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Reconstructing the life appearance of a Pleistocene giant: size, shape, sexual dimorphism and ontogeny of *Palaeoloxodon antiquus* (Proboscidea: Elephantidae) from Neumark-Nord 1 (Germany)

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KEY WORDS - Body mass, morphology, sexual dimorphism, ontogeny, shoulder height, Palaeoloxodon antiquus.

ABSTRACT - Between 1985 and 1996, approximately 70 individual Palaeoloxodon antiquus *specimens were recovered from the lacustrine deposits in the open-cast lignite mine of Neumark-Nord 1 (NN1) in Geiseltal, Sachsen-Anhalt, Germany. This study analyses 11 of the most complete skeletons. Because the studied fossil remains were so well preserved, it was possible to determine the elephants' physical appearance, shoulder height, body mass, sexual dimorphism, ontogenetic growth, and biomechanics. These reconstructions also made it possible to highlight the morphological differences of these straight-tusked elephants against other members of Elephantinae. Some of the most peculiar characteristics of* P. antiquus *are the morphology of the skull, remarkably long tusks, elongated forelimbs, a massive torso, and a body mass three times that of male Asian elephants* (Elephas maximus)*, and twice that of extant bush African elephants* (Loxodonta africana)*. Sexual dimorphism of* P. antiquus *was observed to be more accentuated than in extant elephants, most notably in terms of size difference. The long-bone epiphyseal fusion pattern indicates that NN1 males continued to grow until their fifties, while females may have completed their growth at an age comparable to that of male African elephants.*

RIASSUNTO - [Ricostruzione dell'aspetto della vita di un gigante del Pleistocene: dimensione, aspetto, dimorfismo sessuale e ontogenesi di *Palaeoloxodon antiquus* (Proboscidea: Elephantidae) di Neumark-Nord 1 (Germania)] - *Dai depositi lacustri della miniera di lignite di Neumark-Nord 1 (NN1) (Geiseltal, Sachsen- Anhalt, Germania) sono stati recuperati nel corso di circa dieci anni (1985-1996) centinaia di resti scheletri di* Palaeoloxodon antiquus *(~ 70 individui) che rendono questo sito uno dei più ricchi noti in Europa. Questa ricerca, che presenta i risultati ottenuti dallo studio di undici scheletri più o meno completi, è finalizzata a ricostruire l'aspetto fisico degli elefanti di NN1. La completezza e il buono stato di conservazione dei resti hanno consentito non solo una stima accurata della statura (altezza al garrese in vivo) e della massa corporea, ma anche una migliore conoscenza della morfologia, lo sviluppo ontogenetico, ed il dimorfismo sessuale di questi elefanti, nonché di evidenziarne le differenze in morfologia e proporzioni scheletriche rispetto ad altri membri della sottofamiglia Elephantinae. La particolare morfologia del cranio a doppia cupola che presenta nei maschi adulti un'evidente cresta parieto-occipitale, è una delle caratteristiche più peculiari di* Palaeoloxodon*. Lo sviluppo della cresta parieto-occipitale mostra, tuttavia, una variazione intra-specifica piuttosto ampia, e almeno in parte legata alla differenza di genere e di età. Altri caratteri peculiari sono dati dal notevole sviluppo delle difese, da arti anteriori relativamente lunghi, dal dorso massiccio, e da una massa corporea rispettivamente tre e due volte maggiore a quella mediamente riscontrata nei maschi degli attuali elefanti asiatici e in* Loxodonta africana*. Il processo di ossificazione delle epifisi delle ossa lunghe indica che negli individui di sesso maschile di NN1 la crescita può prolungarsi fino al cinquantesimo anno di età, mentre le femmine in genere completano la loro crescita all'incirca alla stessa età degli odierni individui maschili di* L. africana*. Il dimorfismo sessuale osservato negli esemplari di NN1 indicherebbe una maggior differenza dimensionale sia tra i generi in* P. antiquus *che negli elefanti attuali. I dati riguardanti la crescita e le dimensioni raggiunte dagli esemplari di NN1 in funzione dell'età ontogenetica, indicano che sia i maschi che le femmine di* P. antiquus *di NN1 dovevano essere, in termini di dimensioni corporee, prossimi alle ottimali presunte per la specie.*

INTRODUCTION

The Neumark-Nord 1 (NN1) mine in Geiseltal, Sachsen-Anhalt, Germany is home to Europe's greatest collection of straight-tusked elephant fossils. For over ten years, from 1985 to 1996, more than 1500 remains corresponding to 70 individuals were uncovered, some of which have nearly complete skeletons. The fossils were recovered from discrete, bone-rich complexes from five fossil-bearing layers (Lower Gyttja 4, Middle Gyttja 6, Lower shore zone 6.1, Upper shore zone 6.2, Upper Gyttja 7) (Mania, 1990, 2010c; Fischer, 2003, 2010; Palombo et al., 2010; Fig. 1).

The Neumark-Nord mine consists of deposits from the Middle to Late Pleistocene glacial-interglacial climatic cycles. This extraordinarily rich fossil record mainly comes from the Lower, Middle and Upper Gyttja lacustrine layers, which yield diverse flora and fauna (Mania, 2010a; Mania et al., 2010; Meller, 2010 and references therein). The age of the fossiliferous layers, deposited during an interglacial phase, remains subject to debate. Some authors correlated the NN1 interglacial deposits with an "intra-Saalian" warm phase (Mania, 2010b and references therein) or a late Middle Pleistocene interglacial phase (Grübe, 2003). Others have dated the deposits to the Eemian interglacial phase (Litt & Turner, 1993; Litt, 1994; Kolfschoten, 2000). Recent attempts to determine a concrete chronology have provided conflicting results. ESR dating (Schüler, 2010) and climate inferences from stable isotope analyses (Böettger et al., 2009) indicate an Eemian age, while amino acid racemisation (Penkman, 2010), and thermoluminescence (Braun & Pfeiffer, 2002; Zöller, personal communication) indicate a late Middle Pleistocene age, as may be

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supported by the presence of *Apodemus maastrichtiensis* van Kolfschoten, 1985 (Koenigswald & Heinrich, 1999; Heinrich, 2001, 2010).

Regardless of their age, the fossils from NN1 provide invaluable data for determining the morphology of straight-tusked elephants. This research aims to reconstruct the physical appearance of *Palaeoloxodon antiquus* Falconer & Cautley, 1847 by performing a descriptive, morphometric, and biological study of the NN1 fossils. Using new methodological approaches on both individual pelvic bones and complete skeletons, this research will also highlight the main dimorphic traits between sexes during ontogenetic growth.

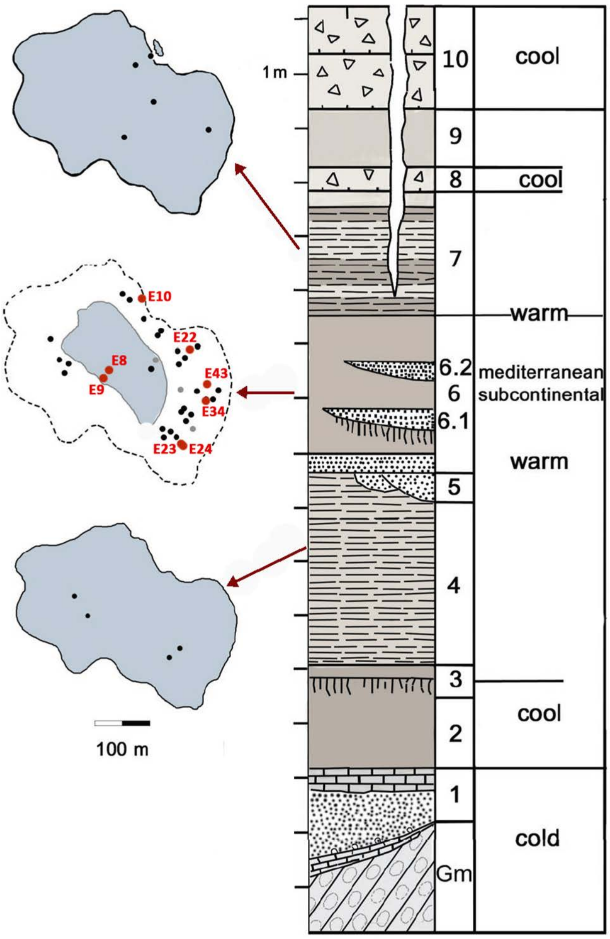

Fig. 1 - Stratigraphy. Sedimentary succession of the Neumark-Nord 1 basin. On the left, the lake at the time of the deposition of the Lower (4), Middle (6), and Upper (7) Gyttja. Labelled dots indicate the position of bone complexes found in the Middle Gyttja (6) and (6.1) levels ("lower shore zone", second regression phase, Middle Gyttja) from which the studied elephants were retrieved. Gm: moraine substrate from Saalian period; (1): fine sands and varved sediments; (2): basin silt; (3): humus band with peat sediments; (4): fine debris with mud and vertebrate deposits of Lower Gyttja; (5): sands and muds deposited in the perilacustrine-littoral zone; (6): silt of Middle Gyttja; 6.1, "lower shore zone", second regression phase and 6.2, "upper shore zone": sands and muds with peat bands and vertebrate assemblage in the perilacustrine-littoral zone; (7): fine debris with mud and vertebrate deposits of lacustrine phase with algae horizons of Upper Gyttja (for geological details see Mania et al., 2010).

