneus (MAR-1-939/635-1). The metacarpal is not
preserved (Fig. 4l); however, the clear space between the
distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
smaller *Capreolus* and the larger *Cervus*.

Although crania or antlers are absent to date from MAR-1, the di-
ination, a distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
smaller *Capreolus* and the larger *Cervus*.

The second cervid is of medium to large size and its presence
was confirmed by some dental and postcraniaal specimens,
including a radius (MAR-1-933/596-82), a metacarpal (MAR-1-939/
637-1) and a calcaneus (MAR-1-939/635-1). The metacarpal is not
preserved (Fig. 4l); however, the clear space between the
distal radius fragment (MAR-1-933/601-6; Fig. 9f) pre-
sests morphological features similar to those of *Dama* (Lister,
1996b) and its dimensions (Table 4) distinguish it from both the
smaller *Capreolus* and the larger *Cervus*.
Hoxne, England, at MIS 11 (~0.4 Ma) (Stuart et al., 1993; Kahlke et al., 2011) [note however, that the Hoxne lutrine is regarded as *Lutra* sp. by Willemsen (1992), thus for the moment the timing of the replacement of the older species by the younger remains uncertain]. The oldest appearances of *Hippopotamus* in Europe are observed in the middle Villafranchian localities Elis (Greece) and Coste San Giacomo (Italy) (Thenius, 1955; Reimann and Strauch, 2008; Bellucci et al., 2012). *Hippopotamus antiquus* (and closely related forms classified as *H. tiberinus* or *H. ex gr. *H. antiquus*)) is recorded in several localities of the late Villafranchian and until the Middle Pleistocene (Palombo, 2014; appendix). The last appearances of this species and its replacement by *H. amphibius* are quite vague. In Italy *H. antiquus* is present at ~0.6 Ma at Isernia la Pineta, Maglianella and Via Portuense (Isernia Faunal Unit, MIS 15), while the first appearances of *H. amphibius* might be traced back to MIS 13 or MIS 11, 0.53–0.45 Ma during the Fontana Ranuccio Faunal Unit (Palombo, 2014; Pandolfi and Petronio, 2015). However, according to Mazza and Bertini (2013) *H. ex gr. H. antiquus* survived until ~0.13–0.11 Ma.

Overall, the MAR-1 large mammal faunal association is common in the Galerian (beginning of Galerian sensu Bellucci et al., 2015) mammal communities of Europe and the current biochronological data indicate that the locality is dated between 0.9 Ma and 0.4 Ma. The study of the micromammals suggests a middle–late Middle Pleistocene age (Doukas et al., this issue). Preliminary post-infrared Infrared Stimulated Luminescence (post-IR IRSL) indicate an age between ~0.5 and 0.4 Ma (Jacobs et al., this issue). The Electron Spin Resonance (ESR) of a mollusk sample from UA2 provided a minimum age at 473 ± 54 ka, while five subsamples of a cervid tooth from UB4c gave an age of 502 ± 13 ka (Blackwell et al., this issue). Finally, the study of the magnetostратigraphy suggests that the find-bearing stratigraphic units (UB4c–UB5 and UA3c–UA4) have an age broadly comprised between ~0.48 Ma and ~0.42 Ma (Tourloukis et al., this issue b). Therefore, the large mammal assemblage is consistent and further supports all of these preliminary age estimates for MAR-1.

5. Palaeoecological remarks

*Palaeoloxodon antiquus* had a wide and flexible ecological adaptation, as the species inhabited mild humid, warm to warm-temperate and moderately wooded to wooded environments, but also wooded or even rather arid grasslands (Palombo et al., 2010). In Northern and Central Europe, the species occurred during the interglacial phases and, with few exceptions, was generally absent from the intervening cold stages of open habitats. During these times, its range was limited to Southern Europe, which acted as a refugium (Tsoukala and Lister, 1998; Lister, 2004). Isotopic and
dental microwear analyses on *P. antiquus* teeth from La Polledrara di Cecanibbio (MIS 9), Casal de’ Pazzi (MIS 7), Neumark-Nord (MIS 7) and Megalopolis Basin [Middle Pleistocene; specimens from several sites within the basin described by Melentis (1961)], showed that the species was a mixed feeder, but with a significant amount of grasses in its diet (Palombo et al., 2005; Grube et al., 2010; Rivals et al., 2012).

