

M.R. Palombo¹ & P. Villa²

¹ Università 'La Sapienza', Roma

² Formia

Sexually dimorphic characters of *Elephas (Palaeoloxodon) antiquus* from Grotte Santo Stefano (Viterbo, Central Italy)

Palombo, M.R. & Villa, P., 2003 - Sexually dimorphic characters of *Elephas (Palaeoloxodon) antiquus* from Grotte Santo Stefano (Viterbo, Central Italy) - in: J.W.F. Reumer, J. de Vos & D. Mol (eds.) - ADVANCES IN MAMMOTH RESEARCH (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999) - DEINSEA 9: 293-315 [ISSN 0923-9308] Published 24 May 2003

To test the sexual dimorphic characters, two almost complete skeletons of *E. antiquus* of late Middle Pleistocene age, which were found in the lacustrine deposit of Grotte Santo Stefano near Viterbo (Central Italy), were examined. Besides dimorphic characters shown in skull, tusks and pelvic morphology, there is some information about the differences between male and female of *E. (Palaeoloxodon) antiquus* in the molar, atlas, epistropheus, carpal and metacarpal bone morphology, and in the biometry. The characters studied seem to indicate that specimens 'A' and 'B' may be considered as female and male individuals, respectively. For the moment however, the differences found between the two specimens cannot be considered conclusive.

Correspondence: Maria Rita Palombo, Dipartimento di Scienze della Terra Università degli Studi di Roma 'La Sapienza', CNR Istituto di Geologia Ambientale e Geoingegneria, Piazzale A. Moro, 5 - 00185 Roma, Italy, e-mail palombo@uniroma1.it; P. Villa, Via della Conca, 59 - 04023 Formia (LT), Italy.

Keywords: *Elephas (Palaeoloxodon) antiquus*, Middle Pleistocene, Italy, sexual dimorphism

INTRODUCTION

The sexual identification of fossil elephant skeletons is generally considered to be an important contribution to understanding the social structure of a population and it can be useful in taphonomical studies. There are several main categories of potential information about the sex of a proboscidean: (1) preserved genitalia, (2) skeleton size and robusticity, (3) skull and tusk morphology, (4) pelvic morphology. Many studies were undertaken to identify efficient dimorphic characters from biometrics and morphology. The greater part of these studies concerns *Mammuthus primigenius* (Averianov 1994, 1996) or other

members of the genus *Mammuthus* (Lister 1996). However, sexual dimorphic characters of *Elephas (Palaeoloxodon) antiquus* are not well known yet (Dubrovo & Jakubowski 1988, Palombo 1986).

In the 1940s and 1950s two almost complete skeletons of *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847 were found in diatomaceous layers, outcropping in the vicinity of Grotte Santo Stefano (Viterbo, Central Italy). The site is situated at a distance of about 10km from the eastern side of the Bolsena Lake (Fig. 1). The first specimen was found in 1941, during mining activities. This specimen - described in detail by

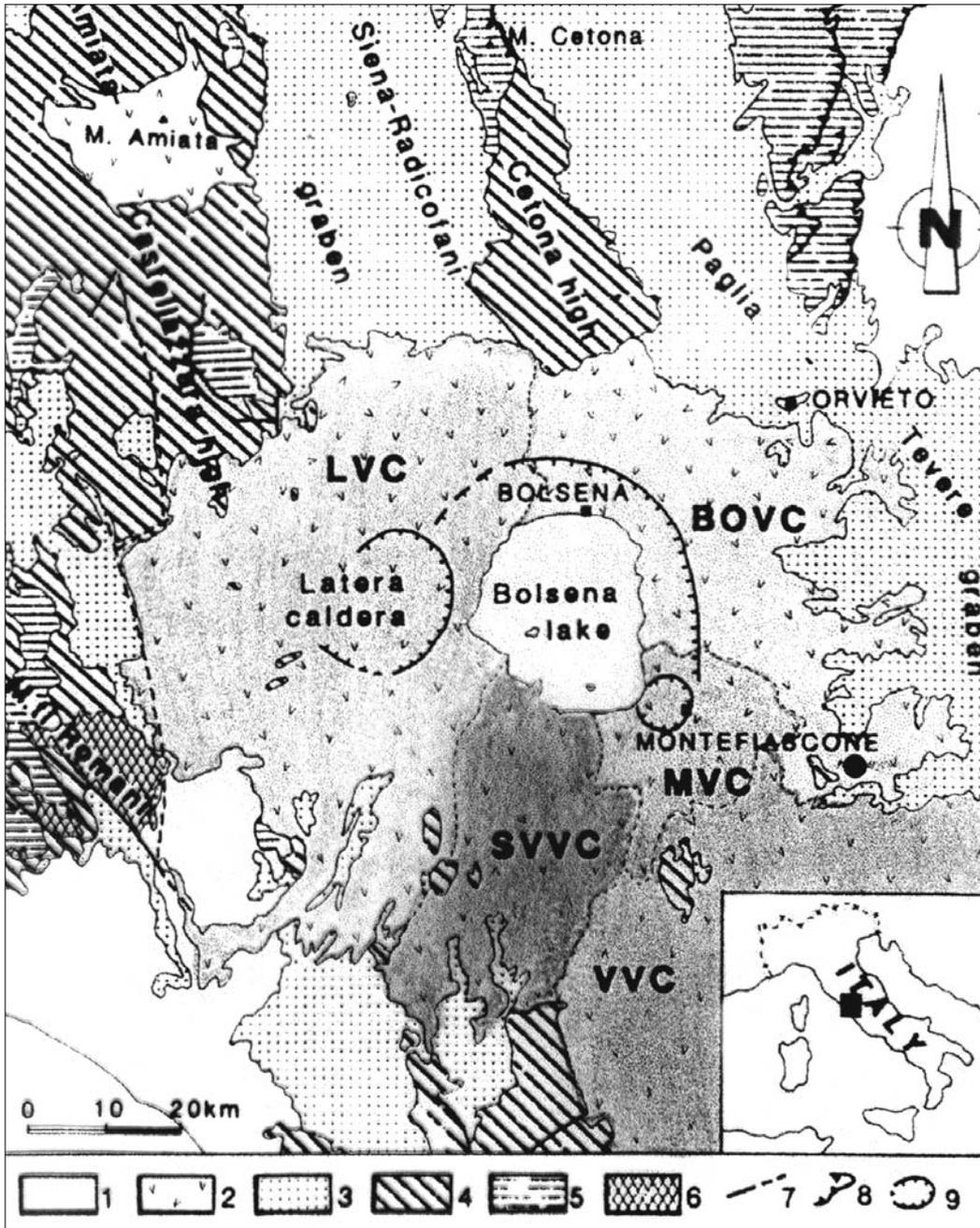


Figure 1. Structural sketch map of Monti Vulsini area. **1:** Quaternary sedimentary deposits, **2:** Volcanics (**LVC** = Latera Volcanic Complex, **BOVC** = Bolsena-Orvieto Volcanic Complex, **MVC** = Montefiascone Volcanic Complex, **SVVC** = Southern Vulsini Volcanic Complex, **VVC** = Vico Volcanic Complex), **3:** Neoautochthonous Sequence, **4:** Liguride and Subliguride Sequence, **5:** non-metamorphic Tuscan Sequence, **6:** Metamorphic Tuscan Sequence, **7:** main faults, **8:** Thrust fronts of the Tuscan Sequence, **9:** Caldera rim. The black circle indicates the fossil flour quarry.

Trevisan (1942, 1949) - underwent several restorations; after strengthening works during the excavation, the restoration was completed in the laboratories of the Geological Department in Pisa. In addition to this, after a second restoration aiming at the recovery of some damaged bones caused by bombing during World War II, the specimen was transferred to the Municipal Museum 'G. Doria' in Genova (North Italy), where it was assembled. Recently, this skeleton was restored again in order to highlight the original parts. In the 1950s, a second skeleton was found in the same diatomaceous deposit. It was also almost complete. The recovery was executed by prof. A. Maccagno and the staff of the Museum of Geology and Palaeontology in Rome. In the 1970s this skeleton was restored and assembled. It is still unpublished. In this assembled skeleton, the dorsoventrally deformed skull (due to crushing) was substituted by a reconstructed model, based on biometrical data of the original specimen. In both specimens of *E. (Palaeoloxodon) antiquus* the penultimate maxillary and mandibular molars are at an advanced degree of wear and the last molars, with the first plates in wear, are present. The individual age of both specimens may be 35-40 years. They may be of the same population, living in a similar environment. A comparison between them becomes very interesting, for checking what characters can be regarded as diagnostic for gender determination of elephantine species. These

characters can be also valid for elephants of *Elephas antiquus-Elephas namadicus* group. Maybe some of these characters depend on the degree of evolution, ontogenetic development or environmental conditions.