MATERIAL AND METHODS

This research focuses on eleven individual straight-tusked elephant (*Palaeoloxodon antiquus*) specimens. The eleven specimens comprise ten more or less complete skeletons and one further pelvic bone (Palombo et al., 2010; Palombo, unpublished data). The fossils were retrieved from eight bone complexes of Middle Gyttja deposits in the NN1 basin. The studied elephants were found in the middle silty clay Gyttja lacustrine deposits of phases 3 and 4 (151-E8, 152-E9, 154-E10A and 154-E10B), and lower shore deposits corresponding to the second lacustrine regression (161-E22A, 175-E23A, 175-E23B, 176-E24A, 176-E24B, 171-E34A, 167-E43A). The gender identification method performed on these fossils is consistent with that already proposed by Palombo et al. (2010) and Marano & Palombo (2013) with the exception of the individual 161-E22A. It was regarded as male by Marano & Palombo (2013), whereas it is here considered a female based on the age, small size, limb-bone robustness, and pelvis proportions and shape (see below for a discussion). As for the other individuals, seven were identified as male (152-E9, 154-E10A, 175-E23A, 175-E23B, 176-E24A, 168-E30, 167-E43A) and four as female (151-E8, 154-E10B, 176-E24B, 171-E34A).

The following skeletons were analysed for this study:

151-E8 (female): partial cranium including maxilla with both M3s, hyoid; complete cervical series (7); complete thoracic series (19); complete lumbar series (4); sacrum; first 10 caudals; all ribs, many of them damaged; right scapula; left scapula (damaged); nearly complete left humerus; partial right humerus; both ulnae; left radius; large portion of the right radius; pelvis; both femora; right tibia; nearly complete left tibia, distal part; right fibula; right tarsals; few metapodial bones.

152-E9 (male): partial skull including maxilla with both M3s; complete mandible; tusks; four cervical vertebrae (C1-C4); one thoracic (T1); four lumbar; sacrum; three caudals (Cd1-Cd3); both scapulae (damaged); left humerus; right humerus, proximal part; left ulna; partial right ulna; left radius; distal right radius; all left side carpal bones; most right side carpal bones; several metapodial bones; nearly complete pelvis; nearly complete left femur; right femur; right tibia; proximal left tibia; right fibula.

154-E10A (male): nearly complete vertebral column; most of the ribs; partial right scapula; partial right humerus; right ulna; right radius; partial femora; left tibia; partial right tibia; several pes elements.

154-E10B (female): sacrum; nearly complete pelvis.

161-E22A (female): skull fragments; mandible; teeth; fragments of tusks; cervical vertebrae; thoracic; lumbar vertebrae; several, mainly broken, ribs; incomplete sternum; right scapula; right humerus; both ulnae; both radii; many carpals and metapodials; nearly complete pelvis; partial femora; right patella; left tibia; partial right tibia; and several tarsals.

175-E23A (male): nearly complete vertebral column; sternum; most of the ribs; complete pelvis; and partial appendicular skeleton elements.

175-E23B (male): partial skull; partial left tusk.

176-E24A (male): partial skull including maxilla with both M3s; nearly complete mandible including both M3s;

partial vertebral column; left scapula; left humerus; other partial limb bone elements; left radius; partial pelvis.

176-E24B (female): complete right scapula and nearly complete left scapula.

171-E34A (female): partial skeleton including long bones and complete pelvic girdle.

167-E43A (male): mandible with m3s; partial vertebral column; several complete ribs; partial scapulae; left humerus; mid portion of the proximal left ulna; left radius; left femur; left tibia; several tarsal bones.

Estimates of body size, age and gender are based on cranial and postcranial skeleton measurements taken by M.R. Palombo and collaborators (E. Albayrak & F. Marano) during two years of research (2008-2009) supported by the Landesmuseum für Vorgeschichte (Halle, Saale) in the framework of the scientific activities planned in view of the exhibition "Elefantenreich Eine Fossilwelt in Europa" (Meller, 2010). Measurements are given in millimetres and were taken with sliding callipers or flexible tapes. In order to estimate the size and appearance of *P. antiquus* from NN1, a rigorous, multi-view skeletal reconstruction was made based on photographs and osteological measurements of the nearly identically sized 152-E9 and 175-E23A male skeletons. The skeletal restoration was made bone-by-bone, applying comparative anatomy of extant proboscideans as in Larramendi (2016). The 175-E23B skull, largely broken into several pieces, but nearly complete, was reconstructed by C. Schauer with the guidance of M.R. Palombo (Fig. 2). We completely reconstructed the shape of the partially incomplete skull of the 152-E9 individual (Fig. 2), based on the morphology of the large preserved fragments and on Schauer's (2010) work. The body volume and body mass of the 152-E9/175-E23B skeleton was estimated using the Graphic Double Integration (GDI) volumetric method (Jerison, 1973; Hurlburt, 1999; Murray & Vickers-Rich, 2004; Taylor, 2009; Larramendi & Palombo, 2015; Larramendi, 2016).

Body size

Several methods, in particular for proboscideans, have been proposed for estimating the height at the shoulder, the body weight, and the relationship between body mass and shoulder height of fossil mammals. The results obtained

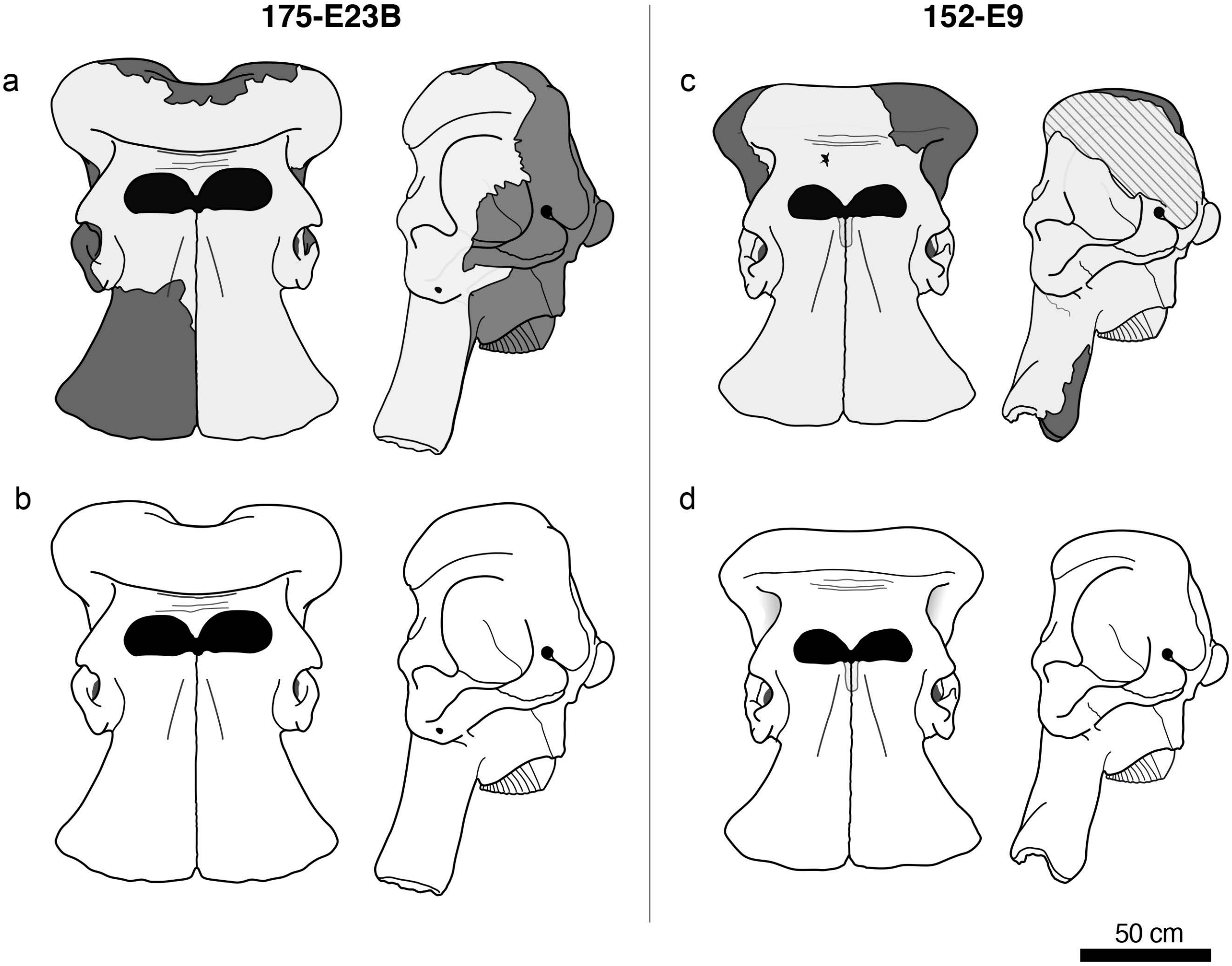

Fig. 2 - *Palaeoloxodon antiquus* from Neumark-Nord 1: restored skulls of 175-E23B (on the left) and 152-E9 (on the right) adult males in lateral and frontal view. a) 175-E23B skull: preserved material is shaded in light grey. b) 175-E23B completely restored skull. c) 152-E9 skull: preserved material is shaded in light grey, whereas the preserved internal cranial pneumaticity is indicated with diagonal lines. d) 152-E9 completely restored skull.