In the MAR-1 fauna, three semiaquatic mammals are present: *Hippopotamus, Castor* and *Lutra*. Morphological and palaeoecological studies on *Hippopotamus antiquus* indicate a rather aquatic habitat with high dependence on water, as the species foraged mainly on aquatic vegetation, in contrast to the grazing (terrestrial) dietary habits of the extant *H. amphibius* (Mazza, 1995; Palmqvist et al., 2003; Madurell-Malapeira, 2012). *Hippopotamuses* are generally considered indicators of temperate climate; however, it is the presence and amount of water (linked to precipitation), rather than temperature, that are of vital importance to this taxon (Mazza and Bertini, 2013). The similar dentition of the otter *Lutra simplicidentis* with the recent Eurasian otter *L. lutra* indicates a comparable diet consisting dominantly of fish (Willemsen, 1992); however, other food sources like frogs, crayfish, crabs, birds, turtles or small mammals would complement its diet (Lanszki et al., 2006; MacDonald, 2009). Although otters forage mainly in water, they spend much of their time resting on land (MacDonald, 2009). *Lutra* is a riparian and semiaquatic species inhabiting ponds, lakes, rivers and streams. Beavers are generalist herbivores with a diet ranging from relatively non-woody plants (e.g., leaves, roots, herbs, ferns, grasses, algae) to shrubs and trees (e.g., aspen, birch, maple, oak, dogwood, fruit trees) (MacDonald, 2009).

*Cervus elaphus* is mainly found today at the edges of woodland, where it can browse the foliage of trees, and also consume grasses and low herbaceous vegetation (Lister, 1984). However, the species presents a high ecological flexibility, as it is encountered from woodlands to open or even treeless environments, feeding on shrubs and tree shoots in the former, and grasses, sedges and rushes in the latter (Lister, 1984; Parfitt, 1999). During the Middle Pleistocene, the species was present during both interglacial and cold stages (Lister, 1984). On the other hand, the presence of *Dama* sp. in the MAR-1 assemblage provides more information. The fallow deer in Northern and Central Europe is generally limited to interglacial stages, as it is less tolerant to open and cold conditions than the red deer and needs temperate climate (Lister, 1984). It mostly inhabits open deciduous or mixed woodland with a well-developed shrub layer, feeding in forest clearings and woodland margins (Parfitt, 1999). Although a specific attribution of the MAR-1 bone is not secure at the moment, the Middle Pleistocene European *Bison* species are generally considered as open landscape dwellers, having a significant grass component in their diet (Palombo, 2016; appendix).

The recent European wildcat is associated with open forest habitats. Small cats are opportunistic and highly effective hunters, killing their own prey (small mammals, amphibians, reptiles, birds, fish), although occasionally they also eat carrion (MacDonald, 2009). Middle Pleistocene European *Vulpes* and *Canis* species are generally ecologically flexible taxa, able to live in shrubland or woodland, as well as in an open landscape, or at the edge of both; foxes are considered as flesh-eaters consuming mainly small mammals, while wolves are bone crushers capable of grinding bones, but also quite efficient in consuming flesh (Palombo, 2016; appendix).