This work represents a first preliminary analysis, which is carried out in order to verify the reliability of a study to individualise every dimorphic character for gender identification of remains of *Elephas (Palaeoloxodon) antiquus*.

MATERIAL AND METHODS

This study is based on two almost complete skeletons of *Elephas (Palaeoloxodon) antiquus*. One of them is stored in the Municipal Museum 'G. Doria' in Genova (c.p. no. 1; C.E. no. 35443). It was studied by Trevisan (1942, 1949) and is here called specimen 'A' (Fig. 2). The second skeleton is stored in the Palaeontological Museum of the University 'La Sapienza', Rome (MPUR/U, assembled skeleton). It is still unpublished and is here called specimen 'B' (Fig. 3). Both skeletons have a damaged, deformed and strongly dorsoventrally pressed skull. In specimen 'A' the best-preserved part of the skull is the dorsal side; it has a frontal, well developed torus and an expanded lateral fan. In specimen 'B' the top of skull is very damaged, whereas the ventral side is more preserved. Therefore, in specimen 'A' the tusks are weakly crushed dorsoventrally, mostly in the proximity of the alveoli. In 'B' the condition



Figure 2 *Elephas (Palaeoloxodon) antiquus*, specimen 'A', Municipal Museum 'G. Doria', Genova c.p. no. 1; C.E. no. 35443.

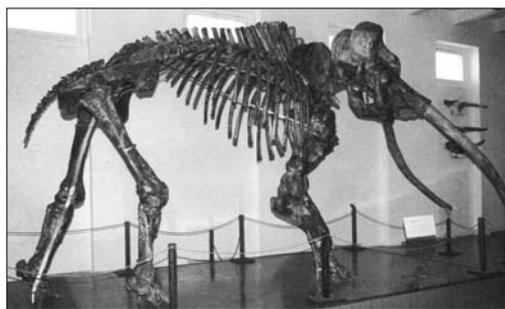


Figure 3 *Elephas (Palaeoloxodon) antiquus*, specimen 'B', Paleontological Museum of the University 'La Sapienza', Rome MPUR/U, mounted skeleton.

of the tusks did not allow recovery, only a trace was made on the sediment. In specimen 'A' the mandible is strongly deformed, while it is incomplete in specimen 'B'. It is absolutely impossible to compare the cranial and mandibular characters of the two skeletons. A valuation of dimorphic characters was carried out in molars, atlas, epistropheus, carpal bones and pelvis. Two skulls of specimens from Viterbo have comparable dimensions, even considering all of the deformations. A first comparison was carried out with the skull of Pignataro Interamna (De Lorenzo & D'Erasmus 1927) (*Hesperoloxodon antiquus italicus*' after Osborn 1942). This specimen, considered to be a female by Osborn (1942), has the penultimate and last molars in function with a more advanced degree of wear than the last molars of specimens 'A' and 'B'. Nevertheless the dimensions are on the average a little smaller.

Both mounted specimens are supported by a steel construction, which caused some trouble when taking measurements. Several morphological and biometrical characters of elephant molars have been examined, and it turned out that in living species males tend to have slightly larger cheek teeth than females (Roth 1992). In various living and fossil homologous populations, especially in *Elephas (Palaeoloxodon) antiquus*, two morphotypes can be recognised in molars with the same degree of wear. These morphotypes can be considered as male and female individuals (Ambrosetti 1968; Palombo 1986, 1995; Roth 1992). In the case of the atlas and epistropheus, which are considered to be diagnostic to determine the sex (Averianov 1996), only a morphological comparison was carried out. As the two specimens of Grotte Santo Stefano show different deformations no measurements could be taken. For the carpal bones, direct comparisons and literature-based confrontations were carried out with more or less complete skeletons from Riano (Early Aurelian; female individual; Maccagno 1962). This specimen is attributable to F.U. of Torre in Pietra (isotopic oxygen stage 9),

therefore it is coeval with the specimens of Viterbo. The comparison was widened to skeletons of Ciechanow (?Eemian; female individual; Dubrovo & Jakubowski, 1988) and of Jowsin (Eemian; male individual; Dubrovo & Jakubowski 1988).

Particular attention was paid to the pelvis, as the morphological and biometrical characters are considered by several authors (Averianov 1996; Deniraygala 1955; Haynes 1990; Lister 1996) to be of great value for identifying the gender, in living as well as in fossil species. The measurements of the pelvic girdle have been taken according to the methodology proposed by Lister (Lister 1996). Some additional dimensions were taken, because the iliac wings of both specimens ('A' and 'B') are deformed and incomplete. In the specimen 'A' the pubic symphysis is incomplete too (see: Appendix 9). It was thought better to measure the pelvis in the mounted skeleton and to take down only the right manus of both specimens.

GEOLOGICAL SETTING

The two specimens of *Elephas (Palaeoloxodon) antiquus* come from surfaced diatomaceous layers in a presently inactive deserted fossil flour quarry. The quarry is near Grotte Santo Stefano, in a locality called Campo del Gatto or Gallo. The fossil drift, potent over 25 m, is formed from diatomite with lemonitic lenses; it is rather thin at the top where there are some deformations by load. A volcanic deposit, which is granular in the base and cineritic in the top, rests on the diatomite. Many diatomaceous layers of Viterbo are deposited within small basins, some of which are swampy. The basin of Grotte Santo Stefano is lacustrine, as it is shown from the notable potency of diatomite and from the predominant presence of *Ciclotellae* diatoms (Clerici 1908). Apart from the almost complete skeletons of elephant, several leaf marks, remains of fishes, amphibians and a complete skeleton of *Bos primigenius* BOJANUS, 1827, have been found within the diatomaceous deposit (Fabiani

1950). The *Bos primigenius* skeleton has large dimensions, comparable with those of Italian ones from the Late Aurelian (Faunal Unit [FU] of Torre in Pietra; Caloi & Palombo 1980). The two specimens of *Elephas (Palaeoloxodon) antiquus* come from the top of a diatomaceous layer, at about 2 m below volcanic layers that are part of the volcanic deposit of the Bolsena-Orvieto Volcanic Complex.

The Vulsinian Volcanic District (Northern Lathium-Southern Tuscany) covers an area of about 2200 km². It includes over 100 volcanoes distributed around a sizeable volcano-tectonic depression largely filled by the Bolsena Lake (Fig. 1). On the basis of stratigraphical studies, four volcanic complexes (the Paleo-Bolsena from 600 to 430 kyr (kyr = 1000 year); the Bolsena-Orvieto, which includes two cycles: the first develops from 430 to 350 kyr and the second one from 350 to 320 kyr; the Montefiascone from 320 to 170 kyr and the Latera from 170 to 14,5 kyr) have been identified in the Vulsinian District.

Each complex is characterised by one or more eruptive cycles. Each eruptive cycle consists of an initial phase of the strombolian type with lucite-bearing lava flows, an explosive plinian type phase and a final phase, characterised by volcano-tectonic collapses, followed by hydromagmatic activity. One of the consequences of the large explosive eruptions was the barrage of river valleys to the slopes of volcanic layers. This has generated several volcanic sedimentary basins, which contained ponds, small water bodies or real lakes, in which relatively potent diatomaceous successions and volcano-clastic deposits are formed, generally related to the plinian phase (Nappi *et al.* 1987, Veroli *et al.* 1987). The deposits of 'Campo del Gatto', made during the second activity period of the Bolsena-Orvieto Volcanic Complex, have been formed in this way.