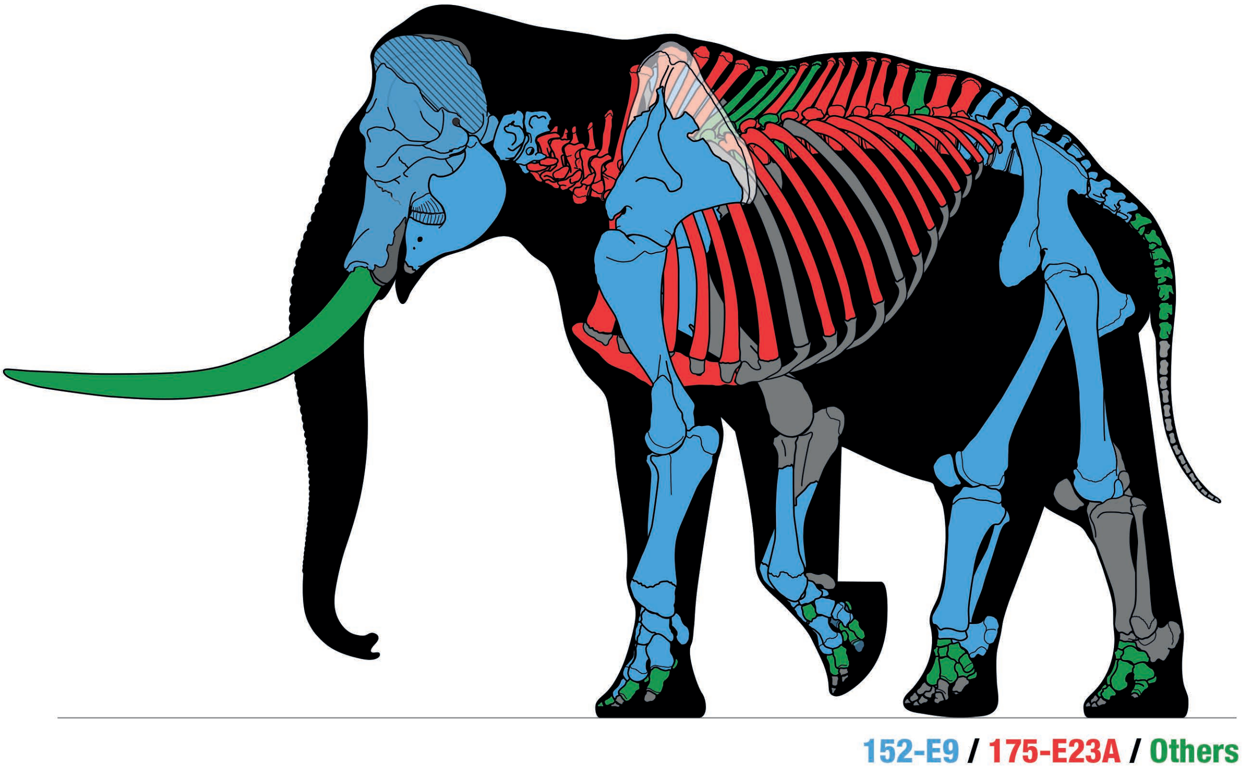

Fig. 3 - (color online) Schematic representation of a *Palaeoloxodon antiquus* skeleton of an adult male from Neumark-Nord 1, composed by means of the best-preserved bones of 152-E9 (blue), 175-E23A (red), as well as multiple skeletal remains of different individuals having scaled (in some cases) to the overall skeleton size (green).

may differ significantly according to the applied method and the elephant species concerned (Osborn, 1942; Hanks, 1972; Laws et al., 1975; Sukumar et al., 1988; Roth, 1990; Christiansen, 2004; Lister & Stuart, 2010; Larramendi, 2016). This highlights the complexity of properly determining the body size of elephants of different gender and ontogenetic age, especially for incomplete specimens. The physical parameters (shoulder height and body mass) of the selected elephants from NN1 were determined for each individual using equations proposed by Larramendi (2016) (see below) and extrapolating the results obtained for the 152-E9 and 175-E23A individuals (Figs 3 and 4).

HEIGHT AT THE SHOULDER (RELATIONSHIPS BETWEEN SKELETAL AND IN VIVO MEASUREMENTS) - The shoulder height and body mass of different individuals have been inferred following the methodology proposed by Larramendi (2016) to estimate the body size of proboscideans. Larramendi (2016) discussed problems about the shoulder height estimations. Osborn (1942), for instance, calculated the skeletal shoulder height of elephants by adding the articular lengths of the foreleg elements, de facto considering the bones as arranged along a straight line, thus slightly overestimating the actual skeletal height. The estimation of the shoulder height based on mounted skeletons may be erroneous. Skeletal shoulder height may be incorrectly estimated if the calculated or measured skeletal shoulder height includes the spines of the thoracic vertebrae. Moreover, the skeletons may sometimes be mounted in an incorrect anatomical position. If so, the percentage of the length of each bone with respect to the shoulder height can neither be correctly calculated, nor be used as an effective value for inferring the shoulder height of a fossil elephant by means of its isolated limb bones (e.g., Shpansky, 2008; Lister & Stuart, 2010; Athanassiou, 2011; Bajgusheva et al., 2011).

Larramendi (2016) scrutinised this issue by analysing more than 20 different proboscidean species. The results obtained show that the skeletal shoulder height of derived proboscidean species, such as Elephantini, can be calculated either through multiplying the sum of the articular length of each forelimb by a factor of 0.98 or through multiplying the sum of the maximum length of long bones by 0.95. Moreover, the author observed that the height of the fore elephantid autopodium is usually 50% of the total length of the radius, and twice the length of the third metacarpal. To calculate the in vivo height at the shoulder for the NN1 elephants following Larramendi's (2015, 2016) method - according to which the true shoulder height of extant elephants, is about 5.5% more than its skeletal shoulder height - it is necessary to add the skin at the back and sole of the foot, the thin layer of cartilage in the bone joints, and the soft tissues - such as muscles, fat and synovial joints - to the measured skeletal shoulder height (e.g., Osborn, 1942; Roth, 1990; Christiansen, 2004; Larramendi, 2015, 2016).

BODY MASS - One of the most common methods for estimating body mass is based on regression equations resulting from measurements of selected skeletal elements