Overall, the large mammal fauna from MAR-1 is consistent with a temperate climate and is indicative of a landscape with substantial woodland components and more open areas. Taking into account the good representation of semiaquatic taxa (*Castor, Lutra, Hippopotamus*), the locality was close to the shore of large and permanent freshwater body. This is also supported by the presence of a rich avian fauna mostly adapted to a lake environment (Michailidis et al., this issue), the water vole *Arvicola* (Doukas et al., this issue) and the dominantly aquatic and waterside vegetation (Field et al., this issue). This lakeshore setting was ideal for the subsistence of several animals. Herbivores (cervids, bovids, elephants) would visit this region in order to drink water and feed on the nearby vegetation, while the small carnivores (*Mustela, Lutra, Felis, Vulpes*) would prey on small mammals, frogs, birds, fishes and invertebrates (all are recorded in the MAR-1 faunal assemblage). Such a location would attract also larger carnivores, such as wolves, which could find a wide range of prey for their survival. This landscape was probably also ideal for early humans, offering the protection and the plant resources of the nearby woodlands, as well as accessible freshwater and a variety of feeding opportunities probably throughout the year, including ungulate and megafauna carcasses, close to the shores of the lake.

### 6. Taphonomical remarks

For the taphonomic investigation of the faunal remains we studied the specimens originating from the upper part of the sedimentary sequence below the Lignite Seam III of Area A and Area B (see Karkanas et al., this issue; Fig. 1b). We treated each of these as one assemblage in order to increase the sample, i.e., one assemblage includes UA2, UA3 and the specimens found at the contact of UA3/UA4 from Area A, and UB3, UB4, UB5 from Area B. However, it should be noted that the majority of the fauna (as well as of the lithics) from Area A and Area B originate from UA3c and UB4c, respectively (Fig. 1b).

The large mammal assemblage examined from Area A includes 136 bones or bone fragments and 28 teeth or tooth fragments. The taxa representation and composition is presented in Table 6 and Fig. 7a. As expected, the majority of the identifiable specimens belong to *Palaeoloxodon antiquus* (skull) or to *Palaeoloxodon antiquus* (79.0%), while *Castor fiber* and cervids represent 9.2% and 6.7% respectively of the assemblage. Because the elephant is the main faunal element in Area A and is of primary interest, its full taphonomic study will be conducted separately, after all the elephant bones of the skeleton are excavated.

The analyzed sample from Area B includes a total of 211 bone/bone fragments and 35 teeth/tooth fragments. *Palaeoloxodon antiquus* is the main faunal component also in Area B, representing 27.3% of the identifiable specimens, followed by fallow deer (25.0%) and red deer (9.1%). The combined cervids are the dominant group (56.8%) of the Area B sample (Table 6, Fig. 7a). Bones from Area B are characterized by a high degree of fragmentation: a) Their maximal diameter ranges from 14.4 mm to 390 mm (mean value: 59.7 mm, standard deviation: 53.1 mm) with the great majority measuring <80.0 mm (Fig. 7b). This size range is much smaller than the expected length of complete long bones (except phalanges) belonging to medium-sized herbivores like cervids (apart from a complete *Cervus* radius all other values over 200 mm correspond to elephant bone fragments), b) Bone fragments make up 93.4% of the assemblage, whereas the percentage of complete/almost complete bones is only 6.6%. The above observations clearly demonstrate the highly fragmented nature of the bone assemblage and account for the low percentage of identifiable bones. Of the 211 bones, only 46 (21.8%) could be attributed to a specific skeletal element, while the rest were unidentifiable (78.2%, mostly splinters or shaft fragments). Bones that could be identified at generic level include 17 specimens (8.1%). Regarding the dental elements, of the 35 teeth specimens, 16
while the latter indicates carcass disarticulation and meat removal. With the overall high bone fragmentation and anthropic fractures, cut marks. The former is created during the knapping of bones, bones indicative of butchering activities include percussion damage taphonomic modi.

Table 6

<table>
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<tr>
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<td>7Hippopotamus antiquus</td>
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<td>164</td>
<td>211</td>
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</table>

are complete (45.7%), while 17 could be identified to genus (48.6%) (Table 6).

