Reassessing diagnostic postcranial traits in Pleistocene elephants: evidence from *Palaeoloxodon antiquus* and *Mammuthus* in Italy

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The fossil elephant remains from the lower Middle Pleistocene site of Contrada Monticelli (Apulia, southern Italy) are described here in detail for the first time. The material, consisting of dental and postcranial bones from a single individual, was analyzed both morphologically and morphometrically. Estimates of shoulder height and body mass were calculated for the specimen. Based on dental characters, the Contrada Monticelli elephant is assigned to *Palaeoloxodon antiquus*. A comparative analysis with *Mammuthus* and *Palaeoloxodon* specimens from the Lower and Middle Pleistocene of Italy indicates the Contrada Monticelli individual represents a medium-sized, old male straight-tusked elephant. The comparative study also demonstrated that several morphological traits of the humerus, ulna, femur, and tibia, previously proposed as diagnostic in distinguishing between *Mammuthus* and *Palaeoloxodon*, are not consistent when intraspecific variability is taken into account. Furthermore, the morphometric analyses revealed no significant differences in size and proportions of the studied limb bones between *Mammuthus meridionalis* and *Palaeoloxodon antiquus* that would allow for a reliable discrimination between the two taxa. The Contrada Monticelli elephant represents one of the few known European straight-tusked elephant skeletons dated to the interval between 0.8 and 0.5 million years ago, corresponding to the dispersal of the genus into Eurasia, and contributes to a better understanding of the biochronological, paleoecological, and paleobiogeographical context of the early evolution of *Palaeoloxodon* in Europe.

Key words: Elephantidae, *Palaeoloxodon*, morphology, anatomy, Middle Pleistocene, Mediterranean Europe, Italy, Contrada Monticelli.

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Introduction

Proboscideans are one of the most commonly found groups of Quaternary large mammals. Although more frequently found at open-air palaeontological sites, their remains are also not uncommon in cave or karstic settings (Schreve and Jones 2005). In Europe, after the extinction of the tetralophodontid gomphothere *Anancus arvernensis* at around 2.0 Ma, proboscideans were represented exclusively by members of the family Elephantidae. Five elephantid species are currently recognized in the Pleistocene of continental Europe: the mammoths *Mammuthus rumanus* (latest Pliocene–early Early Pleistocene), *Mammuthus meridionalis* (Early Pleistocene), *Mammuthus trogontherii* (Middle Pleistocene), *Mammuthus*

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primigenius (Late Pleistocene), and the straight tusked elephant *Palaeoloxodon antiquus* (Middle–Late Pleistocene). All these species are known from the Quaternary of Italy, in many cases represented by complete skeletons (Palombo and Ferretti 2005). The paleoclimatic and paleoenvironment significance of elephantids is well established and elephants are widely recognized as ecologically key-stone species (Haynes 1991). In addition, during the Quaternary humans interacted with elephantids in complex ways, ranging from scavenging and hunting to potential cultural and symbolic association (Konidaris and Tourloukis 2021; Palombo and Cerilli 2021). Identification of elephant fossil remains at the generic or species level is essential in investigating all these aspects.

The straight tusked elephant coexisted in western Europe with *M. trogontherii* and *M. primigenius* during much of the Middle and Late Pleistocene, while the earliest *Palaeoloxodon* record in Europe may be contemporaneous with the latest *M. meridionalis* populations. A major issue in the study of Pleistocene elephants in Europe is that in absence of dental (especially molars) and cranial remains, it is often a difficult task to discriminate between the two genera. As a matter of fact, postcranial elements of different elephant genera, both extant and extinct, are often difficult or even impossible to distinguish, due to their similar size and morphology (Lister and Stuart 2010; Athanassiou 2011). Overall, the role of postcranial bones in the taxonomic attribution of proboscidean fossil remains is still controversial and has not received sufficient attention. As a result, taxonomic attributions are often tentative and based on the biochronological, paleogeographical, and paleoenvironmental context.

In this paper we describe for the first time in detail the elephantid material from the lower Middle Pleistocene site (Galerian; Isernia FU) of Contrada Monticelli (CM) (Apulia, southern Italy), comparing it to several skeletons of *P. antiquus* and *M. meridionalis*, from various Italian sites. Aims of this study is to: (i) provide a definitive taxonomic identification of the CM sample; (ii) investigate in depth the morphological and morphometric characters of the limb bones, in order to verify the validity of the morphological differences between European *Palaeoloxodon* and *Mammuthus* suggested so far by previous authors, and, on the other hand, evaluate the possible identification of new distinctive characters; (iii) determine whether the CM elephantid sample represents a single individual and provide an estimate of its shoulder height (SH), body mass (BM), and sex; (iv) discuss the significance of the CM elephantid sample within the context of the Italian Middle Pleistocene mammal biochronology, biogeography, and paleoecology.

Institutional abbreviations.—IGF, Museum of Geology and Paleontology, University of Florence, Italy; MSTB-CM, Museum of Earth Sciences, University of Bari, Italy; MUST, University Museum of Earth Sciences, University of Rome, Italy.

Other abbreviations.—BM, body mass; CM, Contrada Monticelli; FU, Faunal Unit; GL, greatest length; MIS, Marine Isotope Stages; POC, parieto-occipital crest; SH, shoulder height. We follow standard convention in abbreviating tooth families as I, C, P, and M, with upper and lower case letters referring to upper and lower teeth, respectively.

Geological setting

Contrada Monticelli (Fig. 1; 40°49’50’’N, 17°10’27’’E) is located, near Putignano town in the Apulian region, in the southeastern part of the Italian peninsula. Unfortunately, the fossil site is no longer accessible, as it is now buried beneath a private residence, preventing any further stratigraphic or taphonomic analyses.

The fossiliferous deposit consisted of the infill of a karst cavity formed within the Calcare di Altamura Formation (Azzaroli 1967; Azzaroli et al. 1968), which is regionally dated to the late Turonian–Maastrichtian, Upper Cretaceous (Ciaranfi et al. 1988). The cavity, locally known as a grave (sinkhole), had an opening of approximately 4.5 × 5 m and was about 11 m deep. It was filled with red soil interbedded with several cinerite levels (Luperto Sinni and Colucci 1985).

The walls and bottom of the sinkhole were covered with reddish sands, mixed with fossilized bone remains. The sinkhole likely formed as a result of intensified karst processes along a fracture (or fault?) running NW-SE, parallel to the state road on which the sinkhole was located (Luperto Sinni and Colucci 1985).

Excavations of the deposit began in spring 1978, thanks to the involvement of the Superintendency of Antiquities of Bari and the Institute of Geology and Paleontology of the University of Bari, under the direction of Elena Luperto Sinni. Fossil remains were recovered from depths of approximately 3–11 m below the ground surface. However,

Fig. 1. Geographic location of the Contrada Monticelli fossiliferous site (Apulia, Southern Italy).

a detailed stratigraphic framework of the infill deposits during the fossil recovery is lacking.

Following a pause during the winter of 1978, excavations resumed in the summers of 1979 and 1980 but were subsequently halted due to lack of funding (Luperto Sinni and Colucci 1985).

Over the decades, Contrada Monticelli (CM) has yielded abundant faunal remains of terrestrial mammals such as *Bison* cf. *schoetensacki*, *Canis mosbachensis*, *Dama* cf. *roberti*, *Stephanorhinus hundsheimensis*, furthermore, additional remains of equids, lagomorphs, and rodents were also found, though they are fragmentary and only identifiable at the family or order level (Luperto Sinni and Colucci 1985; Mazza and Varola 1999; Mecozzi et al. 2017; Stefanelli et al. 2021, 2024a, b). In addition to the taxa mentioned, an elephant referred to *Elephas* (=*Palaeoloxodon*) *antiquus* has been reported by Luperto Sinni and Colucci (1985). This Galerian faunal assemblage is biochronologically homogeneous and has been attributed to the Isernia Faunal Unit (lower Middle Pleistocene) by several recent studies (Stefanelli et al. 2021, 2024a, b).

In the Apulian hinterland, calcareous rocks experienced intense karst activity during the Middle to Late Pleistocene, forming a complex network of fissures (Selleri et al. 2003; Selleri 2007). These fissures were later infilled with sediments and occasionally preserved vertebrate fossils. Notable fossiliferous karst sites in Apulia include Pirro Nord, one of the most significant Early Pleistocene sites in Europe (e.g., Pavia et al. 2010; Arzarello et al. 2012; Berto et al. 2024; Duval et al. 2024), and the Maglie area, located in the Salentine Peninsula, which has yielded thousands of remains dated from the late Middle Pleistocene to the Early Holocene (Mecozzi et al. 2021 and references therein).

However, apart from Pirro Nord, most Apulian fossil deposits are attributed to the late Middle Pleistocene or more recent periods. Therefore, CM represents the only known deposit of early Middle Pleistocene age in the region and one of the few in southern Italy, alongside Isernia La Pineta, Loreto, and Notarchirico.

Material and methods

Material.—The elephantid material from Contrada Monticelli is represented by 32 specimens. These include three incomplete molars, four tusk fragments, and 25 skeletal bones (SOM 1: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Stefanelli_etal_SOM.pdf). Further elephant skeletal material is embedded in a block of bone remains cemented with reddish sand (see 3D model in SOM 3). All the CM material is currently preserved at the Museum of Earth Sciences of the University of Bari Aldo Moro, Italy. The catalogued specimens are labelled with progressive numbers preceded by the acronym MSTB-CM (Museo di Scienze della Terra Bari-Contrada Monticelli).