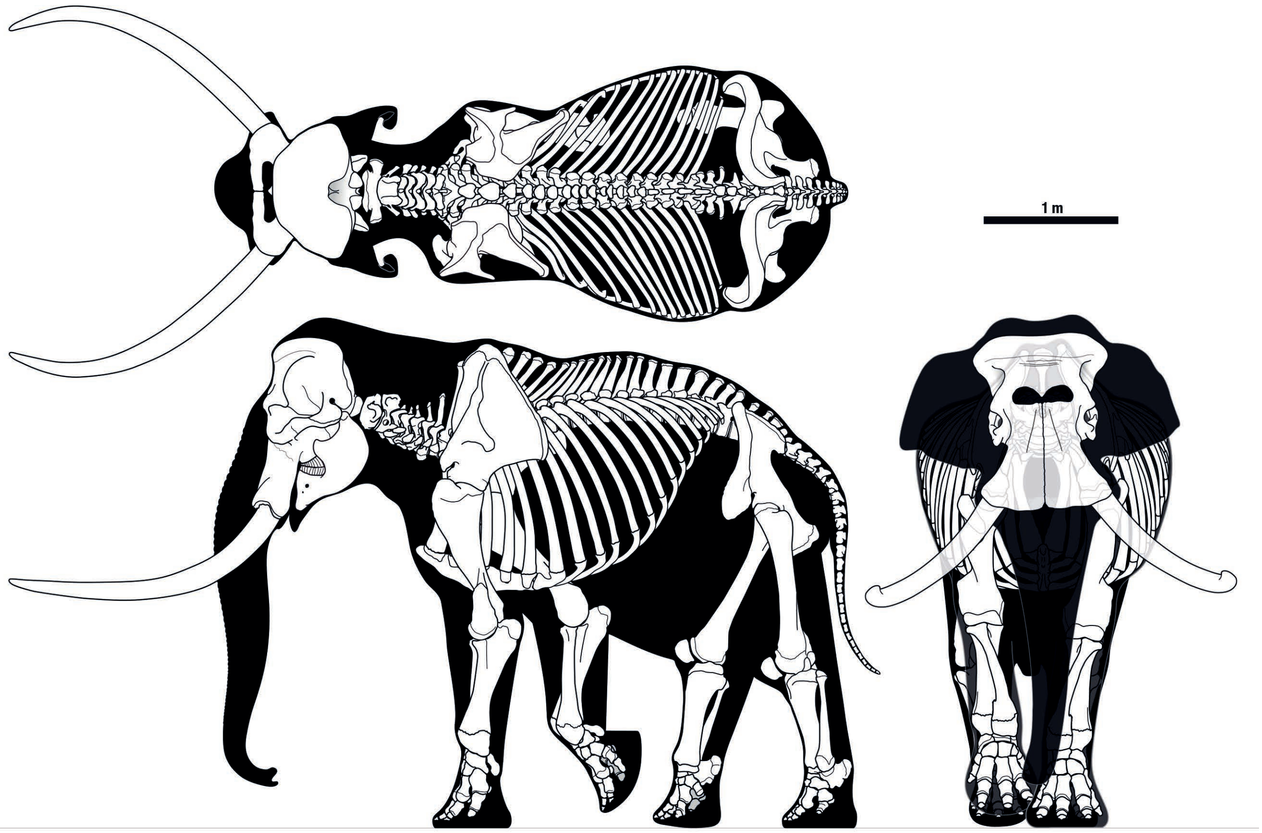

Fig. 4 - Rigorous multi-view skeletal restoration of *Palaeoloxodon antiquus* from Neumark-Nord 1, mainly based on 152-E9 and 175-E23A skeletons.

of living species. In particular, long bone dimensions have been considered by most authors as quite reliable body mass predictors for herbivores of medium to very large sizes, although each species or group of species needs its own particular equation, in accordance with its skeletal structure. Several researchers have shown, however, that allometric methods may be not accurate enough for estimating the body mass of an extinct species (Paul, 1997; Hulburt, 1999; Larramendi, 2016) whose body mass/ bone dimension relationships are different from those of their extant relatives. This is also true of *P. antiquus* as suggested by the strong inconsistencies among body mass estimates obtained for a single individual even when using measurements with the best predictive indices (e.g., Marano & Palombo, 2013). The body masses of some extinct elephants have also been calculated by means of their shoulder height (e.g., Palombo & Giovinazzo, 2005), although this method is highly dependent upon a correct estimate of this parameter (see above). Larramendi (2016) recently proposed a new formula for the estimating the body weight of *P. antiquus* from shoulder height:

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

where BM is body mass in kg and SH is the shoulder height of a live individual in centimetres.

Herein, we have applied the GDI volumetric method, not only because it produces more accurate results (provided that models are technically correct and based on the most complete and well-preserved specimens) (Haynes, 1991; Paul, 1997; Hulburt, 1999; Larramendi, 2016), but also because it may provide the body proportions and life appearance of the restored animal.

Age and gender determination

Marano & Palombo (2013) estimated the ages of many *P. antiquus* from NN1 based on the progress of eruption and degree of wear of lower and upper molariform teeth compared to extant elephants (Laws, 1966; Roth, 1982; Jachmann, 1988; Roth & Shoshani, 1988) and on the status of the epiphyseal-diaphyseal junction of long bones (Roth, 1984; Haynes, 1991). However, both the huge size of *P. antiquus* and a later fusion of the bone epiphysis in comparison with extant elephants (see below) suggest that extinct straight-tusked elephants had a longer lifespan than living species. *P. antiquus* might have had a longevity of 68 years or more, based upon the equation of Blueweiss et al. (1978) and assuming a lifespan of 60 years for *Loxodonta africana* Blumenbach, 1797. Recent findings suggest that the maximum lifespan of *L. africana* is between 70 and 75 years (Lee et al., 2012; Stansfield, 2015; Haynes, 2017). Thus, *P. antiquus* could have had a life expectancy of more than 80 years. However, in this study we consider *P. antiquus* to have a maximum lifespan of 75 years, as it was suggested for *L. africana*.

Accordingly, the ages of the studied individuals, inferred by Marano & Palombo (2013), have been reconsidered taking into account the most recent ontogenetic studies made on African bush elephants (*L. africana*) (Lee et al., 2012; Stansfield, 2015; Haynes,

152-E9/175-E23A	
Body part	Volume (l)
Tusks (pair)	90
Trunk	~280
Head-Neck-Body	8107
Fore limbs (pair)	630
Hind limbs (pair)	406
Ears (pair) and tail	~31
Total volume	9544
Total mass (kg)	9522

Tab. 1 - Volumes and body masses of *Palaeoloxodon antiquus* 152-E9/175-E23A specimen, estimated by Graphic double integration. Masses assume a specific gravity of 1.8 for the tusks and 0.99 for the rest of the body (Larramendi, 2016).

2017). The gender determination proposed in previous works (Palombo et al., 2010; Marano & Palombo, 2013), has been revised providing new data including pelvis proportions.

RESULTS

Neumark-Nord skulls

The *P. antiquus* skulls recovered from NN1 are among the best-preserved known to date. Noteworthy is the completeness of the 152-E9 skull, which is entirely preserved except for some fragments of the parietals and a few parts of temporal bones (Fig. 2).

Additionally, the anterior portion of the 175-E23B skull is also almost entirely preserved (Fig. 2).

The preserved materials from NN1 show that a lateral view of the skull vertex appears rectangular because of the development of the post-temporal crest (a ridge running vertically at the lateral margin of the nuchal plane), a character that distinguishes *Palaeoloxodon* from the *Elephas* genus. In addition, the premaxillaries are fan shaped and extremely wide distally, the jugal arch is relatively slender, and the parieto-occipital bosses (swellings formed on the right and left sides of the occipital and parietal), are large and moderately inflated posteriorly. Of particular interest is the specialized anatomy of the forehead, which is sometimes characterised by the occurrence of a strong parieto-occipital crest. The 152-E9 and 168-E30 skulls have prominent squama frontalis and weak but relatively defined parieto-occipital crests. These skulls show features that match those characterising, according to Saegusa & Gilbert (2008), the so-called "Stuttgart morph". Conversely, in the very large 175-E23B skull, the frontal bone is not well antero-posteriorly extended and the parieto-occipital crest is well developed, similar to skull morphologies of some adult Italian male specimens, including the La Polledrara di Cecanibbio specimens (Anzidei et al., 2012), and the Indian *P. namadicus* Falconer & Cautley, 1846 specimens.

Evidence from NN1 confirms that ontogenetic growth and sexual dimorphism highly influence the development of the parieto-occipital crest, however, the evidence also suggests that other factors (e.g., environmental), which are still difficult to properly define, contribute to its variation.

Body size

The rigorous skeletal reconstruction, based on two male individuals (152-E9/175-E23A) of similar age and size, depicts an elephant 363 cm at high at the shoulder including flesh with a body mass of 9522 kg (Tabs 1 and 2). A body mass of 9802 kg was obtained by applying the equation in Larramendi (2016). This is only 3% more than the estimated body mass obtained from the volumetric restoration, and such consistency supports the accuracy of the results obtained by both methods.

The sizes of 152-E9 and 175-E23A are about twice the average size of *Elephas maximus* Linnaeus, 1758, and 50% more than *L. africana* males (Larramendi, 2016); however, both individuals are smaller than the NN1 males 167-E43A and 154-E10A, yet have a similar age (about 47 African Equivalent Years, AEY). Indeed, 167-E43A and 154-E10A are considerably bigger. Their bone dimensions suggest animals around 390 cm high at the shoulders and weighing about 12 tonnes (Tab. 2). In

Individual	152-E9	175-E23A	175-E23B	167-E43A	176-E24A	176-E24B	154-E10A	161-E22A	154-E10B	151-E8	171-E34A
Gender	Male	Male	Male	Male	Male	Female	Male	Female	Female	Female	Female
Age (AEY)	47	44	~50	47	50	43	47	24	24	37	39
Skeletal shoulder height	344	-	-	365e	359	-	-	276	-	250	280e
Shoulder height in the flesh	363	363e	~400	385e	379	~300	395e	291	+300	264	295e
Estimated body mass (1)	9.5	9.5	~12.7	~11.4	~10.7	~5.5	~12.2	5	+5.5	3.9	4.5
Estimated body mass (2)	9.8	9.8	13	11.6	11.1	5.6	12.5	5.15	5.6	3.9	5.4

Tab. 2 - Physical parameters (height, weight, sex and age) of 152-E9, 175-E23A, 175-E23B, 176-E24A, 167-E43A, E154-E10A male specimens and 151-E8, E154-E10B, 161-E22A, 176-E24B, 171-E34A female specimens. Body mass in tonnes (1): calculated from volumetric models or based on the extrapolation of the results obtained in the 152-E9/175-E23A restoration. Body mass in tonnes (2): calculated from shoulder height after Larramendi (2016) ($BM = 3.63 \times 10^{-4} \times SH^{2.903}$). Shoulder heights are given in cm; e: estimated.