The bone surfaces from both Area A and B do not show traces of rounding, which suggests limited, if any, transport over a short distance and/or for a short time span. Although the number of bones in Area A (excluding the elephant skeleton) is much lower than in Area B, similar weathering percentages are obtained (Fig. 7c): the majority of the bones in both Areas present rather well-preserved surfaces with minor cracking and flaking (weathering stages 0–2 of Behrensmeyer [1978]). This indicates that most bones were buried relatively quickly and/or were kept moist and protected by the lake vegetation [corroborated by the diverse fossil floral assemblage (Field et al., this issue) and the palaeoenvironmental reconstructions of the wider region during that time (e.g., Nickel et al., 1996)].

The good state of the bone preservation allows the identification of taphonomic modifications. Human modifications on the MAR-1 bones indicative of butchering activities include percussion damage and cut marks. The former is created during the knapping of bones, most commonly related to marrow processing (and is also associated with the overall high bone fragmentation and anthropic fractures), while the latter indicates carcass disarticulation and meat removal.

Cut marks were identified on elephant bones belonging to the skeleton from Area A, as well on elephant and other mammal bones from Area B. Specifically, so far identified cut-marked elephant bones from the skeleton include an astragalus (MAR-1-939/674-46) and a tibia (MAR-1-938/673-19). The astragalus shows two almost parallel striations located on its distal side, on the lateral articular facet for the tibia (Fig. 8a and b); while the tibia presents a single, wider groove, located on the plantar side of the diaphysis, and obliquely oriented relative to the long axis of the bone (Fig. 8g). The astragalus and tibia striations are almost straight and V-shaped in cross-section, they show Hertzian cones and they partially preserve internal microstriations (Fig. 8). These characteristics are observed with high frequency in cut marks (e.g., Dominguez-Rodrigo et al., 2009; Fernández-Jalvo and Andrews, 2016), including those created during exploitation of proboscidean carcasses (e.g., Yravedra et al., 2010; Sassà, 2012). Trampling, which mostly creates sinuous trajectories with flat- and broad-based grooves in cross-section (Dominguez-Rodrigo et al., 2009, 2010), is a less likely cause for these modifications, due to the low abrasive nature of the sediment bearing the fossils and the absence of a stony substrate, as well as the minor transportation of the bones and their relatively fast burial/limited time of exposure. Carnivore tooth marks have usually a U-shaped cross-section (scores; Blumenschine, 1985) and carnivore gnawing in general is so far not recognized in any of the elephant bones in Area A. Moreover, the excavation of bones was carried out with wooden tools, so that the possibility these marks (which were originally also filled with fine sediment) to have a recent origin should be excluded. Cut marks on the astragalus are possibly related to the cutting of the joints/ligaments, and the disarticulation of the tarsals, probably to exploit the fat content and the soft tissues enclosed in the distal part of the hindlimb and the foot cushion [Weissengruber et al., 2006; see also Saunders and Daeschler (1994) for the disarticulation of mammoths’ forelimbs including carpal]. On the other hand, the location of the tibia cut mark on the mid-shaft in the plantar side of the bone, where strong muscles are developed (Weissengruber and Forstenpointer, 2004), could possibly be attributed to filleting. Although cut marks on proboscidean bones are rare (see below), a cut-marked astragalus (on the proximal articular facet for the tibia) was recently recorded at the early Homo site HWK EE (Olduvai Gorge, Tanzania; Pante et al., in press). Cut marks on mammoth tibiae have previously been reported at the Late Pleistocene sites Yudinovo (Russia; Germonpré et al., 2008), Dent and Clovis (U.S.A.; Saunders and Daeschler, 1994; Saunders, 2007).