Morphological and morphometric analysis.—Dental measurements were conducted following the protocols of Maglio (1973), whereas skeletal measurements were taken according to Göhlich (1998). All measurements were taken with a tape measure or sliding digital caliper. The original abbreviations used in Göhlich (1998) have been replaced by a number whose correspondence with the original abbreviations is shown in SOM 1: table 2. In the comparative analysis of the CM elephant material we used both published data and direct observation of osteological material, including mounted skeletons of *Mammuthus meridionalis* from Upper Valdarno, housed at the Museum of Geology and Paleontology of the University of Florence, and of *Palaeoloxodon antiquus* from Fonte Campanile, Viterbo, exhibited at the University Museum of Earth Sciences (MUST). Measurements taken on the CM specimens, and on the comparative material are reported in SOM 1: table 2. With the aim to verify the actual reliability of certain morphological traits in distinguishing between European *Palaeoloxodon antiquus* (the only mainland Europe full-sized representative of the genus in the Middle to Late Pleistocene) and mammoths (specifically the Quaternary species occurring in Europe), we compared these diagnostic characteristics, cited in the literature (see below), with skeletal material directly observed on specimens exhibited in the museums of Florence, Rome and Bari, as well as with material illustrated in published sources. To support this analysis, comparative tables were constructed, selecting the main morphological features of the humerus, ulna, femur, and tibia identified by Andrews and Cooper (1928), Maccagno (1962), Melentis (1963), Kroll (1991) and Davies (2002) as taxonomically significant at the generic level: these characters were compared and checked. The most important measurements have been plotted in scatter diagrams and analyzed through Principal Component Analysis (PCA) with PAST v. 4.13 (Hammer et al. 2001).

Tusk dentine Schreger pattern.—A cross-section of a proximal tusk fragment from CM was performed with a circular saw in order to measure the so-called “Schreger angles”. The latter were measured using the ImageJ software. Comparisons were made with a tusk polished section of *Mammuthus meridionalis* (IGF 305) preserved at the Museum of Geology and Paleontology of the University of Florence (SOM 2: fig. 3) and with data taken from the literature.

Body size and sex determination.—To estimate shoulder height of the CM elephant, from single long bone, in our case the femur, the linear regression equation proposed by Larramendi (2016) was used in this work:

$$SH = X \times 2.56,$$

where SH = skeletal shoulder height, X = femur length from caput (mm). Shoulder height, however, must also consider the part of flesh and integument that covers the skeleton of a living animal. Osborn (1942) added 6.67% for flesh, Roth (1990) and Christiansen (2004) added around 5%, and Larramendi (2016) added 5.5%. Following previous authors, 6% was added to skeletal shoulder heights to account for flesh, providing estimates of live shoulder height. In Lister and Stuart (2010) live shoulder heights are estimated at 5%, 6% and 7% above skeletal height. In this work, the live shoulder heights are estimated at 6% as in Erkek and Lister (2021). The shoulder height (both skeletal and with flesh) estimations were calculated based on the greatest length from caput (measurement 1) of the femur.

In this work, the formula recently proposed by Larramendi (2016) was used to estimate the body mass of *P. antiquus* from shoulder height:

$$BM = 3.63 \times 10^{-4} \times SH^{2.903},$$

where BM = body mass in kg and SH = shoulder height (with flesh) in cm.

Differences in body size between males and females are commonly found among many extant and extinct elephants. In this work, to determine the sex, the SH and BM of the CM specimen were compared with the analogous ones calculated for the specimens of *P. antiquus* described in the literature, for which the sex had been established.

For archiving and research purposes, the skeletal elements of the CM elephant were digitalized using a structured-light EinScan-Pro HD 3D scanner equipped with the Color Pack accessory to acquire both geometry and texture. Data acquisition was performed with the dedicated EXScan-Pro software in handheld mode, using a spatial resolution of 0.3 mm with a nominal accuracy of ±0.045 mm and a volumetric accuracy of 0.3 mm/m. With the same software the obtained point cloud was then fixed and the mesh with texture was built.

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Proboscidea Illiger, 1811

Family Elephantidae Gray, 1821

Genus *Palaeoloxodon* Matsumoto, 1924

Type species: *Palaeoloxodon naumanni* (Makiyama, 1924), Sahama Formation (Late Pleistocene), Shizuoka (Japan)

Palaeoloxodon antiquus (Falconer & Cautely, 1847)

Figs. 2–4.

1823 *Elephas priscus*; Goldfuss 1823: 489, pl. 57: 1.
1847 *Elephas antiquus*; Falconer and Cautley 1847: 25–80, pl. 12d: 4, 5, pl. 14a: 1–13, pl. 14b.
1875 *Elephas ausonius* Forsyth Major, 1875; Verri 1886: 453.
1897 *Elephas platyrhynchus*; Graells 1897: 569, pl. 18: 1–11.

Material.—A partial skeleton (detailed list of preserved elements Table 1, see also SOM 1: table 1) from Contrada Monticelli, Italy, Pleistocene.

Description.—*Preservation and minimum number of individuals*: Both the isolated dental and skeletal elements and those still embedded into the cemented block are in a variable state of preservation. Most of the remains are fractured and/or incomplete and covered with a reddish patina. Some of the bones, however, are complete and in a relatively good state of preservation, allowing for a thorough anatomical description. For those elements embedded in the block only general observations could be done.

There is no evidence that suggest the presence of more than one individual in the CM elephantid material. Among the isolated remains, there are no duplicated elements and the molars and the size and developmental stage of the bones support their attribution to a single individual.

Tusks: Four tusk fragments are present in the CM sample; one is from near the proximal end (MSTB-CM QF59a; Fig. 2B), as indicated by a small pulp cavity visible at the center; two represent intermediate sections of the tusk (MSTB-CM 30559, 30668) and one derives from near the distal end of the tusk (MSTB-CM 30560; Fig. 2C). Despite the poor state of preservation and the partial coverage by the encrusting sediment (which did not allow for a reliable measurement of the circumference), only a weak curvature is noted, especially in the distal fragment MSTB-CM 30560. The proximal portion (MSTB-CM QF59a), shows a slightly elliptical cross-section, with diameters of approximately 138 and 120 mm. Overall, being fragments of different parts of the tusk (proximal, intermediate, distal), these can belong to one or a maximum of two tusks, and this is consistent with the presence at CM of a single individual.

Molars: Cheek tooth material is in poor condition. MSTB-CM QF59b (Fig. 2B) is interpreted as rather worn upper third molar (M3) with only a small posterior part missing. The occlusal surface of the molar is cemented with one of the tusk fragments (MSTB-CM QF59a), preventing the observation of the occlusal morphology. However, observing its lateral profile, towards the base of the crown, a lamellar frequency of 5 and a total of 14–15 lamellae can be counted. MSTB-CM 30531 consists of incomplete and poorly preserved and interpreted as rather worn lower third molar (m3) based on the roots that are noticeably curved backwards (see SOM 2: fig. 2). MSTB-CM 30812 (Fig. 2A),

Table 1. List of preserved elements *Palaeoloxodon antiquus* from Contrada Monticelli. L, left; R, right; ? uncertain assignment.

Anatomical portion	Specimen
tusk	MSTB-CM 30559, 30560, 30668, QF59a
tooth	MSTB-CM 30531, 30709, QF59b, 30812(fragm.)
vertebra	MSTB-CM 30582, 30583
rib	MSTB-CM 30564, 30569, 30572–30577, 30676, 30812
scapula	MSTB-CM 30581, 30585(R)
humerus	MSTB-CM 30562(?), 30567(?), 30568(?), 30588
ulna	MSTB-CM 30571(R)
radius	MSTB-CM 30566(R), 30587(?)
femur	MSTB-CM 30570, 30586(L)
tibia	MSTB-CM 30563(R)
metapodial	MSTB-CM 30584