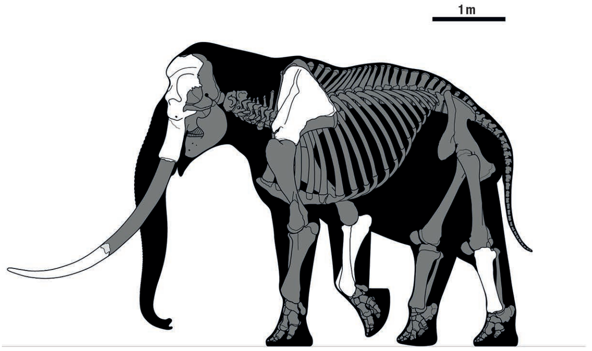

Fig. 5 - Skeletal restoration based on bones (in white) of 175-E23B (tusk, skull and scapula) and 154-E10A (ulna, radius and tibia) of about the same size.

152-E9, however, the distal epiphysis of radius/ulna and the caput femoris, are still incompletely fused, indicating that the animal did not complete its growth; thus, its weight at a later stage of life may have surpassed 10 tonnes. The large size of adult NN1 males is confirmed by the dimensions of two specimens (a skull and a scapula found in the bone place E23), likely belonging to the largest elephant recorded at NN1 (175-E23B in Marano & Palombo, 2013). Both are about 10% larger than those of 152-E9, suggesting an animal of at least 400 cm at the shoulders (Figs 5 and 6). Assuming isometry, this very large elephant would have weighed about 12.7-13 tonnes (Tab. 2).

The female individuals from NN 1 are much smaller. The skeletal dimensions suggest that healthy females reached a height at the shoulders of about 300 cm and a weight of about 4.5-5.5 tonnes (Tab. 2). In the largest NN1 females represented by single bones - 176-E24B by a completely ossified scapula too small to belong to a male, and E10B by a large pelvic girdle - the estimated shoulder height in life may have been more than 300 cm and the weight around 5.5 tonnes.

Gender determination and dimorphic traits

Results obtained show that pelvic proportions greatly differ in male and female elephants from NN1 (Tabs 3 and 4). The ratio between the maximum horizontal pelvis width and the minimum width of the ilium shaft and the ratio between the maximum horizontal width of pelvic aperture and the minimum width of ilium shaft are, respectively, significantly higher and lower in males than in females (Tabs 3 and 4). Values obtained for the NN1 specimens, however, fall in the variation ranges estimated for extinct Elephantini (e.g., Lister & Agenbroad, 1994; Lister, 1996; Göhlich, 2000; Palombo & Villa, 2003).

Other dimorphic characters have been already detected in NN1 elephants (Marano & Palombo, 2013). The mandible morphology of 175-E23A and 176-E24A individuals, for instance, matches the dimorphic traits observed in extant elephant males (Todd, 2010a; Marano & Palombo, 2013), and our observation confirms that, in the vertebrae, the atlas of males has a more robust dorsal tubercle on the arcus dorsalis than females, and that the odontoid process of epistropheus is more developed in males than in females.

It is worth noting that, according to available data, the scaling in size between males and females as calculated for each limb bone seems to differ, suggesting some dimorphic differences in proportion. In NN1 males, the humerii maximum lengths (152-E9: 1220 mm, 176-E24A: 1270 mm, 167-E43A: > 1230 mm) are up to 36% longer than that of the young 161-E22A (934 mm) individual (previously regarded as a male and herein considered as a female, see below), the radii lengths (152-E9: 882 mm, 176-E24A: 910 mm, 167-E43A: 934 mm, 154-E10A: 965 mm) are up to 47% longer than in females (171-E34A: 760 mm, 161-E22A: 685 mm, 151-E8: 657 mm), the femur length (167-E43A: 1398 mm) is more than 30% longer than in females (171-E34A: 1070 mm, 151-E8: 1040 mm) and tibiae lengths (154-E10A: 914 mm) are at least 43% longer than in females (161-E22A: 638 mm, 171-E34A: 624 mm, 151-E8: 576 mm) (Supplementary

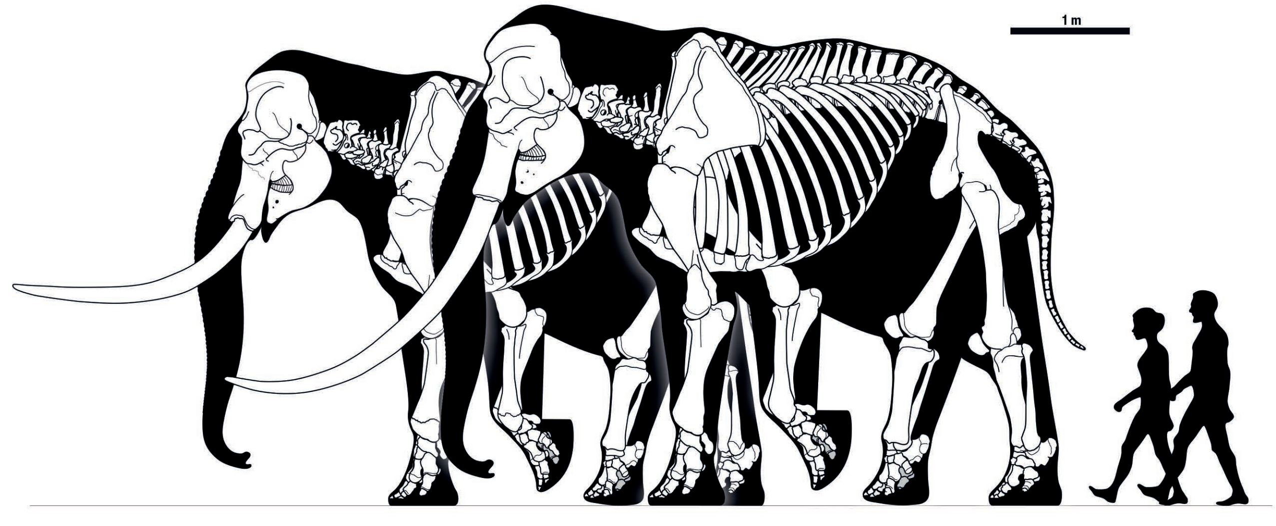

Fig. 6 - Size comparison between 152-E9/175-E23A (smaller) and 175-E23B (larger). The human silhouettes are 165 and 180 cm tall, respectively.

Pelvis	152-E9	175-E23A	161-E22A	151-E8	171-E34A	E154-E10B
Side	1740e	1730	1435e	~1400	1230	1430e
Maximum width	1214	-	855	1000e	-	-
Maximum length	1060	-	872	844	780	1000
Maximum ilium length	277	287	196	152	146	195
Minimum ilium width	540	584	506-550e	470	550	550e
Maximum horizontal width of pelvic aperture	448	-		520	552	564
Maximum height of the acetabulum	198	200	-	170	151	186
Maximum length of the acetabulum	230	220	-	164	144	181
Maximum thickness of tuber coxae	260	-	172	110	158	-
Maximum horizontal width between outer margins of the acetabula	920	960	770c	784	730	776

Tab. 3 - Measurements of pelvic girdles of *Palaeoloxodon antiquus* male (152-E9, 175-E23A) and female 151-E8, 161-E22A, 171-E34A, E154-E10B) individuals from NN1. Measurements are given in mm; e: estimated.

Online Material 1). These differences are generally smaller in extant elephants (Supplementary Online Material 2).

The gender of 161-E22A young elephant - Marano & Palombo (2013) regarded 161-E22A as a male based on the mandible and pelvis morphology. This elephant is a young individual of about 24 AEY according to the progression of the lower teeth (worn m1 with the last 5 plates in an advanced state of wear, m2 with 10 plates in use, and alveolus of m3 open with some isolated plates in an early stage of formation). The age is confirmed by the state of fusion of the epiphyses in long bones (humerus with fused distal and partially non fused proximal epiphyses, radius and ulna with fused proximal epiphyses but incompletely fused distal epiphyses, femur with partially fused distal epiphysis and non fused caput femoris, tibia with partially fused proximal and distal as partially fused distal edges of the scapula and pelvic iliac wings). The small size of the skeleton clearly suggests that the bones belong to a female, contrary to the conclusions by Marano & Palombo (2013). The pelvis of the E10B female, which is about as old as 161-E22A, has roughly the same size and proportions (Tabs 3 and 4). In addition, some tibiae and femora of the NN1 sample are believed to belong to female individuals in their twenties (Palombo & collaborators, unpublished data), which are comparable in size and robustness with 161-E22A.