DISCUSSION

Elephas (Palaeoloxodon) antiquus is one of the more common species in the late Middle Pleistocene mammal assemblages of Southern Europe, especially in the Italian faunal complexes related to the FU of Torre in Pietra (isotopic oxygen stage 9; Fig. 4). Various sites (among the richest are Torralba and Ambrona in Spain, Castel di Guido and Polledrara in Lathium/Italy) have been found, in which the palaeoloxodontine specimens can be ascribed to several individuals. The bone assemblage of some of these seems to be natural. To complete earlier taphonomic studies, it might be interesting to determine the sex in addition to the number of the individuals and their age of each faunal association. This in order to see whether the social structure of the population of *Elephas (Palaeoloxodon) antiquus*, in comparison with the social structure of living popula-

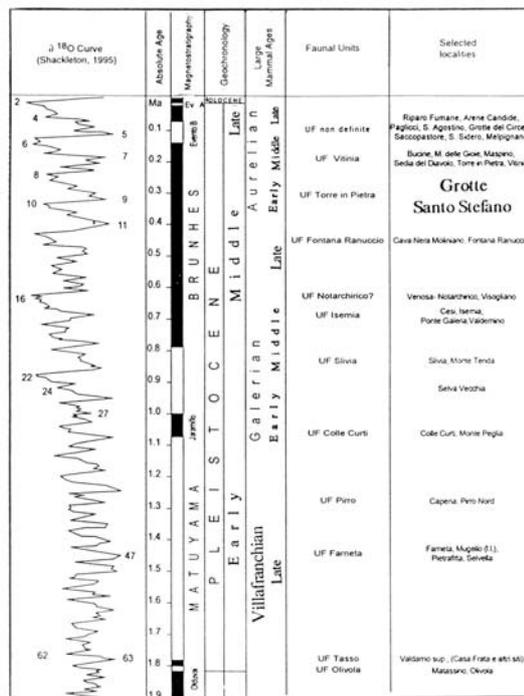


Figure 4 Biocronology of Faunal Units and selected localities of the Italian peninsula from the Early Pleistocene to the Holocene.

tions, is dominated by female individuals (Saunders 1980). Several studies were undertaken to establish which characters may be useful for identifying the gender of fossil elephants. The most indicative characters are generally considered to be: skeletal dimensions (especially those of the skull and tusks), morphology and biometry of pelvis (Deraniyagala 1955; Haynes 1990; Lister 1996). Other possibly useful characters (especially if they go together with more diagnostic characters in the same individual) are the age of fusion of distal extremities (precocious in the female, Roth 1984), morphology and biometry of atlas and epistropheum and morphology of molars (Palombo 1986; Roth 1992).

The molars

In the two specimens ('A' and 'B') both upper and lower molars are very similar in degree of wear, in morphology of enamel loops of worn plates and in dimensions (Fig. 5): maximum length M3 = 280mm in 'A', 290mm in 'B'). The specimen 'A' has M2 larger than B (functional width of M2 = 79mm

in 'A'; 68,5mm in 'B'). In both specimens the push of M3 caused itself some fabric noise (Roth 1992): the first wearing plate and two subsequent are deformed; in the M2's eight functional lamellae and a half of the anterior strongly worn one are present. In both of the specimens the enamel is well plicated, but in 'A' the most worn plications of the plates are sharper than in 'B' and a fold corresponding to the posterior median pillar is still present. This feature is clearer in the lower molars. The plates show an oval shaped occlusal pattern, but the lingual and buccal sides of enamel loop parts are weakly turned backwards. The two specimens are similar in lamellar frequency (M2 = 5,5 both 'A' and 'B'; M3 = 5,5 in 'A'; 6,5 in 'B') and average enamel thickness (it is included between 2,8 and 3). In 'A' the cement is more abundant than in 'B', so that the maximum width is about 80 mm in 'B', whereas the functional width is about the same. Average thickness of enamel, lamellar frequency, and hypsodonty are consistent with the evolutionary degree of *Elephas (Palaeoloxodon) antiquus* of the late

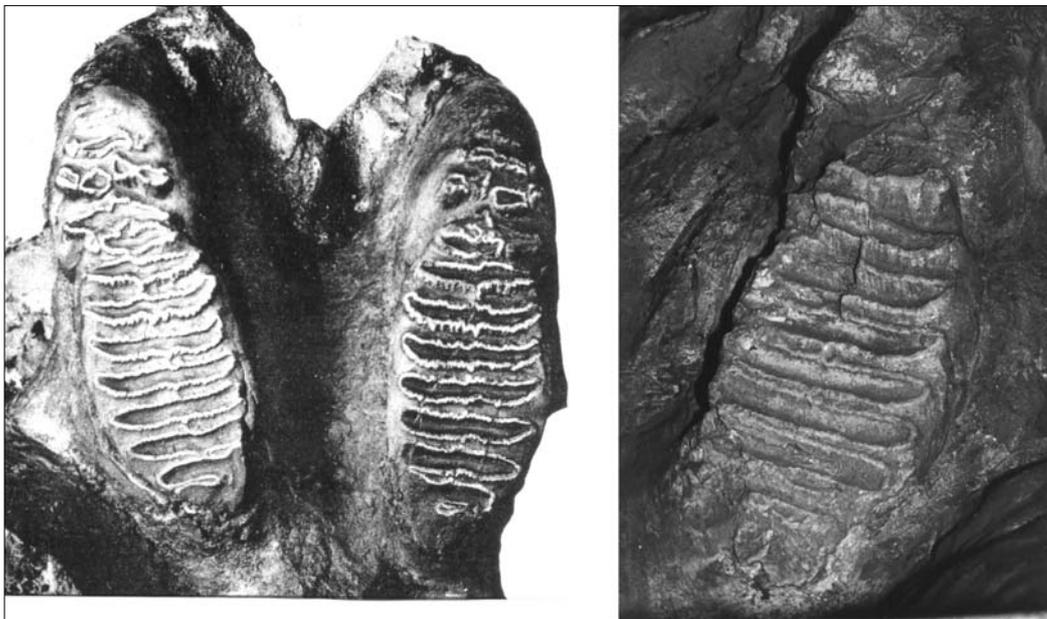


Figure 5 *Elephas (Palaeoloxodon) antiquus*, left: specimen 'A', upper M2 and M3 in occlusal view, right: specimen 'B', upper right M2 and M3 in occlusal view.

Middle Pleistocene of Italy (Palombo 1986, 1995). The observed differences are not enough to justify an attribution to two different sexes. Also, it is considered that in the coeval Italian population (i.e. from La Polledrara and Castel di Guido) two morphotypes are present with the same molars and the same degree of wear. The first one, attributable to a female individual, has thinner and thickly plicated enamel loops and less abundant cement. The second one, attributable to a male individual, has thicker and less thickly plicated enamel loops, and the lamina, especially in lower molars, overhang considerably interposed cement. These characters distinguish males from females in the living species. However, it is possible to observe intermediate morphotypes between the two extreme features. The molars of the examined specimens ('A' and 'B'), even if closer to the male morphotype, do not have all characters typical for male individuals. See Appendix 1.

The carpal bones

Since the beginning of the 19th century, the morphology and structure of carpal bones of proboscideans have been considered by several authors (Baur 1890; Pander 1826; Schlosser 1890) to be useful elements for taxonomic identification of fossil elephants, especially when more diagnostic elements such as teeth or cranial material are lacking. For example a great importance was given to serial (each bone of the distal row corresponds to a bone of the proximal row) or aserial (the medial-lateral width of the lunar exceeds that of the underlying magnum) structure of carpal bones. Trevisan (1949), for example, considered the proboscidean carpal structure as diagnostic for taxonomic and phylogenetic studies. Nevertheless this character is variable in the same phyletic line, like for instance in *Mammuthus* the carpal bones are serial in primitive forms of *Mammuthus meridionalis*, whereas it tends to become aserial in later forms (Lister 1996). On the other hand, Andrews & Cooper (1928) and Dubrovo & Jakubowski (1988) consid-

ered the carpal structure of *Elephas (Palaeoloxodon) antiquus* as typically aserial, whereas it was considered to be serial by Maccagno (1962). The type of carpus structure is closely related to the distribution of load and the way of locomotion. It depends on the load which the skull passes onto the anterior limb by a more or less accentuated ipsycephaly or bathycephaly and on the tusk development. On the other hand, the gait is strictly depending on environmental conditions and some features can have a functional significance. The different carpal structure affects the proportion of development of the articular surfaces of each carpal bone, consequently male or female individuals, living at the same time in a similar environment, can have a different body structure, that can give different morphology and proportions of carpal bones.

Several morphological and biometrical carpal characters have been pointed out to distinguish the females from the males within the same species. Dubrovo & Jakubowski (1988) have examined three skeletons that were found in Poland during last couple of years. Two of them, Jozwin and Ciechanow were more broadly studied, because their bones were completely preserved and they are considered to be male and female, respectively. Actually, our direct comparison with several specimens of *Elephas (Palaeoloxodon) antiquus* show that the structure and morphology of the carpus is characterised by a large individual variability. In spite of this we tried to check the validity of the hypothetical dimorphic characters in the specimens from Grotte Santo Stefano. Dimensions of the carpal bones are given in Appendix 2-8; for illustrations see Figures 6-8.