Elephant bones from Area B showing cut marked surfaces include a broken rib fragment (MAR-1-933/595-71), which presents on the ventral side a single V-shaped mark, as well as a cluster of scrape marks [see e.g., Rodríguez-Hidalgo et al. (2017, Fig. 6b) for similar marks on a bison bone] (Fig. 9a–d). All these traces are present only locally with the rest of the bone lacking any other signs of marks. Cut marks (although of a different pattern compared to the MAR-1 ones) on the ventral side of an elephant rib from Aridos 2 (Spain) have been attributed to evisceration, which occurs at the very early stages of carcass consumption (Yravedra et al., 2010). The intensive effort applied in the form of the observed cluster in theMAR-1 rib might be related to the removal of the periosteum during butchery or to the cleaning of the bone from fat before breaking it (Voormolen, 2008; Starkovich and Conard, 2015; Fernández-Jalvo and Andrews, 2016; Gingerich and Stanford, in press and references cited therein). Indeed, on the dorsal side of the rib, the absence of cortical layer (classic peeling) in the fractured region (Fig. 9e) indicates that the bone was broken when it

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was still fresh. Butchering marks on the rib accompanied by peeling indicates early access to an elephant carcass by hominins (Pickering et al., 2013).

Apart from elephants, ungulate exploitation is indicated by a cut-marked distal radius epiphysis (MAR-1-933/601-6) of a fallow deer, showing four short and parallel striations (Fig. 9f and g). Their location is possibly related to the disarticulation of the joint between the radius and the carpals (Rabinovich et al., 2008; Soulier and Costamagno, 2017). Furthermore, a spiral fractured humerus diaphysis fragment of a small/medium-sized mammal (MAR-1-
Fig. 8. Modifications on Palaeoloxodon antiquus bones from the Marathousa 1 (Area A) skeleton. a–f, right astragalus, MAR-1-933/591-71: a, distal view, in the rectangle the region of the cut marks, shown in ‘b’; b, close view of the cut marks; c, detail of the cut marks, dashed line indicates the location of the profile shown in ‘d’; d, profile of the cut mark at 50% of its length; e, detail of the morphology of the cut mark in 3D; f, 3D model of the cut marks; g–k, left tibia, MAR-1-938/673-19; g, plantar view (proximal to the right), in the rectangle the region of the cut mark; h, detail of the cut mark, dashed line indicates the location of the profile shown in ‘i’; i, profile of the cut mark at 30% of its length; j, detail of the morphology of the cut mark in 3D; k, 3D model of the cut mark.
Fig. 9. Modifications on bones from Area B. a–e, *Palaeoloxodon antiquus*, rib fragment, MAR-1-933/591-71: a, ventral view, in rectangle the region of modification shown in ‘b’; b, detail of the rib showing the cut mark (rectangle, originally filled with sediment) and the scrape marks; c, detail of the cut mark, dashed line indicates the location of the profile shown in ‘d’; d, profile of the cut mark at 60% of its length; e, classic peeling, detail of the dorsal side of the rib showing the region of missing cortical layer; f–g, *Dama* sp., distal fragment of left radius with cut marks, MAR-1-933/601-6; f, caudal view; g, detail of the cut marks; h–i, spiral fractured humerus diaphysis fragment of small/medium-sized mammal with cut marks and percussion damage, MAR-1-933/600-113; h, medullary view; i, cortical view and detail of the cut marks.
933/600-113), shows oblique cut marks relative to the axis of the bone and a percussion notch with its negative scar (Fig. 9h and i). Finally, the presence in Area B of bone flakes/tools, as well as of a bone shaft fragment (possibly belonging to an elephant) with flute and impact scars, is indicative of bone knapping (Tourloukis et al., this issue a).

Carnivore gnawing is recorded in Area B and includes one sinus process of an elephant vertebra (forrowing, crenellation, salivary rounding; Fig. 40), one diaphysis of a cervid radius (salivary rounding) and one mandibular (corpus) fragment of fallow deer, which presents single and overlapping notches on its ventral side (Fig. 4m–n). Although overlapping notches may result from dynamic loading (hammerstone percussion), they are produced in higher frequency through static loading (carnivore pressure) due to the close-set carnivore teeth and the simultaneous bite of adjacent teeth cusps, creating closely spaced impact points (Dominguez-Rodrigo and Barba, 2007). Moreover, in contrast to humans who usually break mandibles transversely into segments and produce rather clean and straight fractures, carnivores produce irregular edges (Stiner, 1994, pp. 140–144).