Age and long bone ossification sequence

The inferred ontogenetic ages (Tab. 2) highlight some differences in tooth eruption and long bone epiphyseal fusion between *P. antiquus* and extant elephants, especially with regard to females. Based on the stage of eruption and wear of teeth, the epiphyseal-diaphyseal fusion of long bones occurred later in *P. antiquus* males than in *L. africana* (Roth, 1984; Haynes, 1991), although these differences are considerably less accentuated when comparing the results with Haynes' (2017) recent study. Following Roth (1984) and Haynes (1991, 2017), for instance, the femur head of African elephants is completely fused to the diaphysis when males are between 36 and 43 years old. Conversely, in the 152-E9 skeleton the femur head is not totally fused despite the advanced wear stage of the lower teeth, which suggests an age of about 47 AEY (XXV Laws' group). It is interesting to note that the females of *P. antigus* from NN1 show an ossification pattern similar to that of *L. africana* males, and clearly different from that of *L. africana* females. In 161-E22, a female of about 24 AEY (XV Laws' group), for instance, the ossification degree of long bones looks like that of a *L. africana* male. In particular, the distal epiphyses of femur and tibia are not fused, while in *L. africana* females they generally fused to the diaphysis in the early twenties (Haynes, 1991, 2017). The hypothesis that differences in the ossification sequence between *P. antiquus* and bush African elephants may be somehow related to their notable differences in size cannot be ruled out.

DISCUSSION

The body proportions and the body profile in any land vertebrate directly depend on the cranial and postcranial bone dimensions, ratios and morphology (Paul, 1997).

Pelvis	152-E9 (male)	175-E23A (male)	161-E22A (female)	151-E8 (female)	171-E34A (female)	E154-E10B (female)
1:5	0.159	0.166	0.137	0.109	0.119	0.136
1:3	0.31	0.338	0.353	0.336	0.447	0.385
2:3	0.83	-	-	1.11	1.0	1.03
3:5	1.95	2.03	2.58-2.81	3.09	3.77	2.82
2:5	1.62	-	-	3.42	3.78	2.89

Tab. 4 - Comparison of different ratios in *Palaeoloxodon antiquus* pelvic girdles (152-E9, 175-E23A, 161-E22A, 151-E8, 171-E34A, E154-E10B) after Lister (1996). 1: maximum horizontal pelvis width; 2: diagonal height of pelvic aperture; 3: maximum horizontal width of pelvic aperture; 4: width of ilium wing; 5: minimum width of ilium shaft.

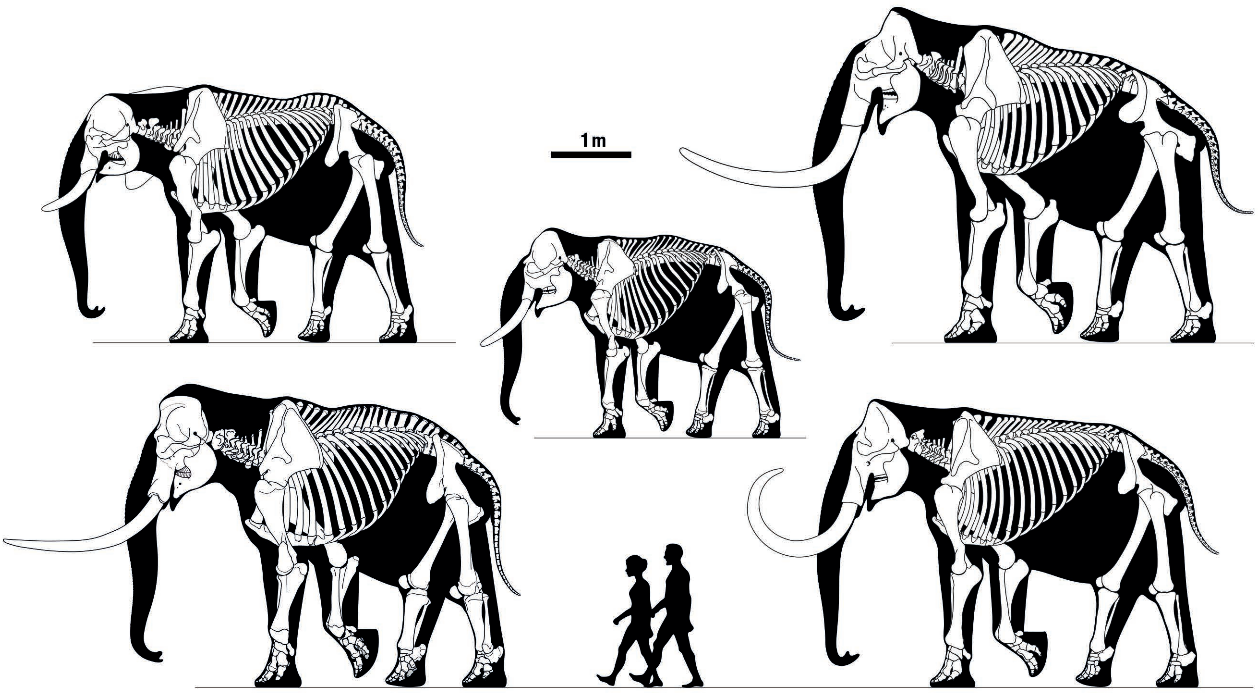

Fig. 7 - Rigorous skeletal restorations of some extant and fossil Elephantinae drawn to scale, and in the same posture in order to highlight the differences in body proportions and skeletal structure among species. *Loxodonta africana* (young adult bull) - AMNH 3283 (top left), SH: 323 cm, BM: 6.15 tonnes. *Elephas maximus* (young bull) - A. 1225 (centre) SH: 253 cm, BM: 3.1 tonnes. *Mammuthus meridionalis* (old bull) - Scoppito (top right) SH: 397 cm, BM: 10.7 tonnes. *Palaeoloxodon antiquus* (adult bull, still growing) - 152-E9/175-E23A (bottom left) SH: 363 cm, BM: 9.5 tonnes. *Mammuthus primigenius* (adult bull) - Siegsdorf (bottom right) SH: 349 cm, BM: 8.2 tonnes. Data from Larramendi (2016). The human silhouettes are 165 and 180 cm tall, respectively. SH: height at the shoulder; BM: body mass.

The shape and proportions of the skeleton of the male *P. antiquus*, as suggested by the result obtained from NN1 specimens, distinguish it from the extant elephants *L. africana, L. cyclotis* Matschie, 1900 and *Elephas maximus,* and additionally from *Mammuthus* representatives (Figs 7-9; Tab. 5).

Body proportions and life appearance of Palaeoloxodon antiquus *from NN 1*

THE INTRIGUING QUESTION OF THE DEVELOPMENT OF THE PARIETO-OCCIPITAL CREST - The morphology of the *Palaeoloxodon* skull is somehow unique among Elephantinae. It is characterised by a flat dorsal profile and a double-domed vertex (Saegusa & Gilbert, 2008; Palombo et al., 2010). The most peculiar feature of the genus is the strong parieto-occipital crest, however, which shows a notable intraspecific variability relating, among other factors, ontogenetic age and probably gender. Juvenile skulls, for instance, lack a parieto-occipital crest, and the latter is usually less developed (or absent) in adult females (Palombo & Ferretti, 2005, 2010; Ferretti, 2008). In adult males, the shape and position - such as the relative shifting - of the parieto-occipital crest towards the nasals, as a result of the anterior bending of the occipital squama of the parieto-occipital crest, differ in the various specimens from infolded (overhanging a deep ventral transverse furrow) to a nearly vertically step-like structure, from close to the nasals (obliterating the fronto-parietal plane) to dorsally displaced with a relatively long fronto-parietal plane.

Saegusa & Gilbert (2008) recognise two distinct morphotypes among Eurasian palaeoloxodontine elephants that, in their opinion, would be represented by a German "primitive Stuttgart morph", and a "more derived *namadicus* morph", epitomised by the Italian skulls from La Polledrara di Cecanibbio (Anzidei et al., 2012). The distinctive morphological traits of the alleged "*namadicus*" morph would be the strongly developed parieto-occipital crest, the anterior surface of the nuchal plane visible in frontal view, the strong "nuchal crest" running along the ventral margin of the parieto-occipital crest, and the rounded lateral margins of the external choanes.

In Italian skulls (e.g., from La Polledrara when minor deformations are taken in consideration, and the well-preserved skulls of the insular species from Puntali cave, Sicily) the dorsal surface of the nuchal plane is not always clearly visible in frontal view, and the shape of the external nares is highly variable (Ferretti, 2008; Anzidei et al., 2012). Although German specimens generally do not show the extreme morphology shown by the so-called "*namadicus*" morphotype, the development of the parieto-occipital crest in male skulls may vary as demonstrated by the morphology of the Neumark-Nord 1 specimens, as already noted by Palombo et al. (2010).