Navicular The shape of articular surfaces for the radius is narrower in female individuals. The male bone is relatively wider than the female. The width/length ratio of the articular facet for the radius shows that in 'A' and Ciechanow the facet is narrower than in 'B' and Jozwin. In addition, the articular surface for the trapezoid is quadrangular in 'B' and Jozwin,

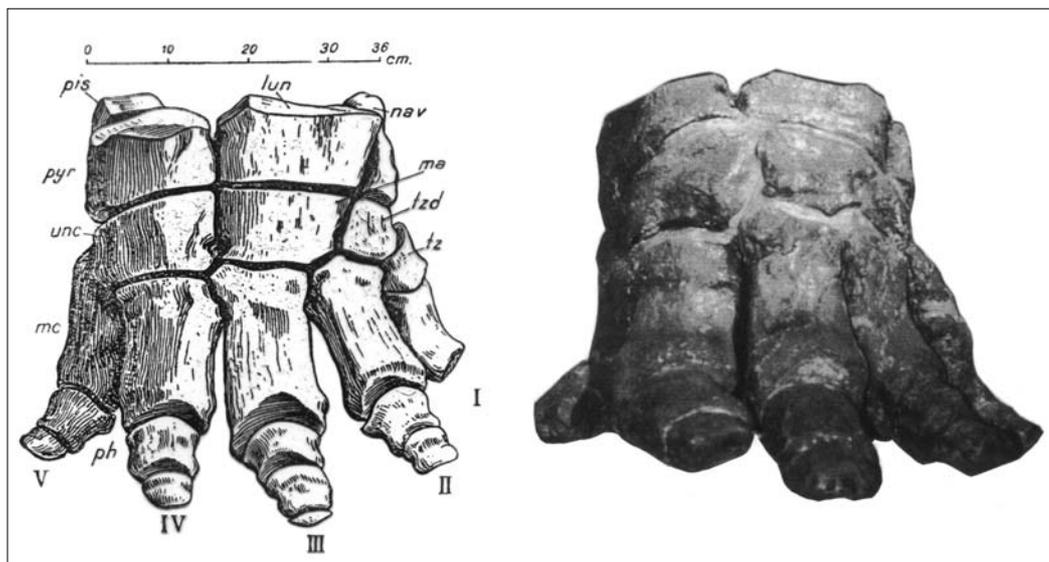


Figure 6 *Elephas (Palaeoloxodon) antiquus*, anterior view of manus. Left: specimen 'A' (after Trevisan 1949, modified), right: specimen 'B'.

whereas it is oval in 'A', Riano (Maccagno 1962) and Ciechanow. See Appendix 2.

Lunar The articulation for the ulna has a trapezoidal form in the lunar bone of the male individuals, the proximal articular surface for the cuneiform is small, flat and semi-lunar. In the female individuals both surfaces are oval. Nevertheless the separation between the articular surface for ulna and radius is sharper in the male than in the female. In the specimens 'B', Riano and Jozwin the articulation for ulna is trapeziform in outline, while in 'A', Upnor and Ciechanow it is extended more oval. The sinus of the medial border is more marked in the male; the outline of the lateral border of the ulnal facet is continuous in the female, sharply delimited by a notch from the border of the radial facet in the male. The two articular facets for the pyramidal are situated anteriorly on the lateral wall. The proximal one is small, semi-lunar in 'B' and Jozwin or elongated oval in 'A', Riano and Ciechanow. In addition, in 'B' and Jozwin have a not much extensive posterior tuberosity, in opposite to the specimen 'A', Riano and Ciechanow. This is proved by

maximum width/height ratio. See Appendix 3.

Pyramidal A large variability characterises this bone. Useful elements to identify the gender may be differences in proportions of the bones and of some articular surfaces. The articular surface for the unciform largely overlaps the hooked process in the male, whereas in the female the overlap is less marked or absent. The shape and extension of articular surface for unciform are similar in 'A' and 'B' as well as in Jozwin. The proportion of cuneiform are variable, it is observable from maximum thickness/height ratio that specimens 'A' and 'B' are taller than Riano, Ciechanow and Jozwin. See Appendix 4.

Pisiform Sculpture on the anterior and proximal side (stronger in the male), shape and dimension of articular surface for pyramidal (the roughness prolongs laterally down of the facet for pyramidal lower in the female than in the male). This surface is very similar in 'A', 'B' and the Jozwin specimen, whereas it is smaller in Riano and Ciechanow. See Appendix 5.

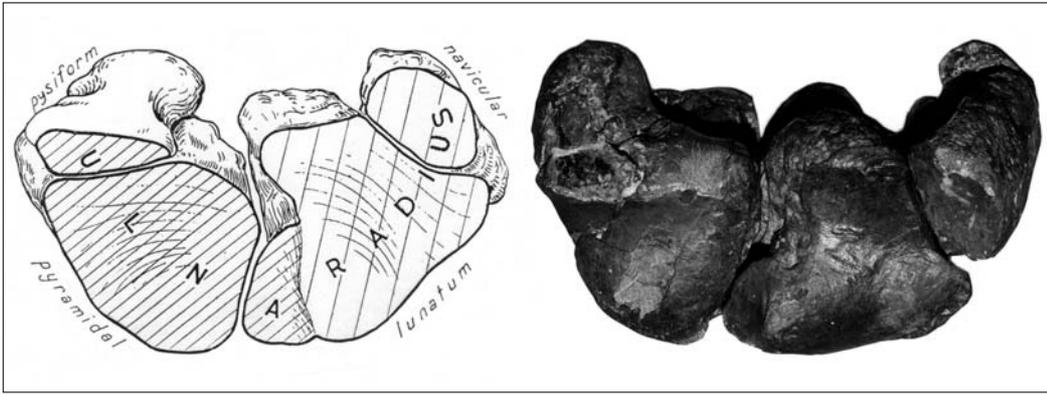


Figure 7 *Elephas (Palaeoloxodon) antiquus*, first line of carpal bones. Left: specimen 'A' (after Trevisan 1949, modified), right: specimen 'B'.

Trapezoid Important are number, shape and dimension of articular surfaces for the magnum. There are three distinct facets in the male, two in the female. In the specimens 'A' and 'B' the articulations of the magnum are confluent in various degrees: in 'B' and Jozwin there are three distinctly separated facets (proximal-anterior, proximal-posterior and distal-anterior); whereas in Ciechanow and Ujnor the anterior, proximal and distal facets are joined. In 'A' and Riano we can see three facets, but they are not remarkably distinguished, and the anterior ones are slightly confluent. In addition, we can observe that the articular surface for the trapezium is broader and more round in 'B' and Jozwin than in 'A', Riano and Ciechanow. See Appendix 6.

Magnum The magnum has a very variable shape and proportions, as showed by dimensional data (see Appendix 7). The extension of the proximal articular facet for the unciform is variable and subrectangular in 'A', 'B' and Ciechanow; whereas the posterior side of this facet is about twice as high as the anterior one in Jozwin and Riano. The distal small articular facet in specimens 'B' and Jozwin is separated from the proximal one, whereas specimens 'A', Riano and Ciechanow have only one anterior facet covering the whole height of the anterior wall surface.

Unciform Shape and proportion of articular surfaces for metacarpal V elongated and straight in the male, short in the female; presence in the male individuals and absence in the female individuals of growth on the

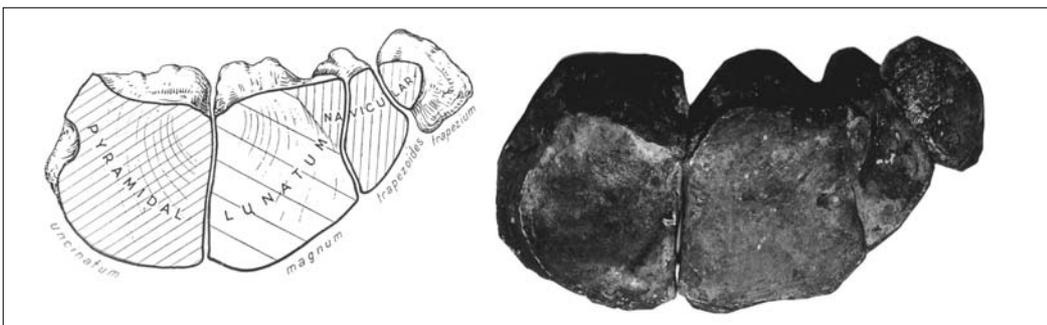


Figure 8 *Elephas (Palaeoloxodon) antiquus*, second line of carpal bones. Left: specimen 'A' (after Trevisan 1949, modified), right: specimen 'B'.

medial surface. Nevertheless, in the unciforms of Grotte Santo Stefano the morphology and proportion of several articular surfaces are quite similar. The only difference is the presence of a groove on the medial surface of 'B'. This feature is in connection with the different morphology of proximal articular surface for the magnum. In the Grotte Santo Stefano specimens the structure is serial in 'A' and aserial in 'B', whereas in Riano it is almost serial. In both Polish specimens most differences with the Italian specimens are the more transversal development of the lunar, whereas the magnum bone decreases proportionally its extension. In connection with different development of the lunar, the first line of carpal bones, observed in dorsal view, present an anterior profile more regularly curved in 'A', Riano and Ciechanow than in 'B' and Jozwin. Nevertheless, the articular facet for the ulna of the lunar bone is more vertical in Ciechanow and Riano, whereas in 'A', 'B' and Jozwin it is oblique and tends to join the

articular surface for the ulna of the unciform. In this way, the ulna has more possibilities to discharge the load also on central finger.