Cut marks on the MAR-1 elephant skeleton, as well as in other elephant and mammal bones, indicate butchering activities by humans. This is in accordance with the traits of the lithic industry and its spatial association with the mammal bones (Giusti et al., this issue; Panagopoulou et al., this issue; Tourloukis et al., this issue a). Cut marks occur in mammals ranging in size from the small/medium fallow deer to elephant (megafauna), indicating a rather wide spectrum of exploitation by humans. The fact that carnivore gnawing occurs in the same taxa as cut marks could potentially suggest a certain degree of carnivore-human competition for early access to the animal carcasses.

Proboscideans, the largest terrestrial animals during the Pleistocene, constituted an ideal food package and one of the most attractive targets for early humans (Ben-Dor et al., 2011; Reshef and Barkai, 2015; Agam and Barkai, 2016). The human engagement in proboscidean assemblages, as well as the degree of their interaction is not always straightforward. For the MAR-1 skeleton in particular, the small number of cut marks observed to date does not necessarily indicate that the human activity was minor, as cut marks are rarely produced during the exploitation of large carcasses. Firstly, the thick cartilage and periosteum impede the penetration and contact of stone tools with the bone and prevents its modification by cut marks, while careful butchering by experienced individuals may not leave direct evidence on the bone cortical surfaces (e.g., Haynes and Klimowicz, 2015). Second, if meat stripping rather than the need of elephant bones for the primary goal for the early humans, this could have resulted in the decrease/absence of the bone damage, i.e., cut marks and green-broken bones, as well as in less time of carcass exploitation (Haynes and Klimowicz, 2015; Gingerich and Stanford, in press).

Whether elephant exploitation was the result of hunting or scavenging is difficult to ascertain; however, according to Yravedra et al. (2010) after 1.0 Ma human exploitation of megafauna was more than a marginal strategy for protein obtainment.

7. Conclusions

In this article, we presented preliminary results from the ongoing excavation in the open-air site Marathona 1 of the Megalopolis Basin. This is the first study of a fossil mammal assemblage from the basin with stratigraphic control and with spatial association with Palaeolithic cultural remains, and therefore human activity. Although the excavation of the elephant skeleton is in progress, it is already the most complete one known from the Megalopolis Basin, and together with the skeletons of P. antiquus from Ambelia and Perdikass (Western Macedonia; see Tsoukala et al., 2011) among the most complete skeletons of this species ever found in Greece. Apart from the elephant, other macro-mammals are so far poorly represented in MAR-1; however, Canis sp. [reported also in Athanassiou et al. (this issue)], Mustela sp., Felis sp. and Lutra simplicidens are recorded for the first time in the Megalopolis Basin, while L. simplicidens is documented for the first time in Greece.

During recent decades a significant number of localities documenting proboscidean exploitation by hominins has been discovered (Santucci et al., 2016, table 4 and references cited therein), considerably enriching our knowledge on the subsistence strategies of Homo and their interactions with megaherbivores. The preliminary dating of Marathona 1 to ca. 0.5–0.4 Ma places the locality among the oldest in Europe, where both lithic artefacts and cut marks are associated with a butchered elephant. It is also the first such locality to be discovered in Southeastern Europe. The recovery of additional faunal material from MAR-1 in the future will be essential for refining the biochronological, palaeoecological and taphonomic interpretation of the site, enhancing our understanding of the Lower Palaeolithic hominin food acquisition strategies and subsistence behavior, as well as enriching our knowledge about human-proboscidean interactions in the Palaeolithic.

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