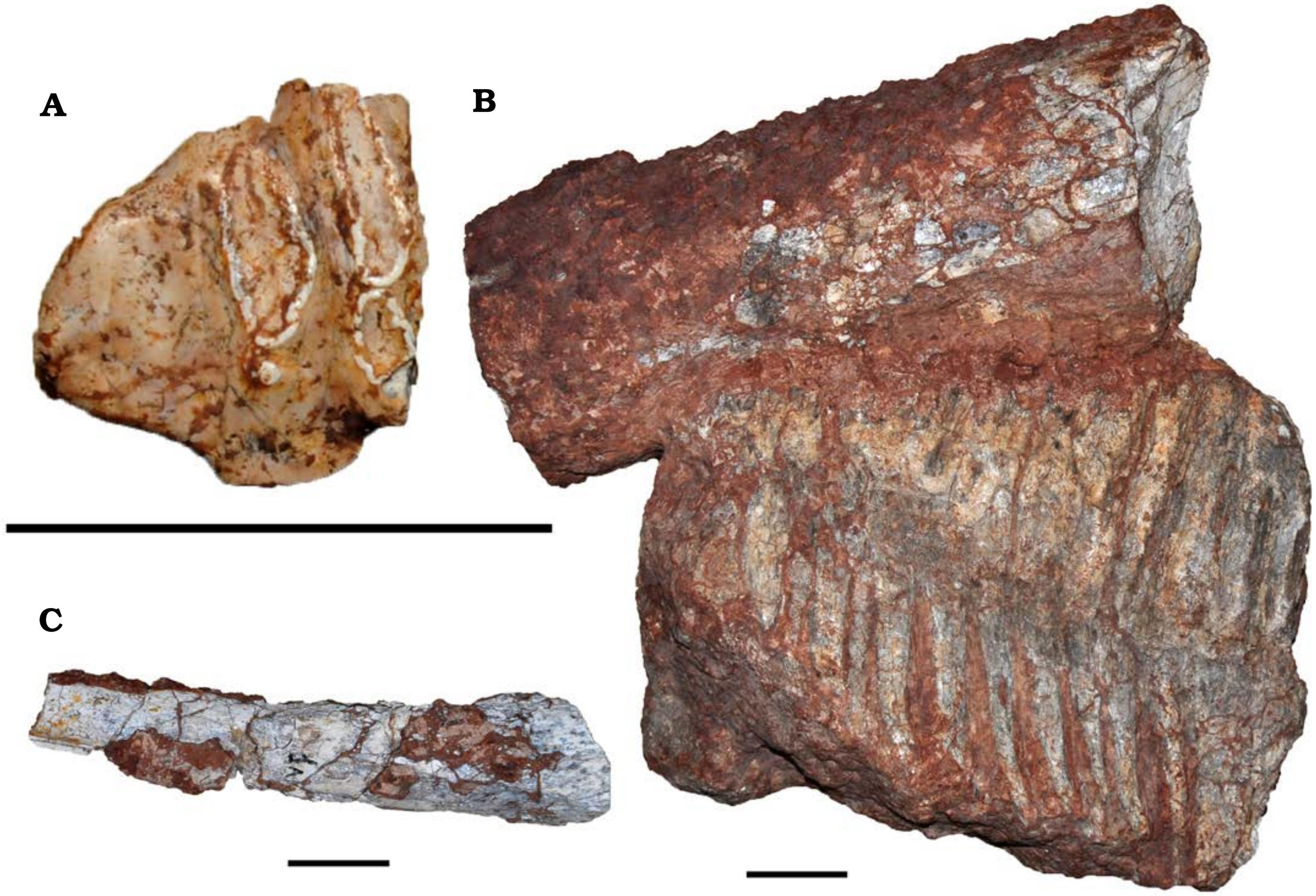

Fig. 2. Dental remains of *Palaeoloxodon antiquus* (Falconer & Cautely, 1847) from Contrada Monticelli, southern Italy, lower Middle Pleistocene. **A**. MSTB-CM 30812, tooth fragment in occlusal view. **B**. MSTB-CM QF59a and b, proximal tusk fragment and M3 cemented together in lateral view. **C**. MSTB-CM 30560, distal tusk fragment in lateral view. Scale bars 50 mm.

consists of a small tooth fragment that, however, has a clean occlusal surface. This molar fragment reveals the initial wear pattern of the lamellae, characterized by a distinctive dot-dash-dot configuration.

Vertebrae: MSTB-CM 30582, 30583, are two fragmentary vertebrae, MSTB-CM 30582 consists of the very large body of a thoracic vertebra.

Ribs: MSTB-CM 30564, 30569, 30572–30577, 30676 and 30812, represent either intermediate or proximal rib fragments, which are the most abundant bone element in the elephantid sample from CM. Their state of preservation prevents the identification of their position along the rib cage. In some cases, the rib fragments are attached to other unidentified bone fragments. Further fragmentary ribs were recognized on the surface of the cemented bone block (see SOM 2: fig. 1: 4, 5).

Scapulae: MSTB-CM 30581, highly abraded fragment and MSTB-CM 30585, the articular portion of the right scapula, characterized by a large elliptical glenoid cavity and the supraglenoid tubercle that extends ventrally lower than the articular surface. The articular portion of the left scapula MSTB-CM 30581 is embedded within the cemented bone block (see SOM 2: fig. 1: 2).

Humerus: The humerus is represented by the portion of the diaphysis (MSTB-CM 30562), two very fragmentary remains (MSTB-CM 30567, 30568) and a left distal fragment preserving part of the medial side of the diaphysis and the entire epiphysis (MSTB-CM 30588; Fig. 3A). It is not possible to determine with certainty whether the previous fragments belong to the same bone. In cranial view, the diaphysis of MSTB-CM 30588 appears rather broad and flattened, with a slightly arched medial profile. The humeral crest is pronounced and ends at approximately the same level as the epicondylar crest. The latter is slightly damaged both in its ascending portion, where it then joins the diaphysis, and in its descending lateral branch, where a substantial portion is missing. Above the trochlea is a large radial fossa that is not very deep and approximately elliptical in shape. The trochlea has a medial lip that is approximately the same height as the medial one, but wider. The trochlear groove is wide and shallow. The medial margin of the trochlea is slightly convex and vertical, while the lateral margin is flat and slightly inclined in a medial direction. The trochlea has a moderately

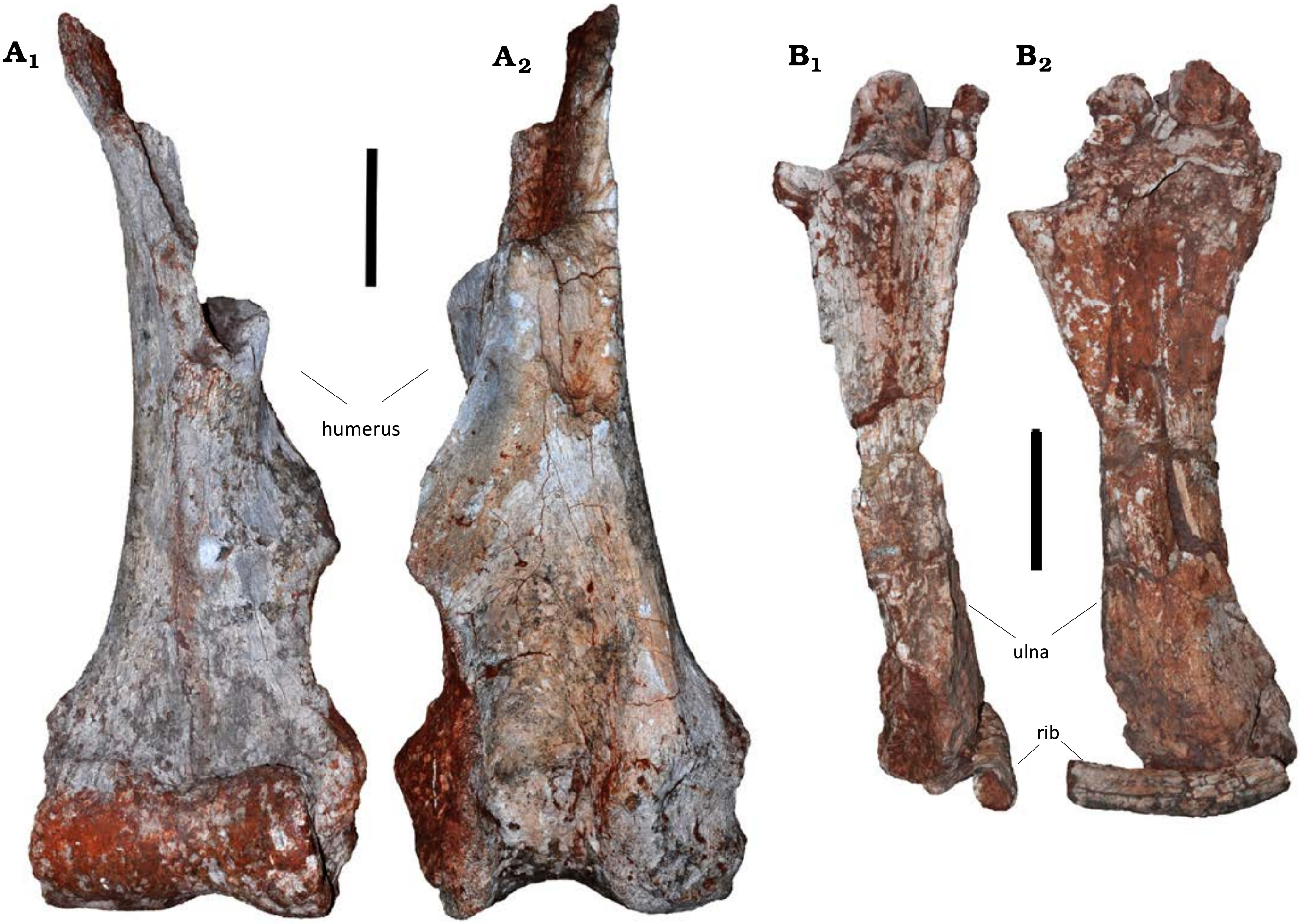

Fig. 3. *Palaeoloxodon antiquus* (Falconer & Cautely, 1847) from Contrada Monticelli, southern Italy, lower Middle Pleistocene. **A**. MSTB-CM 30588, left humerus in cranial (A_1) and caudal (A_2) views. **B**. MSTB-CM 30571, right ulna and unnumbered rib fragment in cranial (B_1) and caudal (B_2) views. Scale bars 20 mm.

cylindrical shape, with quite sharp edges. In caudal view, the olecranon fossa is high, wide, but shallow. On either side of it, the epicondyles are very different from each other, with the medial one being clearly more massive than the lateral one.