In the Ciechanow specimen aseriality is taken in the right manus by superposition of the lunar bone on the trapezoid bone and no unciform bone; this happens in the left manus of the same individual. In addition it is observable that in 'A', Riano and Ciechanow the anterior edge of the second line of carpal bones is more convex (in comparison with unciform and magnum bones) than in 'B' and Jozwin. See Appendix 8.

The pelvis

The pelvis takes a very important position among the different main categories that may provide information about the gender of proboscidean skeletons. We now know that the morphology of the pelvis of *Elephas (Palaeoloxodon) antiquus* shows a larger pelvic aperture in the females than in the males, but it is very difficult to establish datum-measures. In

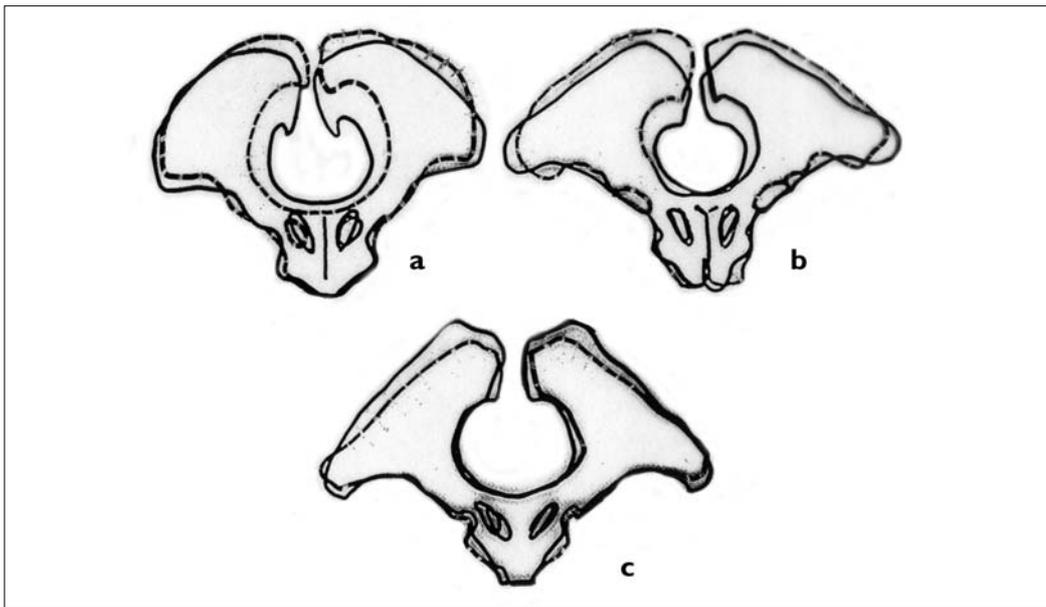


Figure 9 Pelvises in ventral view of **a:** *Elephas maximus* (after Deraniyagala 1955, modified), **b:** *Loxodonta africana* (after Haynes 1990, modified), **c:** *Mammuth primigenius* (after Lister 1996, modified). Interrupted outline: female individuals, continuous outline: male individuals.

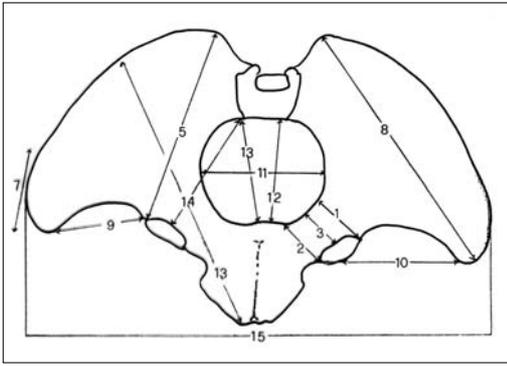


Figure 10 Measurements taken on pelvic bones of *Elephas (Palaeoloxodon) antiquus*. See Appendix 9.

fact the pelvic aperture of Asian and African elephants is characterised by a notable increase of both the distance ileum epiphysis-pubis, and of the transverse diameter. Moreover, in females of Asian and African elephants the wing of the ileum is wider than in the males. In *Mammuthus* (see Figure 9) it is just the opposite (Lister 1996). A series of measurements (Fig. 10) was taken on the two Viterbo specimens ('A' and 'B'; Fig. 11) using flexible tape and calipers. The resulting data are presented in Appendix 9. We have compared the pelvis from Grotto Santo Stefano with pelvis of the Upnor *Elephas antiquus* (Osborn 1942). The three specimens have very similar dimensions and proportions, moreover the Upnor specimen is more similar to a female of *Loxodonta africana*.

The main differences that can be noticed between 'A' and 'B' - taking permanent deformations into consideration - are a lower edge of the iliac wing towards acetabulum in specimen 'B' (Fig. 12). In specimen 'A' the bending radius is smaller and the tuber coxae is in a higher position, in relation to the pubic symphysis, than in specimen 'B'. Specimen 'A' is a little more robust antero-posteriorly. The pelvic aperture of 'A' is somewhat wider both transversally and dorsally than in 'B'. The differences between the two pelvis are not remarkable, nevertheless they give the two a different shape. Moreover, the differences are not easy to explain; in fact the dis-

tinctive elements for the gender determination work in opposite way in the different genera. For example specimen 'A' has a feature that in *Mammuthus* would indicate a female. However, in 'A' the shape of iliac wing and the width of the pelvic aperture are similar to those of a male African and Asian elephant. The pelvic aperture of 'B' appears as male, whereas the shape of wing is similar to male individuals of *Mammuthus* and female of Asian and African elephants. In spite of the ischium of 'B', which is a little more robust than in 'A', the differences between the two specimens do not appear completely sufficient to detect the sex.

CONCLUSION

The analysis of several characters, considered to be essential for gender determination, showed us that the two specimens of the Grotto Santo Stefano seem to be morphologically and biometrically comparable to each other. Especially the skull, the molars and the tusks. For the larger dimensions of the skull 'A' compared to those of Pignataro Interamna, which is considered to be a female by Osborn (1942), and for greater strength of the teeth, Trevisan considered specimen 'A' to be a male individual. Accepting this assumption specimen 'B' could also be a male individual. The morphological and biometrical characters of the pelvis do not contradict the attribution of the two skulls to male individuals. Really the ischium is very little wider in 'A' than in 'B', whereas the tuber coxae in specimen 'B' is more downward turned (as in the female specimens of *Elephas*). In several elephantine lines the trend of the iliac wing is usually rather variable, but in the two specimens of Grotto Santo Stefano the width of the pelvic aperture can be an individual variability. In fact specimens of the subgenus *Palaeoloxodon* MATSUMOTO, 1924 with wider pelvic aperture exist. Considering what is mentioned before, the morphological and biometrical characters of the carpal bones do not appear sufficient to distinguish male from female individuals. The differences in extension and shape of