THE GENERAL SHAPE OF *PALAEOLOXODON ANTIQUUS* FROM NN1 - The most peculiar aspect of *P. antiquus* from NN1 is the high position of the shoulders, as documented by the limb-bone ratios. The proportionally longer

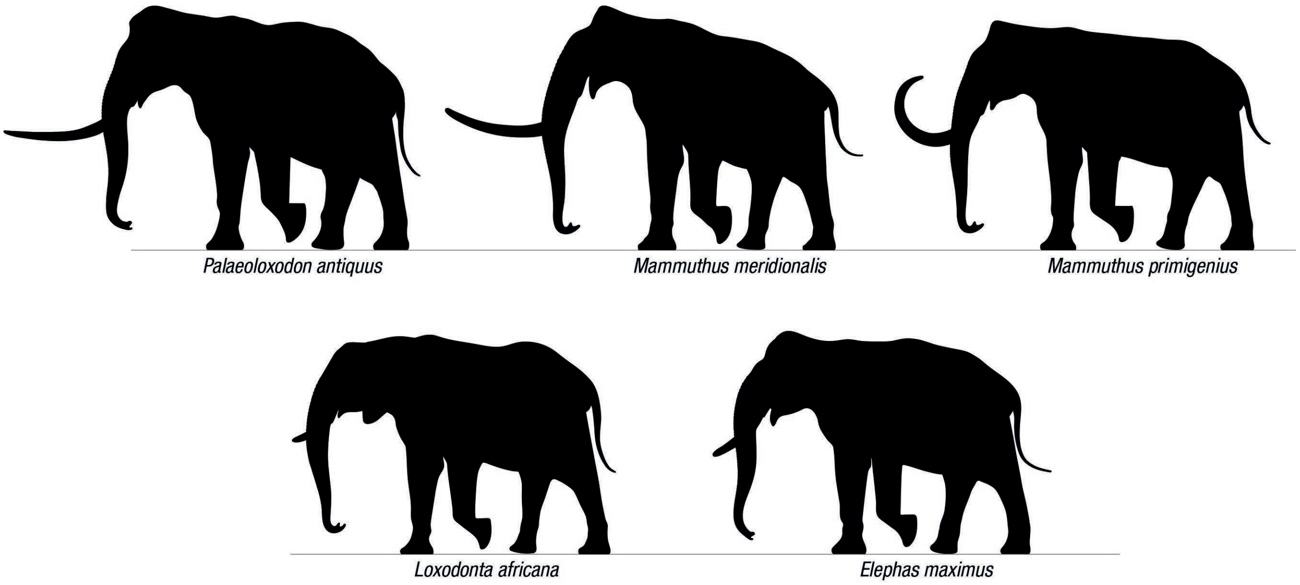

Fig. 8 - Side views of different elephant taxa, scaled to the same femur length to highlight the notable difference in body shape among different living and extinct species. Extinct large taxa were considerably more high-shouldered than living species; their head is the highest point of the body. Conversely, in the living species, the shoulder is the highest part in *Loxodonta africana*, while in *Elephas maximus* head and back are placed nearly to the same level. *Palaeoloxodon antiquus* has a high and massively domed head with somewhat rectangular shape, long and barely curved tusks, massive body, a convex, sloping back, robust legs and a relatively long tail. *Mammuthus meridionalis* has a high domed head, long massively built and relatively curved tusks, very pronounced sloping and slightly convex back, fairly robust legs and a rather small tail. *Mammuthus primigenius* (European morph) has a very high domed head, long, massive and extremely curved tusks, straight pronounced sloping back, fairly robust legs and a very short tail. *Loxodonta africana* has low and flat skull, gently curved, no particularly robust tusks, concave back, quite slender legs and a long tail. *Elephas maximus* has large domed forehead, convex back, generally small, gently curved tusks, quite robust legs and a long tail.

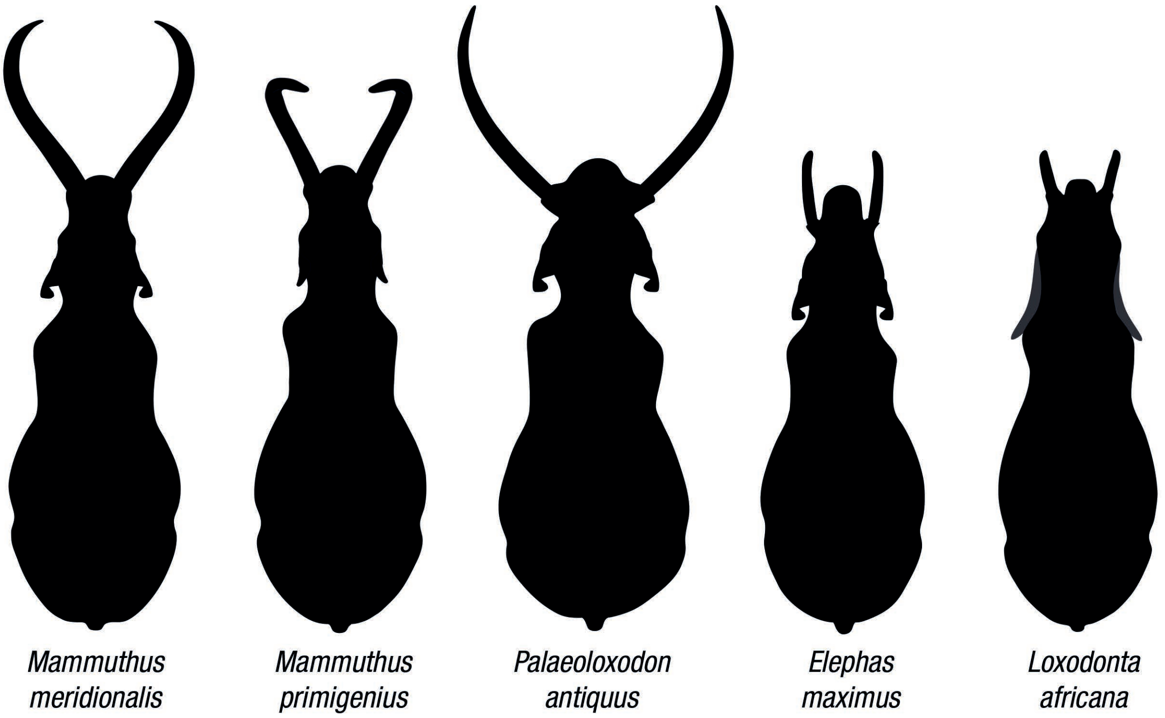

Fig. 9 - Top views of selected living and extinct elephant taxa, scaled to same femur length to stress the notable differences in body proportions among species. *Palaeoloxodon antiquus* is clearly the broadest and most robust animal, showing the most massive head. Mammoth species are similarly built and considerably massive. *Loxodonta africana* is the slenderest among the species compared here. The stoutness of *Elephas maximus* is between mammoths and African elephant, while it has the shortest body.

	Palaeoloxodon antiquus		*Loxodonta africana*		*Loxodonta cyclotis*		*Elephas maximus*		*Mammuthus meridionalis*		*Mammuthus trogontherii*		*Mammuthus primigenius*	
Shoulder height	>300 cm ♀	400 cm ♂	260 cm ♀	320 cm ♂	160 - 200 cm ♀	220 - 280 cm ♂	240 cm ♀	275 cm ♂	330 cm ♀	400 cm ♂	370 cm ♀	400 cm ♂	230 -260 cm ♀	280 - 315 cm ♂
Body mass	>5.5 t ♀	13 t ♂	3 t ♀	6 t ♂	0.75 t - 1.5 t♀	2 t - 4t ♂	2.7 t ♀	4 t ♂	7 t ♀	11 t ♂	9.5 t ♀	11 t ♂	2.8 - 4 t ♀	4.5t - 6 t ♂
Number of ribs	19		Up to 21		-		Up to 20		Usually 19		Usually 19		19 - 20	
Highest point	head		shoulders		shoulders and hips at the same level. Hips in females		usually the back or the head		head		head		head	
Back shape	sloping and irregular		concave		concave		humped		sloping and irregular		sloping and straight		sloping and straight	
Body	very broad		narrow		narrow		rather broad		broad		broad		broad	
Fur	probably very sparse		very sparse		very sparse		sparse		probably sparse		dense		very dense	
Ears size	probably large		extremely large		very large		medium		probably medium or large		probably small		very small	
Head	high double domed		low single dome		low single dome or flat		double domed		middle high single domed		high single domed		very high single domed	
Tusks morph	somewhat robust and from barely curved to straight. Very long		somewhat curved and rather robust. Middle length		straight and slim. Middle length		barely curved and rather robust. Middle length		very robust and curved. Very long		robust and very curved. Very long		robust and very curved. Very long	
Trunk tip	unknown		2 equal “fingers”		2 equal “fingers”		1 “finger”		unknown		unknown		1 short and, 1 long “finger”	
Tail length	medium		long		long		long		medium		short		very short	

Tab. 5 - Differences in physical parameters among straight-tusked elephants, mammoths and extant elephants.

forelimb of *P. antiquus* with respect to *L. africana* depends on the relative longer humerus and scapula, being the ulna articular length proportionally similar in adult males of both species (Supplementary Online Material 2).

The different proportions determine the overall body shape. In the 152-E9 male, for instance, with an estimated shoulder height in life of 363 cm, the femur is 1320 mm long, while in two large males of *L. africana*, having a similar femur length (1330 mm) (Haynes, 1991), the height at the shoulder in the flesh estimated from the dimension of forelimb bones for these individuals, is about 333 cm (Supplementary Online Material 2). The difference is remarkable, because at this shoulder height, an African elephant is expected to weigh 6.7 tonnes (see Tab. 7 in Larramendi, 2016), which is 42% lighter than a *P. antiquus* with the same femur length. This significant body mass difference between the two species accounts for their different ratio between the maximum pelvis breadth and the femur length. The considerably higher ratio of 1.32 in 152-E9 compared to the 1.0-1.05 in *L. africana* (Supplementary Online Material 2), indicates that males of *P. antiquus* from NN1 were much more robustly built than *Loxodonta*.