Ulna: MSTB-CM 30571 (Fig. 3B) is a complete ulna, although it is extensively fractured. Part of the olecranon tuberosity is missing, while a bone fragment (probably a rib) is attached to its distal part. In cranial view, the trochlear notch (incisura semilunaris) has a saddle-shaped basis and is also quite wide in a medio-lateral direction. The cranial surface of the diaphysis is slightly concave. The distal epiphysis does not expand much transversely, though it is heavily fractured. In medial view, the notable antero-posterior elongation of the proximal epiphysis is evident. The anconeal process is moderately curved forward and a deep fossa for articulation with the radius is evident.

Radius: MSTB-CM 30566 consists of the proximal two thirds of the right radius, exhibiting a significant degree of fracturing and abrasion. The proximal epiphysis presents an articular surface for the humerus that is approximately triangular in proximal view, with rounded corners. In cranial view, the radial tuberosity and the coronoid process are quite prominent. Immediately distal to the proximal epiphysis, the diaphysis exhibits a strong torsion around its axis and has a distinctly curved profile.

Femora: Two femora are present in the CM elephantid sample. MSTB-CM 30570 consists of an articular head; MSTB-CM 30586 (Fig. 4) is a nearly complete left femur. In cranial view, the articular head is large, spherical and facing upwards, with a short neck. In both bones there are no traces of a fovea capitis. The portion of the greater trochanter is the only slightly damaged part of the bone. Proceeding distally, the diaphysis narrows and, in its central part, has a straight columnar shape, then widens again near the distal epiphysis. The patellar surface is rather small and hourglass shaped in distal view. It is oriented towards the medial side and its lateral lip is slightly more pronounced than the medial one. These two parts are separated by a rather deep groove. The medial epicondyle is more prominent than the lateral one, which is flatter. In caudal view, the trochanteric fossa is elliptical in shape, rather narrow and elongated downwards, but not very deep. The intertrochanteric crest is poorly marked. The condyles, although partially covered by a large fragment of another strongly cemented bone, are large and rounded, close to each other and with the lateral one noticeably more voluminous than the medial one. The intercondylar fossa is narrow and shallow. The right femur is embedded within the cemented bone block from which only the side of the proximal epiphysis emerges.

Tibia: MSTB-CM 30563 is a right tibia missing the proximal end. In cranial view, there is a rather pronounced tibial crest and the medial malleolus is prominent. In caudal view, a broad distal articular surface (tibial cochlea) with a pronounced concavity occupies the entire distal end.

Stratigraphic and geographic range.—Lower Middle Pleistocene–Upper Pleistocene; Europe and Western Asia.

Results

Tusks and molars.—Although fragmentary, the tusk remains from CM lack the pronounced, often twisted curvature characteristic of mammoths. Instead, they display a pattern characteristic of *P. antiquus*. Consistently, the molar fragment MSTB-CM 30812 shows the typical dot-dash-dot wear pattern of *Palaeoloxodon*, while *Mammuthus* molars are characterized by either a dash-dot-dash wear pattern or a row of uniformly sized enamel rings (Albayrak and Lister 2012).

Appendicular skeleton.—In this section we examine the various morphological characters of the limb bones considered in the literature to distinguish between *Mammuthus* (European Pleistocene species) and *Palaeoloxodon antiquus*. For each character (Table 2) we compare descriptions provided by previous authors with our own direct observation of several elephant skeletons (see Material and methods). We then assess how each character appears in the CM specimens.

Humerus (Table 2): (i) Melentis (1963) reported that *Palaeoloxodon* has a less spherical articular head than *Mammuthus*. According to our direct observations, however, there are no evident differences in the degree of curvature of the articular head between *Palaeoloxodon* and *Mammuthus*. The shape of the humeral articular head is, in fact, much more flattened than that of the femur, so much so that osteological measurement protocols (e.g., Göhlich 1998) only include measurements of the diameters of the femoral articular head. In the humerus, the anteroposterior and transverse diameters of the entire proximal epiphysis are measured (see measurements 4 and 5 of the humerus in SOM 1: table 4). In the CM specimen the articular head is not observable because the proximal part of the humerus is missing.

(ii) According to Kroll (1991) and Davies (2002), *Palaeoloxodon* has a triangular-shaped groove along the lateral side of the diaphysis (deltoid fossa), while this feature is absent in *Mammuthus*. Our comparative study demonstrates that a deltoid fossa may be either present or absent in both *Palaeoloxodon* and *Mammuthus*, as previously noted by Ferretti (2008). In the CM specimen the presence of groove midway along the diaphysis is not observable because part of the diaphysis is missing.

Fig. 4. *Palaeoloxodon antiquus* (Falconer & Cautely, 1847) from Contrada Monticelli, southern Italy, lower Middle Pleistocene. MSTB-CM 30586, left femur and MSTB-CM 30587, left radius fragment in cranial (A_1) and caudal (A_2) views. Scale bar 20 mm.

(iii) Melentis (1963) noted that the angle of the lateral epicondyle could vary between 110–115° for *Palaeoloxodon* and 140–145° for *Mammuthus*. According to our direct observations, the amplitude of the angle formed by the lateral epicondyle is not particularly different between *Palaeoloxodon* and *Mammuthus* (see Table 2: humerus character 3). In the CM specimen, the part relating to the lateral epicondyle was slightly damaged, therefore it was not possible to make an adequate estimate of the angle.

(iv) According to Maccagno (1962) there are differences in the proportion of the distal epiphysis between the two genera, with *Palaeoloxodon* having a broader epiphysis than *Mammuthus*. Although the number of *M. meridionalis* specimens directly examined by us is rather low, the data seem to support Maccagno's (1962) observation: the width of the distal epiphysis, relative to the length of the humerus, tends to be greater in *Palaeoloxodon antiquus.* In the CM individual the distal epiphysis is notably wide, with a transversal width among the highest recorded (see SOM 1: table 4).

(v) Melentis (1963) reports that the trochlear articular surface (distal articular surface) is characterized by a deeper central groove in *Palaeoloxodon* than in *Mammuthus*. According to our direct observations, the depth of the trochlear groove is variable in both *Palaeoloxodon* and *Mammuthus* with no consistent difference between the two genera (SOM 2: fig. 4). Regarding the depth, the CM individual has a shallow trochlear groove (Fig. 3A_1).

(vi) According to Melentis (1963), the trochlear articular surface is relatively wider in *Palaeoloxodon* and narrower in *Mammuthus*. Based on our direct observation, the trochlea of *Palaeoloxodon* is wider than that of *Mammuthus* (see measurement 10 of the humerus in SOM 1: table 4). The CM individual has a particularly wide trochlea (see measurement 10 in SOM 1: tables 2, 4).

(vii) Melentis (1963) observed that the medial and lateral edges of the trochlear articular surface are sharp in *Palaeoloxodon*, while in *Mammuthus* are blunter. From observations made directly on the comparative material, the edges of the trochlea tend to be indeed sharper in *Palaeoloxodon* than in *Mammuthus* (see SOM 2: fig. 4). In the CM specimen, the edges of the trochlea are quite sharp (see Fig. 3A_1).

(viii) Andrews and Cooper (1928) noted that *Mammuthus* has a more cylindrical trochlea than *Palaeoloxodon*, which, according to them, possesses medially and laterally enlarged condyles, producing an hourglass-like shape. In our comparative sample, there do not seem to be particular differences between *Palaeoloxodon* and *Mammuthus* regarding the degree of cylindricity of the trochlea in cranial view (e.g., for *P. antiquus* see Maccagno 1962: pl. 12: 2b). In the CM specimen, the trochlea is cylindrical (see Fig. 3A_1).

Ulna (Table 2): (i) In Davies (2002), *Palaeoloxodon* is described as possessing a saddle-shaped trochlear notch, while this is flat in *Mammuthus*. According to our direct observations, the trochlear notch is more pronounced in *Palaeoloxodon* and, in general, the articular surface with the trochlea of the humerus has a wavy saddle-like shape. This surface in *Mammuthus* is more flattened. In the CM specimen the trochlear notch is saddle-shaped (see Fig. 3B_1).

(ii) According to Davies (2002), the olecranon in *Palaeoloxodon* is large and overhanging, while in *Mammuthus* it is smaller and more upright. Direct observations have shown that in *Palaeoloxodon* the olecranon is smaller and more elongated backwards, while in *Mammuthus* it is more robust and projected dorso-caudally. Unfortunately, the olecranon part is damaged in the CM specimen, therefore it is not possible to evaluate this character.

(iii) Maccagno (1962) reported that the two articular processes of the ulna for the humerus (processus coronoideus lateralis and processus coronoideus medialis*)* were more extended transversely in *Palaeoloxodon* and more extended antero-posteriorly in *Mammuthus*. According to our direct observation, however, no significant differences between *Mammuthus* and *Palaeoloxodon* were found in the transverse and antero-posterior development of the articular surface for the humerus. In the ulna of the CM specimen, the proximal articular processes for the humerus are relatively broad and antero-posteriorly short (see Fig. 3B).

Femur (Table 2): (i) According to Melentis (1963), the articular head of the femur is less spherical and more medially projected in *Palaeoloxodon* than in *Mammuthus.* In directly observed specimens, there does not appear to be any particular differences in the degree of sphericity and medial projection of the articular head between *Mammuthus* and *Palaeoloxodon* (see SOM 2: fig. 5). The CM specimen has a spherical and moderately medially projected femoral head (Fig. 4).