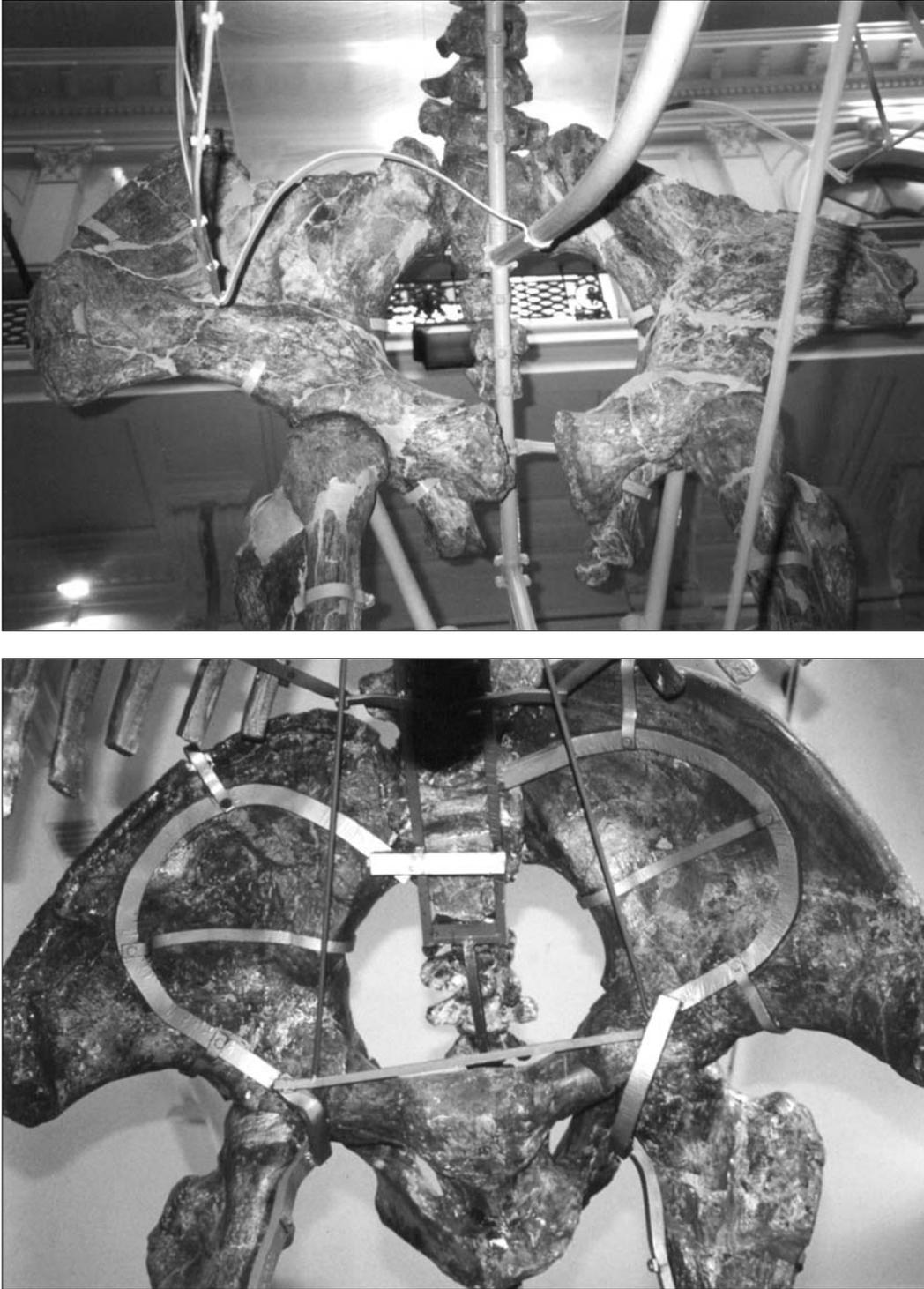


Figure 11 *Elephas (Palaeoloxodon) antiquus* pelvis in ventral view. Above: specimen 'A', below: specimen 'B'.

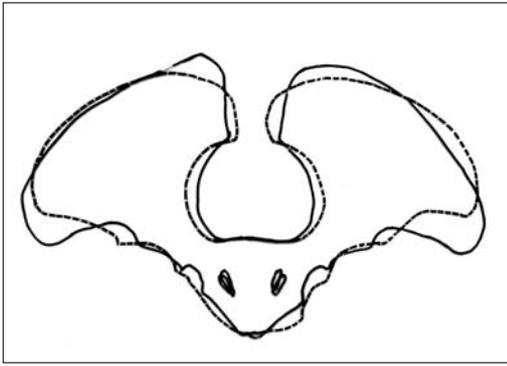


Figure 12 *Elephas (Palaeoloxodon) antiquus*: pelvis in antero-ventral view, adjusted to the same maximum width and corrected for deformations. Interrupted outlined: specimen 'A' (Municipal Museum 'G. Doria', Genova), continuous outline: specimen 'B' (Paleontological Museum, University of Rome).

articular surfaces found between various examined specimens seem due to large individual variability. This applies also to individuals belonging to the same population. Some characters of magnum, trapezoid, pyramidal and especially the trend of outline of the first and second line of carpal bones seem to differentiate in a rather constant way the male from the female morphotypes. Considering these characters as diagnostic for gender identification, we may ascribe 'A' and 'B' to female and male individual respectively. These data are partly in accordance with the pelvic and atlas morphology; in fact in the atlas of specimen 'B' the vertebral spine to attach the muscles is more marked than in the atlas of specimen 'A'. Anyway, the comparative analysis of the two specimens of *Elephas (Palaeoloxodon) antiquus* shows the difficulty to fix diagnostic characters for gender identification. Moreover, other data are necessary to check the validity of some characters, which seem to be diagnostic, if they are present in a conjoint way, such as the pelvic aperture; the width of the iliac wing; the width/length ratio of the navicular articular facet for the radius; the two lunar articular facets for the pyramidal; the morphology of the distal small articular facet of the magnum. Because of not completely proved

validity of these characters, for the moment the differences found between the two specimens 'A' and 'B' cannot be considered conclusive.

ACKNOWLEDGEMENTS

We are grateful to the director dr Poggi of the Municipal Museum 'G. Doria' (Genova) for allowing us to examine the fossil remains and curator dr Raineri and technician mr Borgo of the same museum for support and hospitality. We are also grateful to the director prof. Nicosia of the Paleontological Museum of the University of Rome for access to collections, to dr Manni and to dr Onniboni for help in taking the measurements.

REFERENCES

- Ambrosetti, P., 1968 - The Pleistocene dwarf elephants of Spinagallo - *Geologica Romana* 3: 277-398
- Andrews, C.W. & Cooper, C.F., 1928 - On a specimen of *Elephas antiquus* from Upnor, with further notes on the teeth and skeleton - *British Museum (Natural History)*, Clowes, London
- Averianov, A.O., 1994 - Kutomanov mammoth - *Trudy Zoologicheskogo Instituta* 256: 35-111
- Averianov, A.O., 1996 - Sexual dimorphism in the mammoth skull, teeth, and long bones - in: Shoshani, J. & Tassy, P. (eds.) - *The Proboscidea*, Oxford University Press, Oxford, pp. 260-267
- Baur, G., 1890 - A review of the charges against the palaeontological department of the U.S. Geological Survey and of the defense made by Prof. O.C. Marsh - *American Naturalist* 24: 288-304
- Caloi, L. & Palombo M.R., 1980 - Resti di mammiferi del Pleistocene medio di Malagrotta (Roma) - *Bollettino Serv. Geol. Ital.* 100 (1979)
- De Lorenzo, G. & D'Erasmus, G., 1927 - *L'Elephas antiquus* nell'Italia meridionale - *Atti R. Accad. Scienze Fis. e Mat. Napoli*, s. 2°, 17 (11): 1-105
- Deraniyagala, P.E.P., 1955 - Some extinct elephants, their relatives and the two living species - *Ceylon National Museums Publication*: 24-127
- Dubrovo, I.A. & Jakubowski, G. 1988 - The carpus morphology of the forest elephant (*Palaeoloxodon*) and its significance for taxonomy - *Prace Muzeum Ziemi* 40: 65-95
- Haynes, G., 1990 - The mountains that fell down: life

- and death of heartland mammoths - in: Agenbroad, L.D., Mead, J.I. & Nelson, L.W. (eds.) - *Megafauna and man: discovery of America's heartland - The Mammoth Site of Hot Springs Inc., South Dakota*, Scientific Papers 1: 22-31
- Lister, A.M. 1996 - Sexual dimorphism in the mammoth pelvis: an aid to gender determination - in: Shoshani, J. & Tassy, P. (eds.) - *The Proboscidea* - Oxford University Press, Oxford, pp. 254-259
- Maccagno, A.M., 1962 - Gli elefanti fossili di Riano (Roma) - *Geologica Romana* 1: 33-131
- Nappi, G. *et al.*, 1987 - An evolutionary model for the Paleo-Bolsena and Bolsena Volcanic Complexes: a structural and petrographic study - *Per. Mineral.* 56: 241-267
- Osborn, H.F., 1942 - *Proboscidea* Vol. 1 - The American Museum Press, New York: 802 pp.
- Palombo, M.R. 1986 - Observations sur *Elephas antiquus* Falconer & Cautley du Pleistocène moyen d'Italie: essai d'évaluation des caractères dentaires - *Geologica Romana* 23: 99-110
- Palombo, M.R., 1995 - Gli elefanti del pliocene superiore e del pleistocene dell'Italia centrale peninsulare: alcune considerazioni - *Studi Geologici Camerti*, Vol. spec. 1994 (B): 447-457
- Pander, C.H., 1826 - *Histoire naturelle de la Boukharie - Geologie*: 349-371
- Roth, V.L., 1984 - How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species - *Journal of Vertebrate Paleontology* 4: 126-145
- Roth, V.L., 1992 - Quantitative variation in elephant dentitions: implications for the delimitation of fossil species - *Paleobiology* 18: 184-202
- Schlosser, M., 1890 - Ueber die Modifikationen des Extremitätenskelets bei den einzelnen Säugetierstammen - *Biologisches Zentralblatt* IX: 684-689, 716-729
- Trevisan, L., 1949 - Lo scheletro di *Elephas antiquus italicus* di Fonte Campanile (Viterbo) - *Palaeontographia Italiana* 44 (1948-49): 1-78
- Vezzoli, L., *et al.*, 1987 - Stratigraphy of the Latera Volcanic Complex: proposals for a new nomenclature - *Per. Mineral.* 56: 89-110
- Weithofer, K.A., 1888 - Einige Bemerkungen über der Proboscidier - *Morphologisches Jahrbuch* 14: 507-516

Received 09 July 1999

APPENDIX I Measurements (in mm) of skull, tusk and molar of *Elephas (Palaeoloxodon) antiquus* specimen A and B, compared with the specimen from Pignataro.

MEASUREMENTS OF SKULL, TUSKS AND MOLAR (in mm)	SPECIMEN A c.p. n° 1; C.E. n°35443	SPECIMEN B MPUR/U assembled skeleton	PIGNATARO DeLorenzo & D'Erasmus (1927), Osborn (1942)
SKULL			
Width between parietal eminence	/	c.1500	1500
Distance between distal edge of fan-top of skull	/	c.1000	800
Maximum width of fan	980	c.1130	900
Minimum distance between alveoli of tusks	560	c.570	500
Maximum length of fan	/	850	750
TUSKS			
Length of bending	2200	/	2200
Length of chord	2050	/	/
Circumference to 50 cm from alveolum	570	550	470
UPPER MOLAR 2			
Functional length	175(dx); 179 (sx)	156,5	
Maximum width	87(dx); 86 (sx)	79,87	76
Functional width	79(dx); 79 (sx)	68,5	/
Functional lamina	9(dx); 9 (sx)	8	6
Laminar frequency	5,5(dx);5,5 (sx)	5,5	5,5/6
Average thickness of enamel	2,6(dx); 2,9 (sx)	2,9	
UPPER MOLAR 3			
Functional length	81(dx); 71 (sx)	93,5	
Maximum length	>275(dx);>260 (sx)	>234	
Maximum width	63(dx); 72 (sx)		
Functional width	61(dx); 66 (sx)		
Functional lamina	4(dx); 4 (sx)	5	
Total lamina	19(dx); 19 (sx)	>12	
Laminar frequency	6(dx); 6 (sx)	6	
Height	210 (dx); /	/	

APPENDIX 2 Dimensions (in mm) of the navicular of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Maximus height	163	157	165,5	182	129
Anterior height	/	97	101	/	/
Thickness (a-p) at proximal end	87	89	83	99	82
Thickness (a-p) at midpoint	115	115,5	112	129	92
Thickness (a-p) at distal end	/	127,5	150,5	158	103
Width (m-l) at proximal end	66	64,3	52,5	71	51
Width (m-l) at distal end	84	83,4	70	81	56
Dimensions of articular facet for radius	82(a-p); 45(m-l)	88(a-p); 63(m-l)	82,5(a-p); 55(m-l)	79(a-p); 55(m-l)	70(a-p); 38(m-l)
Dimensions of proximal articular facet for lunar	80(a-p); 42(m-l)	78(a-p); 32,5(m-l)	63(a-p); 24,5(m-l)	89(a-p); 26(m-l)	54(a-p); 22(m-l)
Dimensions of distal articular facet for lunar	/	/	63(a-p); /	89(a-p); 26(m-l)	54(a-p); 22(m-l)
Dimensions of art. facet for magnum, trapezium and trapezoid	110(a-p); 85(m-l)	102(a-p); 74(m-l)	120(a-p); 88(m-l)	125(a-p); 88(m-l)	>78(a-p); 62(m-l)
Minimal distance between articular facets for lunar	45	42	44	48	33
Maximum width/height ratio	70,5	81,2	90,9	86,8	79,8
Maximum thickness/height ratio	51,5	53,1	42,3	44,9	43,4

APPENDIX 3 Dimensions (in mm) of the lunar of *Elephas* (*Palaeoloxodon*) *antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n*1;C.E.n*35443	SPECIMEN B MPUR/U mounted skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Thickness (a-p)	168	170	170	177	133
Maximum width (m-l)	191,5	175	157	171	>126
Height (max)	104	99	101	102	73
Height (medial)	83,5	65	68,7	/	/
Heigth (min.)	72	57	65	/	/
Dimensions of articular for radius	150,5(a-p); 164(m-l)	142(a-p);148(m-l)	144(a-p);143,2(m-l)	138(a-p);137(m-l)	105(a-p);110(m-l)
Dimensions of articular facet for ulna	83,5 (a-p); 52,5(m-p)	68(a-p);46,5(m-l)	78,3(a-p);45(m-l)	>54(a-p);52(m-l)	55(a-p);30(m-l)
Dimensions of distal articular facet	164(a-p);160(m-l)	156(a-p);143,5(m-l)	145(a-p);135,7(m-l)	143(a-p);146(m-l)	114(a-p);113(m-l)
Dimensions of proximal articular facet for scaphoid	99(a-p);40,5(pr-d)	94(a-p);30(pr-d)	75,7(a-p);21,1(pr-d)	84(a-p);32(pr-d)	>79(a-p);28(pr-d)
Dimensions of distal articular facet for scaphoid	83(a-p); 26(pr-d)	68(a-p);21,5 (pr-d)	73(a-p);27(pr-d)	83(a-p);25(pr-d)	65(a-p);>18(pr-d)
Dimensions of proximal articular facet for cuneiform	67(a-p);14,5(pr-d)	50(a-p);12,5(pr-d)	—	50(a-p);13(pr-d)	>40(a-p);13(pr-d)
Dimension of distal articular facet for cuneiform	65(a-p);22,5(pr-d)	>56(a-p);13,5(pr-d)	>54(a-p);22,5(pr-d)	>65(a-p);29(pr-d)	56(a-p);>17(pr-d)

APPENDIX 4 Dimensions (in mm) of the pyramidal of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U mounted skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANÓW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Maximus width (m-l)	245(?)	223	171,5	245	190
Maximus thickness (a-p)	155(?)	184	199	158	—
Height (min.)	72	64	72,5	/	/
Height (max. medial)	88	76	77,3	/	/
Height (max. anterior)	89,5	73	85,5	/	/
Height (max)	123,5	101	93	96	64
Dimensions of articular facet for ulna	142,5 (a-p); 162 (m-p)	120,7 (a-p); 140 (m-l)	125,7 (a-p); 142 (m-l)	115 (a-p); 170 (m-l)	95 (a-p); 128 (m-l)
Dimensions of articular facet for unciform	160,5 (a-p); 199 (m-l)	150 (a-p); 132 (m-l)	132 (a-p); 142,5 (m-l)	136 (a-p); 199 (m-l)	110 (a-p); >125 (m-l)
Dimensions of articular facet for pisiform	67 (pr-d); 94 (m-l)	49 (pr-d); 87 (m-l)	44 (pr-d); 70(m-l)	49 (pr-d); 86 (m-l)	50 (pr-d); 65 (m-l)
Dimensions of articular for metacarpal V	—	—	—	49 (a-p); 92 (m-l)	39 (a-p); 71 (m-l)
Height/Width ratio	50,4	45,3	54,2	39,6	—
Thickness/Width ratio	63,3	82,5	116?	64,2	—