(ii) Andrews and Cooper (1928) observed that the head of the femur and the greater trochanter are at about the same height in *Palaeoloxodon*, while the head of the femur rises more above the greater trochanter in *Mammuthus*. We observed in our comparative sample that this trait is quite variable both in *Mammuthus* and *Palaeoloxodon*, with the femoral head ranging from slightly to markedly higher than the greater trochanter (see SOM 2: fig. 5). In the CM specimen, this trait cannot be assessed as a large portion of the greater trochanter is missing. However, the articular head appears significantly elevated.

(iii) Melentis (1963) and Davies (2002) describe the diaphysis of the femur of *Palaeoloxodon* in frontal view as possessing a straight lateral profile, while that of *Mammuthus* would be characterized by curved medial and lateral edges. From our observation, there does not appear to be significant differences in the shape of the diaphysis and the degree of curvature of its medial and lateral edges between *Mammuthus* and *Palaeoloxodon* (see SOM 2: fig. 5). The diaphysis of the CM specimen is straight in anterior view (Fig. 4).

(iv) According to Maccagno (1962), the distal epiphysis of the femur is relatively broader (transversally) in *Palaeoloxodon* and narrower in *Mammuthus*. Although our *M. meridionalis* sample is limited, it supports Maccagno's (1962) conclusion that the femur distal width, relative to greatest length of the bone, is generally greater in *P. antiquus* than in *Mammuthus*. In the CM specimen the distal epiphysis is rather broad (see SOM 1: table 4).

(v) According to Melentis (1963), the angle of the trochlear groove is larger in *Palaeoloxodon* (ca. 145°) than in *Mammuthus* (ca. 130°). However, according to our direct observation, the amplitude of the trochlear groove angles shows a certain variability, with values for *Palaeoloxodon* and *Mammuthus* overlapping in the range of ca. 130–145° (see Table 2: femur character 3). The CM specimen displays a trochlear groove with an angle of approximately 130°.

(vi) Davies (2002) reported that the distal condyles, in posterior view, are very close together in *Palaeoloxodon*, whereas they are more widely spaced in *Mammuthus*. Among the directly observed specimens, there do not appear to be significant differences in the degree of separation

Table 2. Selected anatomical characters of the humerus, ulna, femur and tibia considered diagnostic for distinguishing between *Palaeoloxodon* and *Mammuthus* species, as described by previous authors and in this study. *observed in *M. primigenius* (Ferretti 2008)

Character number	Reference	Character	*P. antiquus* (from references)	*M. meridionalis* *M. primigenius* (from references)	*P. antiquus* (this study)	*M. meridionalis* (this study)
Humerus						
1	Melentis 1963	shape of articular head	less spherical	more spherical	spherical or approximately spherical	spherical or approximately spherical
2	Kroll 1991; Davies 2002	lateral groove, midway along the diaphysis	present	absent	variably present	absent*
3	Melentis 1963	angle of the lateral epicondyle	110–115°	140–145°	117–140°	125–147°
4	Maccagno 1962	distal epiphysis	relatively broad	relatively narrow	relatively broad	relatively narrow
5	Melentis 1963	trochlear furrow	deep	shallow	shallow to deep	shallow to deep
6	Melentis 1963	trochlea width	relatively broad	relatively narrow	relatively broad	relatively narrow
7	Melentis 1963	medial and lateral edges of the trochlea	sharp	rounded	sharp	rounded
8	Andrews and Cooper 1928	shape of trochlea in anterior view	hourglass-shaped	cylindrical	variable degree of cylindricity	variable degree of cylindricity
Ulna						
1	Davies 2002	shape of trochlear notch (incisura semilunaris)	saddle-shaped	flat	saddle-shaped	flat
2	Davies 2002	olecranon	larger and overhanging	smaller and more upright	smaller and more elongated backwards	more robust and dorso-caudally projected
3	Maccagno 1962	coronoid processes	extended transversely	extended antero-posteriorly	variably extended transversely	variably extended transversely
Femur						
1	Melentis 1963	head shape and orientation	less spherical and more medially projected	more spherical and less medially projected	distinctly spherical and moderately medially projected	distinctly spherical and moderately medially projected
2	Andrews and Cooper 1928	height of head relative to greater trochanter	about the same height	head of the femur rises more above the greater trochanter	head of the femur rises more above the greater trochanter	head of the femur rises more above the greater trochanter
3	Melentis 1963; Davies 2002	shape of the diaphysis	straight diaphysis	diaphysis with curved medial and lateral edges	straight diaphysis	straight diaphysis
4	Maccagno 1962	proportion of distal epiphysis with respect to bone length	relatively wide	relatively narrow	relatively wide	relatively narrow
5	Melentis 1963	angle of trochlear groove	ca. 145°	ca. 130°	ca. 130–145°	ca. 130–145°
6	Davies 2002	intercondylar spacing	distal condyles very close to each other	distal condyles further apart	rather close to each other	rather close to each other
7	Melentis 1963	width of distal articular surface	relatively narrow	relatively broad	relative breadth similar in the two taxa	relative breadth similar in the two taxa
8	Melentis 1963	width of caudal part of lateral condyle	relatively broader	relatively narrower	relative breadth similar in the two taxa	relative breadth similar in the two taxa
Tibia						
1	Andrews and Cooper 1928	lateral proximal articular surface (condylus lateralis)	relatively wider antero-posteriorly	relatively narrower antero-posteriorly	shape of the lateral articular surface does not differ between the two taxa	shape of the lateral articular surface does not differ between the two taxa

of the condyles between the two genera (see SOM 2: fig. 5). In the CM specimen the distal condyles are positioned very close to each other (Fig. 4A$_2$).

(vii) Melentis (1963) reported that the distal articular surface for the tibia (seen in distal view) is relatively narrow transversally in *Palaeoloxodon* and broad in *Mammuthus*. According to our direct observation, there do not appear to be any significant differences in the shape of the articular surface for the tibia between *Mammuthus* and *Palaeoloxodon* (see measurement 12 of the femur in SOM 1: table 3).

In the CM specimen, the breadth of the articular surface for the tibia falls between the minimum and maximum values observed in the comparative sample.

(viii) Melentis (1963) states that the caudal part of the lateral condyle is relatively broader (transversally) in *Palaeoloxodon* and narrower in *Mammuthus*. In directly observed specimens, the caudal part of the lateral condyle does not show particular differences in width between *Palaeoloxodon* and *Mammuthus* (see SOM 2: fig. 5). Like the other Elephantidae examined, the CM individual also appears to have a rather broad caudal part of the lateral condyle.

In addition to the characters discussed above, we observed that the studied femora of *Mammuthus* have a deeper trochanteric fossa than those of *Palaeoloxodon*. Indeed, this appear to be the only character that distinguishes the observed individuals of *M. meridionalis* from *P. antiquus*. The CM specimen exhibits a shallow but rather wide trochanteric fossa (see SOM 2: fig. 5).

Tibia (Table 2): (i) According to Andrews and Cooper (1928), the tibia of *Palaeoloxodon* differs from that of *Mammuthus* in the relative position of the lateral proximal articular surface for the femur (condylus lateralis), which is much lower than the medial one and in being wider antero-posteriorly. In the specimens we examined, however, *Palaeoloxodon* and *Mammuthus* seem not to differ in these traits. In the CM individual, this character is not observable as the entire proximal extremity is missing.

Schreger pattern analyses of tusk dentine.—In MSTB-CM QF59a the Schreger angles ranges 95–110° (Fig. 5). These values are higher than that typically observed in *Mammuthus,* while are consistent with the observed range in *Palaeoloxodon* (Espinoza and Mann 1993; Palombo and Villa 2001; Trapani and Fisher 2003). Schreger angles measured on the tusk section of *M. meridionalis* (IGF 305) ranged from 75° to 90°, consistent with the reported range in *Mammuthus* (Espinoza and Mann 1993; Palombo and Villa 2001; Trapani and Fisher 2003).

Morphometric analysis.—The state of preservation of the molars from CM and their advanced stage of wear does not allow determining the original total number of plates and crown heigh, two important parameters in species identification. The most complete molar, MSTB-CM QF59b, presents however a rather narrow crown and a lamellar frequency which are consistent with and attribution to *P. antiquus*. Regarding the postcranial skeleton, our morphometric analysis did not reveal significant differences in size and robustness between the studied *M. meridionalis* and *P. antiquus* specimens. As the femur is the most complete long bone in the CM elephantid sample, we conducted a PCA on our femur sample, based on five measurements (measurements 1, 6, 7, 10, and 11; see SOM 1: table 4). PC1 accounts for most of the sample total variance (96.32%) and is highly correlated with variable 1 (GL) and therefore with overall size. Accordingly, a scatterplot of the first two principal components (Fig, 6) shows a clear separation of male and female specimens along PC1. In contrast, the ranges of variation of the two species largely overlap as the analysis revealed no clear distinction between the femora of *P. antiquus* and *M. meridionalis* (Fig. 6). None of the other PCs improved species discrimination.

Shoulder height, body mass, and sex.—To calculate the SH, the equation of Larramendi (2016) was applied both to the Contrada Monticelli individual and to the other comparison specimens of *P. antiquus* (see SOM 1: table 5). The results obtained showed a flesh SH for the CM individual of 3636 mm, a height comparable to that of medium-high sized male specimens (Fig. 7).