APPENDIX 5 Dimensions (in mm) of the pisiform of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1:C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Height (pr-d)	185	—	183	195	155
Width (m-l) at proximal end	102	90,3	83	93	62
Width (m-l) at midpoint	68	87	64	62	48
Width (m-l) at distal end	—	—	—	59	63
Thickness of proximal end (a-p)	70,5	62	62	70	49
Thickness of distal end (a-p)	—	—	—	59	43
Dimensions of articular facet for pyramidal	87,5(a-p);61,5(pr-d)	76(a-p);59(pr-d)	93,5(a-p);47,5(pr-d)	82(a-p);46(pr-d)	59(a-p);34(pr-d)
Dimensions of articular facet for ulna	83(a-p);38(m-l)	74(a-p);42(m-l)	71,5(a-p);40(m-l)	77(a-p);38(m-l)	54(a-p);31(m-l)
Proximal width/height ratio	55,1	—	45,3	47,7	40
Distal width/height ratio	—	—	—	30,2	40,6

APPENDIX 6 Dimensions (in mm) of the trapezoid of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Maximus cranial width (m-l)	87,5	86,5	88,5	100	72
Maximus thickness (a-p)	152,5	140	145,5	161	128
Maximus height	75,5	69	75,5	93	72
Dimensions of proximal cranial articular facet for magnum	70(a-p); 60(pr-d)	68,5(a-p); 52(pr-d)	55,5(a-p); 58(pr-d)	69(a-p); 57(pr-d)	67(a-p); 58(pr-d)
Dimensions of caudal articular facet for magnum	70(a-p); 39,5(pr-d)	45,5(a-p); 43(pr-d)	63,5(a-p); 41(pr-d)	60(a-p); 42(pr-d)	38(a-p); 30(pr-d)
Dimensions of distal cranial articular facet for magnum	47(a-p); 18,5?(pr-d)	31(a-p); 43(pr-d)	—	38(a-p); 25(pr-d)	—
Dimensions of articular facet for trapezium	108(a-p); 65(pr-d)	84,5(a-p); 55(pr-d)	92,5(a-p); 52,5(pr-d)	92(a-p); 58(pr-d)	69(a-p); 49(pr-d)
Dimensions of articular facet for navicular	119 (a-p); 74,5(m-l)	109(a-p); 65(m-l)	111(a-p); 75(m-l)	143(a-p); 61(m-l)	92(a-p); 48(m-l)
Dimensions of articular facet for metacarpal II	67 (pr-d); 94 (m-l)	49 (pr-d); 87 (m-l)	44 (pr-d); 70(m-l)	49 (pr-d); 86 (m-l)	50 (pr-d); 65 (m-l)
Width/Thickness ratio	57,4	61,8	60,8	62,1	56,2
Height/Thickness ratio	49,5	49,2	51,9	57,7	56,2

APPENDIX 7 Dimensions (in mm) of the magnum of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Maximum thickness (a-p)	187	175,5	160	170	140
Width on cranial side (m-l)	159	134,5	123	127	90
Width on caudal side (m-l)	126	129,5	119	130	100
Height on cranial side (pr-d)	98	92	99	100	83
Height on caudal side (pr-d)	162,5	134	128	147	112
Dimensions of proximal articular facet for unciform	136(a-p);86(pr-d)	122(a-p);67,5(pr-d)	124(a-p);65(pr-d)	132(a-p);76(pr-d)	105(a-p);56(pr-d)
Dimensions of distal articular facet for unciform	94(a-p);23(pr-d)	75(a-p);11,3(pr-d)	66 (a-p); 8?(pr-d)	106(a-p);17(pr-d)	95(a-p);15(pr-d)
Dimensions of articular facet for lunar	158(a-p);147(m-l)	143,5(a-p);142(m-l)	136(a-p);139(m-l)	143(a-p)134(m-l)	111(a-p);100(m-l)
Dimensions of proximal cranial articular facet for trapezoid	121(a-p);60,5(pr-d)	—	65(a-p);55(pr-d)	76(a-p);55(pr-d)	72(a-p);56(pr-d)
Dimensions of distal cranial articular facet for trapezoid	50(a-p);19,5(pr-d)	—	31(a-p);16(pr-d)	34(a-p);18(pr-d)	—
Dimensions of proximal caudal articular facet for trapezoid	67(a-p);40(pr-d)	—	54,5(a-p);49(pr-d)	54(a-p);43(pr-d)	33(a-p);33(pr-d)
Dimension of articular facet for metacarpal II	134,5(a-p);58(m-l)	122,5(a-p);53,5(m-l)	110,5(a-p);46(m-l)	115(a-p);45(m-l)	94(a-p);39(m-l)
Dimension of articular facet for metacarpal III	104(a-p);147,5(m-l)	116,5(a-p);83(m-l)	127(a-p);83,5(m-l)	120(a-p)	102(a-p)
Caudal width/thickness ratio	67,4	73,8	74,4	76,5	67,8
Cranial width/thickness ratio	85	76,6	76,9	58,8	60,1

APPENDIX 8 Dimensions (in mm) of the unciform of *Elephas (Palaeoloxodon) antiquus* specimen A and B compared with specimens from Riano, Jozwin and Ciechanov.

CHARACTERISTICS	ELEPHAS (PALAEOLOXODON) ANTIQUUS, FALCONER & CAUTLEY				
	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton	RIANO (MACCAGNO 1962)	JOZWIN MOK/P/289 (DUBROVO, JAKUBOWSKI 1988)	CIECHANOW MZZ/P/127 (DUBROVO, JAKUBOWSKI 1988)
Thickness (a-p)	157,5	173,5	163	167	140
Width on cranial side (m-l)	178	143	169	167	135
Max. cranial height (pr-d)	104	102	102,5	114	92
Max caudal height (pr-d)	154	120	135	151	114
Dimensions of art. facet for pyramidal	151(a-p);173(m-l)	147(a-p);139,5(m-l)	127(a-p);150(m-l)	136(a-p);143(m-l)	125(a-p);105(m-l)
Dimensions of proximal articular facet for magnum	132(a-p);77,5(pr-d)	120(a-p);62(pr-d)	131(a-p);40(pr-m)	131(a-p);78(pr-d)	105?(a-p);51(pr-d)
Dimensions of distal articular facet for magnum	127,5(a-p);12(pr-d)	>75(a-p);8,2(pr-d)	60(a-p);9,5(pr-d)	103(a-p);14(pr-d)	91?(a-p);11(pr-d)
Dimensions of articular facet for metacarpal III	126(a-p);66(m-l)	120(a-p);40,5(m-l)	122,5(a-p);45(m-l)	123(a-p);42(m-l)	103(a-p);35(m-l)
Dimensions of articular facet for metacarpal IV	138(a-p);125(m-l)	128(a-p);117(m-l)	12,5(a-p);108,5(m-l)	114(a-p);106(m-l)	98(a-p);93(m-l)
Dimension of articular facet for metacarpal V	129(a-p);86(m-l)	116,5(a-p);72(m-l)	115(a-p);84(m-l)	112(a-p);77(m-l)	87(a-p);60(m-l)
Width/thickness ratio	113	82,4	104	100	96,4
Max. height/thickness ratio	97,8	69,2	82,8	90,4	81,4

APPENDIX 9 Measurements (in mm) of pelvic bones of *Elephas (Palaeoloxodon) antiquus* specimen A and B. See Fig. 10.

MEASUREMENTS OF PELVIC BONES (in mm)	SPECIMEN A c.p.n°1; C.E.n°35443	SPECIMEN B MPUR/U assembled skeleton
1 Minimum width of ilium shaft	246	259
2 Anterior-posterior diameter of ischium	128	135
3 Distance between midpoint of acetabulum edge-ischium	162	199
4 Distance between medial edge of acetabulum-ischium	122	161
5 Distance between lateral edge of acetabulum-iliac wing	810	?
6 Thickness lateral edge of iliac wing	139	141
7 Height tuber coxae-iliac wing	325	350
8 Maximum width of iliac wing	1000	1050
9 Distance between lateral edge of acetabulum-ilium	452	470
10 Distance between medial edge of acetabulum-ilium	680	650
11 Maximum diameter of pelvic aperture	582	560
12 Diagonal height of pelvic aperture	440	400
13 Maximum distance between distal edge of pube- proximal edge of ilium	630	/
14 Distance between midpoint of iliac wing-midpoint of acetabulum	118	120
15 Maximum horizontal width of pelvic girdle	181	180

DEINSEA - ANNUAL OF THE NATURAL HISTORY MUSEUM ROTTERDAM
P.O.Box 23452, NL-3001 KL Rotterdam The Netherlands