BM was estimated using the equation of Larramendi (2016) applied both to the individual from CM and to the other specimens of *P. antiquus* and *M. meridionalis* in the comparative sample (see SOM 1: table 5). The results obtained showed a BM for the CM individual of 9881 kg, and a shoulder height with flesh of 3.6 m, comparable to that of medium-large male *P. antiquus* specimens (Fig. 7).

The Upnor specimen was not included in the comparison, as only the proximal part of the femur is preserved, the rest is restored and its total length (1545 mm, according to Andrews and Cooper 1928) is most likely exaggerated (Asier Larramendi personal communication, 2025).

A reliable method for estimating the sex of an elephant skeleton is based on pelvis proportions (Lister 1996). In the absence of this skeletal element, as is the case for the CM elephant, body size, bone robustness, and tusk dimensions can be used as a proxy to estimate the sex of the animal, as elephants display a marked sexual dimorphism in these traits. Comparing the SH and BM estimates obtained for the CM elephant, based on linear measurements of the femur (MSTB-CM 30586), the CM elephant appears to belong to a large adult male, although its tusks are relatively slender. A principal component analysis (PCA) based on five femoral measurements did not clearly separate *P. antiquus* and *M. meridionalis*, which formed two largely overlapping clusters (Fig. 6). On the other hand, male and female individuals are separated along the PC1 axis, which correlates primarily with measurement 1 (femur GL), and thus reflects overall size. The CM specimen fell well within the male *P. antiquus* cluster.

Discussion

Taxonomy, sex, and age of the Contrada Monticelli elephant.—The CM elephantid was referred to as *Elephas* (= *Palaeoloxodon*) *antiquus* by Luperto Sinni and Colucci (1985), the most common elephant species in the Middle Pleistocene of central and southern Italy, although they did not provide supporting evidence for their taxonomic attribution. Our morphological and morphometric analysis of the entire CM sample allows us to confirm this preliminary attribution to *Palaeoloxodon antiquus*, based on dental morphology. In particular, the occlusal surface of the molar MSTB-CM 30812 (Fig. 2A), shows the dot-dash-dot initial wear pattern

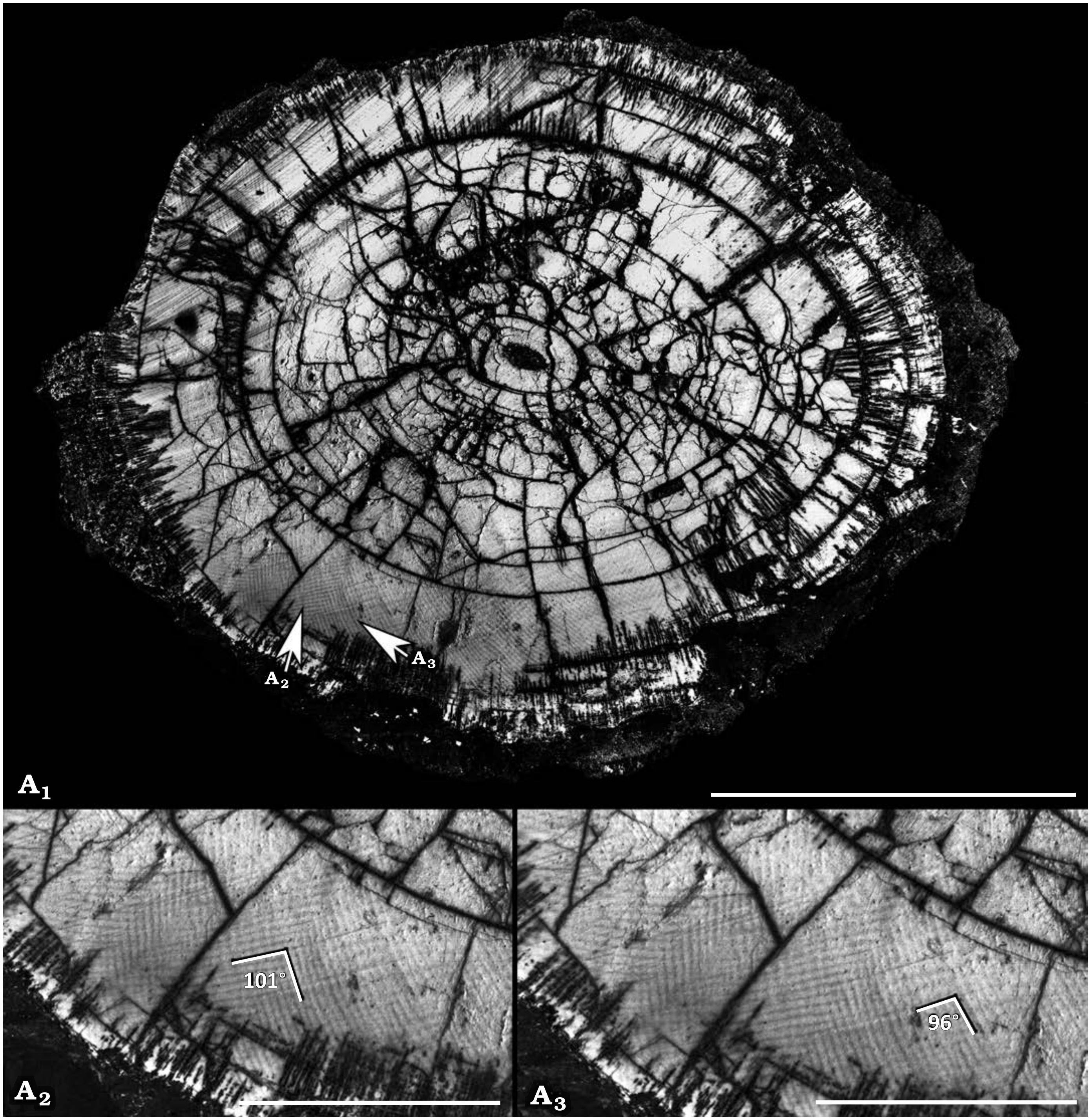

Fig. 5. Transverse section of the proximal portion of the tusk of *Palaeoloxodon antiquus* (Falconer & Cautely, 1847) from Contrada Monticelli, southern Italy, lower Middle Pleistocene. MSTB-CM QF59a, photo with enhanced contrast (A_1), Schreger angles in the outer portion of the tusk section vary from about 101° (A_2) to about 96° (A_3). Scale bar A_1 50 mm, A_2, A_3 10 mm.

typical of *Palaeoloxodon*, and different from those usually observed in *Mammuthus*. The M3 (MSTB-CM QF59b) possesses a relatively narrow crown (SOM 1: table 3), compatible with the known range of variability observed in Italian samples of *P. antiquus* (Palombo and Ferretti 2005).

Based on the preserved fragments, the tusks of the CM elephant appear to have been only slightly curved, resembling the tusk morphology of *Palaeoloxodon antiquus* and contrasting with the spirally curved tusks of mammoths. Consistently, the dentine of the CM tusk shows Schreger angles ranging from 95° to 110° (Fig. 5), which fall within the observed range of *Palaeoloxodon*, and of extant *Loxodonta* and *Elephas*. In contrast, *Mammuthus* possesses distinctly narrower angles (Palombo and Villa 2001),

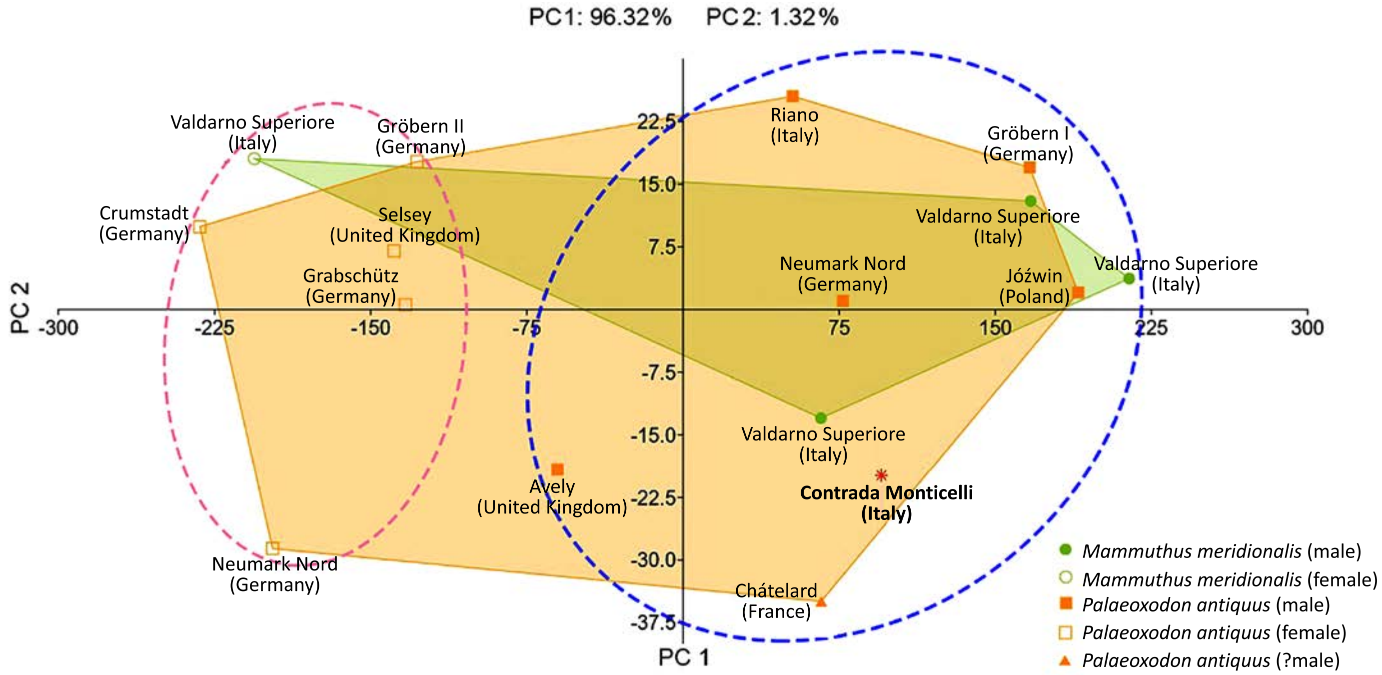

Fig. 6. 2D scatterplot of PC1 and PC2 from the Principal Component Analysis of femur variables 1, 6, 7, 10, and 11 in the studied sample of *Palaeoloxodon antiquus* and *Mammuthus meridionalis*. The analysis did not separate the two taxa. PC1, which primarily reflects size variation, distinguishes females (pink dashed oval) from males (blue dashed oval) individuals. Original measurements are reported in SOM 1: table 2.

further confirming the utility of this trait in discriminating among elephantid taxa (Athanassious 2011; Katona et al. 2012; Virág 2014; Kevrekidis and Mol 2016).

The arrival of elephants of the genus *Palaeoloxodon* from Africa into Eurasia occurred at the end of the Early Pleistocene (approximately 0.9–0.8 Ma, MIS 21–19; Palombo and Ferretti 2005; Lister 2016; Mecozzi et al. 2025b). From a dental perspective, these forms are similar to the African species *P. recki*. In particular, the total number of lamellae and the degree of hypsodonty show substantial stasis throughout the time span in which the genus existed in Eurasia. In contrast, the skull shows morphological evolution in the Eurasian forms, especially evident in the development of a peculiar structure of this genus known as the parieto-occipital crest (POC; Larramendi et al. 2020).

European remains of *Palaeoloxodon* are commonly attributed to a single species, *P. antiquus*. The earliest finds of this species come from northern Italy (Slivia, MIS 21) and England (Pakefield, MIS 17), which attest to its wide latitudinal distribution in Europe during the 0.9–0.7 Ma time interval (Stuart and Lister 2001; Palombo and Ferretti 2005). It is worth noting that the skull of *P. antiquus* is only known starting from MIS 12 (e.g., Marathousa 1, Greece; Konidaris et al. 2018; Athanassiou 2022), at which point the development of the POC is already well pronounced.

In the Middle East (a likely dispersal route between Africa and Eurasia followed by *Palaeoloxodon*) and Central Asia, elephant skulls attributable to this genus have been found, dated between 0.8 and 0.7 Ma, which, however, do not show development of a POC, and have been assigned to different species (*P. recki* and *P. turkmenicus*, respectively; Dubrovo 1960; Saegusa and Gilbert 2008). In the absence of cranial remains showing the dorsal portion, it is currently not possible to determine the degree of development of the POC in pre-MIS 12 European *Palaeoloxodon* populations, which includes the Italian material from CM, Isernia La Pineta, and Notarchirico. As a matter of fact, although these earlier specimens are indistinguishable from late Middle and Late Pleistocene *P. antiquus* based on dental and postcranial features, they may nonetheless represent a distinct taxon. For this reason, sites dated between 0.9 and 0.5 Ma, such as CM, are of particular importance for our understanding of the diversity of early European palaeoloxodont elephants.

Our estimates of shoulder height (SH) and body mass (BM) for the CM elephant are close to the averages calculated for adult male *Palaeoloxodon antiquus* from various European localities (Erkek and Lister 2021), suggesting it was a medium-sized male individual (M3 in use), with relatively slender tusks. The specimens studied by Erkek and Lister (2021) originate from sites younger than the Isernia FU. No size estimates currently exist for *P. antiquus* specimens older than MIS 12, except for the nearly complete skeletons from Contrada Calorie (Palombo et al. 2024) and CM. Interestingly, the SH and BM estimates reported for the Contrada Calorie elephant are very similar to those proposed here for the CM elephant (see Fig. 7). At present, due to the scarcity of well-preserved early *P. antiquus* skeletal material, it is not possible to determine whether the extreme body sizes observed at younger sites, such as Neumark

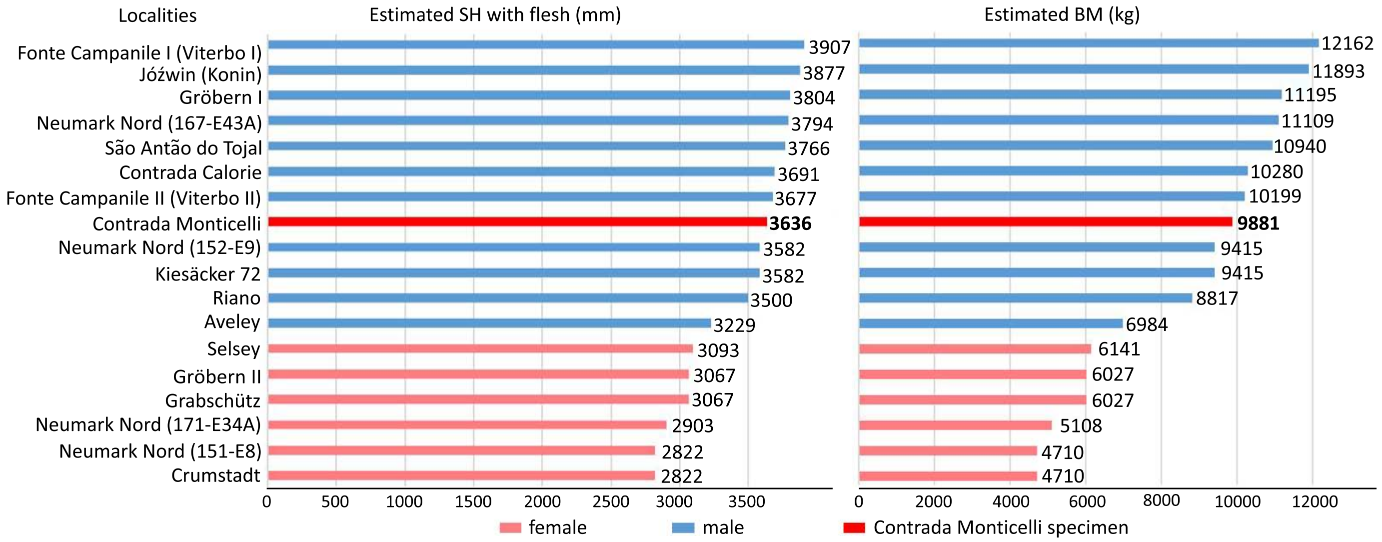

Fig. 7. Bar-charts comparing the estimated shoulder height with flesh (SH, in mm, following Larramendi 2016) and the estimated body mass (BM, in kg, following Larramendi 2016) of the *Palaeoloxodon antiquus* specimen from Contrada Monticelli with that of 17 other skeletons of *P. antiquus*. Data and relative references are reported in SOM 1: table 5.

Nord 1 (MIS 7/5; Larramendi et al. 2017), already characterized the earliest European populations of *P. antiquus*.

On the other hand, the available evidence suggests that *P. antiquus* did not exhibit a latitudinal gradient in body size across its European range (Larramendi et al. 2017; Erkek and Lister 2021; Palombo et al. 2024).

Diagnostic value of the post-cranial skeleton.—All Elephantimorpha (the clade that includes derived proboscideans with horizontal tooth progression) exhibit a rather stereotypical skeletal structure, likely linked to their graviportal adaptations for supporting their very large body size. Only a few minor postcranial characters have been identified that appear to differentiate Mammutidae, Gomphotheriidae, and Elephantidae (Tassy 1985; Ferretti 2010), while differences within families are more elusive and mostly concern bone proportions and robusticity (Reggiani 2001; Larramendi 2016). These, however, are difficult to assess with small samples, considering that postcranial bones change in proportion during growth, and that males are generally more robust than females. In fact, the only consistently marked difference between elephantid genera is the well-known variation in the dorsal silhouette of the vertebral column, which is primarily due to differences in the length and inclination of the vertebral spinous processes (Shoshani 1996). However, this complex feature can only be assessed in sufficiently complete and well-preserved vertebral columns, a rather rare occurrence.

Our comparative anatomical analysis of four long bones (humerus, ulna, femur, and tibia) previously considered by several authors to possess diagnostic traits distinguishing *Palaeoloxodon* from *Mammuthus*, revealed that most of these traits are subject to extensive individual variation, or that traits regarded as diagnostic for one genus were also observed in the other. These therefore cannot be used to discriminate between the two genera.

The humerus, ulna, and femur do appear to show some consistent differences between the two genera; however, these need to be tested on a larger sample to confirm their diagnostic value. As first observed by Maccagno (1962) and Melentis (1963), *Palaeoloxodon* is characterized by a proportionally wider distal humerus compared with *Mammuthus*, as indicated by the greater widths of both the distal epiphysis and the distal articular surface, relative to the bone length. Consistently, the CM humerus is characterized by a particularly broad distal epiphysis. We were also able to confirm Melentis' (1963) observation that the distal articular surface of the humerus of *Palaeoloxodon* possesses distinctly sharper edges with respect to *Mammuthus*.

Regarding the ulna, we confirmed Davies' (2002) observation that in *Palaeoloxodon*, the trochlear notch (incisura semilunaris) is clearly saddle-shaped, whereas in *Mammuthus* it is relatively flat. Davies (2002) also highlighted differences in the robusticity and orientation of the olecranon between the two genera. We observed consistent differences in the development of the olecranon as well, although they differ from the traits described by Davies (2002). Specifically, in *Mammuthus*, the olecranon is more robust and projects in a dorso-caudal direction, while in *Palaeoloxodon* it appears less pronounced and positioned lower. Additionally, the distance from the anconeal process to the posterior edge of the olecranon is greater in *Palaeoloxodon* than in *Mammuthus*.

Regarding the femur, Maccagno's (1962) observation on the proportions of the distal epiphysis is supported: *Palaeoloxodon* exhibits a larger relative distal width than *Mammuthus*, consistent with pattern observed in the humerus. Furthermore, another feature that seems to distinguish *M. meridionalis* from *P. antiquus*, is the different depth of the trochanteric fossa. The *Mammuthus* femora examined have a deeper trochanteric fossa than those of *Palaeoloxodon*.

The morphometric analyses did not reveal significant size differences between the *Mammuthus* and *Palaeoloxodon* specimens studied.

Despite this, significant individual size differences were observed among individuals of the same genus, but these are attributable to sexual dimorphism. As is well known, both extant and extinct elephants exhibit pronounced sexual dimorphism, particularly in body size, with males being considerably larger than females (Haynes 1991; Shoshani 1996; Sukumar 2003). Healthy, fully grown males of *E. maximus* are approximately 15% taller and weigh 48% more than females, whereas males of *L. africana* are 23% taller and weigh twice as much (100%) as females (Larramendi 2016). Larramendi et al. (2017) found that sex differences in size were even greater in *P. antiquus* from Neumark Nord 1, with fully grown males being approximately 33% taller and weighing approximately 136% more than females, suggesting greater sexual dimorphism than in extant elephants. Consistently, several authors have used the size of the postcranial elements to distinguish sexes of extinct elephantids (e.g., Kroll 1991; Averianov 1996; Tsoukala and Lister 1998; Palombo and Villa 2003).

Biochronological, paleobiogeographical, and palaeoecological remarks.—Faunal assemblages from southern Italy, such as those from Isernia La Pineta (MIS 15) and the upper levels of Notarchirico (MIS 16), dated to approximately 0.58 and between 0.66 and 0.61 Ma, respectively, and referred to the Isernia FU, exhibit a taxonomic composition similar to that of CM (Sala 2006; Breda et al. 2015; Peretto et al. 2015; Mecozzi et al. 2024b). These assemblages are characterized by the occurrence of *Bison* cf. *schoetensacki* and *Stephanorhinus hundsheimensis,* and the primitive fallow deer *Dama roberti*, whose known fossil record spans from 0.7 to 0.5 Ma (Breda and Lister 2013; Mecozzi et al. 2024a). During this interval, *Palaeoloxodon antiquus* had already achieved a wide geographical distribution across Europe, ranging from the British Isles to southern Italy, and from the Iberian Peninsula to Greece (Palombo et al. 2010). Despite this wide range, complete or partial skeletons of this species are extremely rare in Europe prior to MIS 12–11, and, as stated above, no complete skulls, preserving the dorsal part, are known. The CM specimen therefore represents one of the few straight-tusked elephant partial skeletons known from this time interval in Europe, along with those from Contrada Calorie (Palombo et al. 2024) and Notarchirico (Mecozzi et al. 2024b).

In the Italian Peninsula, the straight-tusked elephant reached as far south as southern Calabria during the Middle Pleistocene and eventually colonized Sicily (Palombo and Ferretti 2005).

P. antiquus represents the most frequently recorded elephant species in the Middle Pleistocene of Italy, whereas findings of *Mammuthus* are extremely rare. No Italian sites are currently known to feature both genera in clear stratigraphic association, with the sole exception of the Ponte Galeria Formation near Rome. The classic "Ponte Galeria fauna" (Ponte Galeria 2) originates from the sand and gravel beach deposits underlying the *Venerupis senescens* clays, dated to approximately 0.7 Ma (Milli 1997). The faunal list includes, among others, *Mammuthus trogontherii* and *Palaeoloxodon antiquus* (Milli and Palombo 2005). Due to the scarcity of remains and the impossibility of verifying the exact stratigraphic position of specimens belonging to historical collections, it cannot be excluded that, actually, the two species may originate from different depositional layers (Petronio and Sardella 1999). This would be consistent with the hypothesis that *P. antiquus* and *M. trogontherii* had distinct ecological requirements and thus occupied different niches.

In Italy, *Mammuthus trogontherii* is considered exceptionally rare and is only reported as far south as Lazio and Abruzzo (Palombo and Ferretti 2005). During the coldest phases of the Late Pleistocene, *M. primigenius* expanded into the Italian Peninsula, reaching its southernmost range at Cardamone, located at the southern tip of Apulia (Rustioni et al. 2003).

Mesowear and stable isotope analyses from other European contexts indicate that *M. trogontherii* maintained a predominantly grazing diet, while *P. antiquus* displayed a broader range of dietary strategies, often classified as a mixed-feeder with a browsing tendency (Saarinen and Lister 2016; Tsakalidis et al. 2025). This degree of dietary plasticity may have allowed *P. antiquus* to exploit a wider array of environments and vegetational structures. Isotope data obtained from the dental enamel of *P. antiquus* from Europe suggest in fact that these animals lived in different environmental and climatic conditions (e.g., Grube et al. 2010; Briatico and Bocherens 2023; Roditi et al. 2024). For example, the straight-tusked elephant sample from Steinheim an der Murr and Mauer (Germany) indicated cooler and more humid conditions compared to that of other European samples (Grube et al. 2010). As a general trend, stable isotopic data indicate a transition from a wooded landscape and humid climate in Europe during the mid-Middle Pleistocene (MIS 15–11), to more open and arid environments at the end of Middle Pleistocene (MIS 7) (Mecozzi et al. 2025a). Due to the poor preservation of dental remains from the CM locality, mesowear analysis could not be performed. Nevertheless, the overall composition of the faunal assemblage from CM suggests the presence of mild climatic conditions and a heterogeneous landscape, characterized by open habitats interspersed with areas of tree cover. This environmental setting would have supported mixed-feeding strategies and reduced potential trophic competition among large herbivores.

Conclusions

The complete early Middle Pleistocene elephant sample from Contrada Monticelli has been studied here for the first time. The material consists of 32 dental and skeletal elements belonging to a single adult (M3 in use) male individual. Molar traits and Schreger pattern of the tusk dentine allowed us to confidently refer the specimen to *Palaeoloxodon antiquus*, the straight-tusked elephant. Diagnostic features of the humerus, ulna, and femur of the CM elephant are consistent with such an attribution. The CM elephant had an estimated shoulder height with flesh of approximately 3.6 m and a body mass of nearly 10 t, corresponding to a medium-sized male *P. antiquus* individual (Larramendi 2016; Erkek and Lister 2021), comparable to the specimen from Contrada Calorie (Palombo et al. 2024).

Our morphological comparison of the limb bones of late Early Pleistocene *Mammuthus meridionalis* from Upper Valdarno (Tasso FU) and various Middle Pleistocene *Palaeoloxodon antiquus* from Italian sites indicates that most of the morphological characters previously reported as diagnostic between *Mammuthus* and *Palaeoloxodon* are not reliable, when intraspecific variability is taken into consideration. However, the two genera appear to differ in specific traits of the distal articular surface of the humerus and femur, and the proximal epiphysis of the ulna. These differences merit further investigation by using a larger comparative sample that should also include other *Mammuthus* species. The morphometric analysis we conducted did not reveal any differences between *Mammuthus* and *Palaeoloxodon* in terms of the size and proportions of the long limb bones. On the other hand, the size of the long bones analyzed (humerus, ulna, femur, and tibia), particularly their greatest length, clearly distinguishes adult male and female individuals in both genera. The elephant from Contrada Monticelli represents one of the few European skeletons of straight-tusked elephant known from the 0.8–0.5 Ma interval, corresponding to the early dispersal of the genus in Eurasia. Although it provides no information on the cranial morphology of these early European palaeoloxodontine populations, particularly regarding the degree of development of the POC, the CM specimen nonetheless contributes to our understanding of the biochronological, paleoecological, and paleobiogeographical context of *Palaeoloxodon* early evolution in Europe. The presence of the straight-tusked at CM, along with other mixed-feeder herbivores such as *Bison* cf. *schoetensacki*, *Dama* cf. *roberti,* and *Stephanorhinus hundsheimensis*, suggests a temperate climate and a landscape with substantial woodland components as well as more open areas, as indicates the occurrence of *Equus* sp. in the CM assemblage. In this varied environment, different herbivores likely took advantage of the diverse vegetation, using their dietary flexibility to minimize competition.

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