The greater body mass of *P. antiquus* from NN1 with respect to woolly mammoths results from the relatively larger skull, greater stature and more sturdily built body (with a pelvis proportionally wider than that of mammoths). The large Siegsdorf *Mammuthus primigenius*, with a femur length of 1330 mm, was 349 cm high at the shoulders and had a body mass of 8.2 tonnes (Larramendi, 2016). The difference in height depends on the relatively longer humerus (by 80 mm) and scapula (by 88 mm) and the higher manus of 152-E9 from NN1, which compensate for the shorter radius (by 48 mm).

In *M. primigenius* from Siegsdorf, the ratio between skeletal shoulder height (sSH) and femur length (FL) is greater (2.5) than that of both large males of *L. africana* (2.38) and the small Taymir mammoth individual (2.41) (Supplementary Online Material 2). This ratio is very high in males of *P. antiquus* from NN1 (2.61 and 2.65 in 152-E9 and 167-E43A respectively), about 0.05-0.09 more than the average value found by Larramendi (2016) for this species (Supplementary Online Material 2).

Larramendi (2016) noted that the average sSH/FL ratio in the larger mammoth species (*M. meridionalis*, *M. trogontherii* and *M. columbi*) ranges from 2.52 to 2.56, reaching a value of 2.6 in the largest specimens, suggesting that as elephants get bigger, the femur becomes proportionally shorter. Therefore, extinct large elephants were relatively higher-shouldered than extant species, possessing very long forequarters. The influence of longer forelimbs on biomechanics and mobility is sometimes difficult to discern (see Haynes, 1991, p. 17 for a discussion). Probably the scaling factor may be among the most influential causes (McMahon, 1973, 1975). In *P. antiquus,* the positive allometric growth of the humerus and scapula may be related to the need to support its heavy wide skull and the long straight tusks, while balancing the body's centre of gravity. The muscles that originate from the skull and neck and insert on scapula and humerus, such as cutaneous trunci, levator scapulae, occipito-scapularis, trapezius, splenius capitis, masto-humeralis and occipito-humeralis (Edgeworth, 1935; Shindo & Mori, 1956), were probably very well developed. Assuming that the scapula and humerus scale isometrically in larger elephant species, the cross section and the mass of the muscles attached to these bones will increase respectively by the square and the cube of the scaling factor. When the size of a structure augments, its volume grows more than the surface area (Galileo, 1638). Accordingly, as an elephant's skull gets bigger, the mass of muscles accountable for supporting its weight increases as the cube of the scale factor, while the muscles' power increases only as the square. Given that muscular strength does not increase as fast as muscular mass, it may be expected that with the enlargement of the skull, the muscles and the proximal limb bones become proportionally larger too.

The development of the large parieto-occipital crest characterising the straight-tusked elephants may support this hypothesis. On this peculiar bone structure, indeed, is inserted a well developed additional muscle known as the splenius capitis superficialis that extends over the splenius muscle (Marchant & Shoshani, 2007; Schauer, 2010; Larramendi, 2016) and supplies additional strength to the splenius profundus muscle and ligaments such as the ligamentum nuchae and laterale atlantis (Marchant & Shoshani, 2007; Schauer, 2010; Larramendi, 2016).

It is interesting to note that the 151-E8 female from NN1 is considerably shorter at the shoulder than males (sSH/FL = 2.4), suggesting that the NN1 adult males may have had a femur proportionally longer than that of females, and, consequently, a less pronounced sloping back, as recorded in other elephant species (Supplementary Online Material 2). In females, this feature is consistent with smaller and thinner tusks, less bulky heads, and smaller overall sizes when compared with males.

Although the forelimbs of *P. antiquus* are proportionally longer than those of extant elephants, the peculiar length of the vertebral spines makes this feature hardly detectable from its silhouette, which does not show a very pronounced sloping back (Fig. 8). In *P. antiquus*, indeed, the spines of the posterior thoracic, lumbar and sacral vertebrae are very long, as in *Loxodonta* and longer than in *Elephas* and *Mammuthus,* whereas the length of the spines of the middle thoracic vertebrae are similar to that of *Elephas*, but more elongated than in *Loxodonta* and *Mammuthus* (Fig. 10). The difference in height between the top of the scapula and the highest point of the pelvis in *P. antiquus* is, however, quite significant and the distance between these points increases as elephant size gets bigger (Fig. 10).

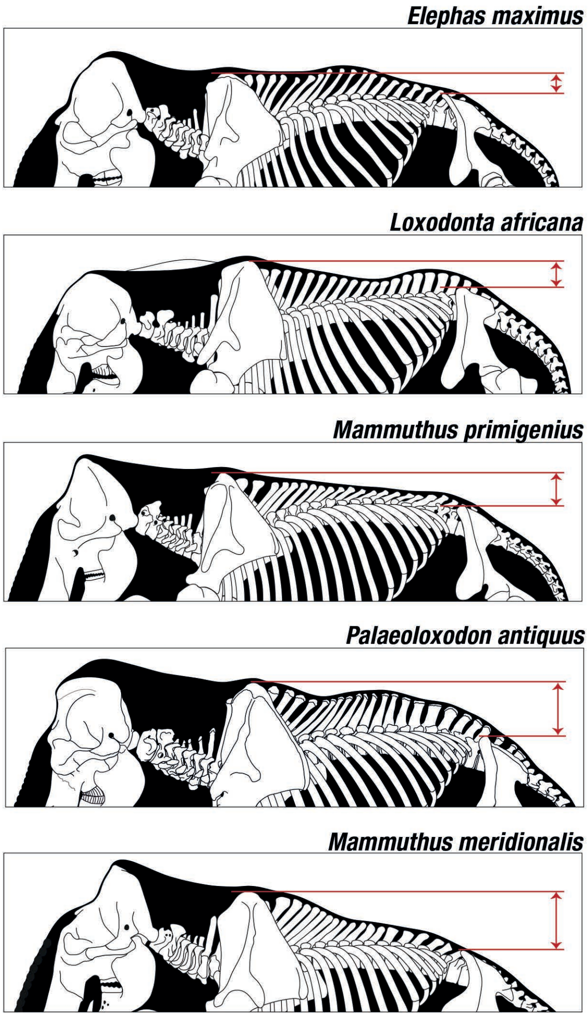

Fig. 10 - Comparison between the position of the highest points of the scapula and pelvic girdles in selected extant and extinct elephant species. The taller and bigger an elephant is, the larger the difference between the fore and rear-limbs. The significant difference in back morphology among species mainly depends on the different asset and length of their vertebral spines.

P. antiquus from NN1 were impressive and powerful animals. Their great stature, robustness, extremely wide skulls and huge tusks make them extraordinary elephants (Figs 10-13). Their skull morphology and size indicate that the domed foreheads of these elephants were much more developed than in extant Asian elephants (Figs 7 and 13). The exceptionally wide premaxillary bones contribute to a very broad rostrum that, together with the massive foreheads and giant tusks, likely made the front view of these animals spectacular (Fig. 13). The markedly developed thoracic spines indicate that the animals' back showed a notable prominence or ridge. The enormous body size, and therefore a very high body volume to skin surface ratio, along with the warm climatic period, indicate that the straight-tusked elephants must have been covered by a very sparse hair cover similar to the modern elephants, where the sparse hair distribution would have increased the heat transfer coefficient (Myhrvold et al., 2012). Although palaeontological evidence supports a close relationship between *Palaeoloxodon* and *Elephas*, from which the African palaeoloxodonts possibly stemmed at around 3.5 Ma. This statement conflicts with the results of recent genetic analyses, according to which the *Palaeoloxodon* lineage would be most closely related to African forest elephants, and *Elephas* would be a sister group of the *Loxodonta cyclotis,* *L. africana* and *Palaeoloxodon* clade (Meyer et al., 2017). Paleontological data per contra fail to effectively support such hypotheses (Todd, 2010b; Lister, 2013). Advances in genetic analysis indicate that *L. cyclotis* is closely related to *P. antiquus* (e.g., Meyer et al., 2017), although the divergence of the forest African species from the bush elephants possibly largely postdates the appearance of *Palaeoloxodon* in Africa (cf. Lister, 2013). Palaeoloxodont elephants actually converge in some morphological features with *Loxodonta.* These apparent similarities (e.g., cranial and dental morphology as well as elongated and antero-posteriorly developed spines in the last thoracic and lumbar vertebrae) prompted some past authors (e.g., Matsumoto, 1924; Osborn, 1942) to include *Palaeoloxodon* and "*Hesperoloxodon*" (= *Palaeoloxodon*) in the subfamily Loxodontinae. Whatever the phylogenetic relationships between *Palaeoloxodon* and *Loxodonta* may be, the physical appearance of the latter cannot be by no means of support to infer some particular aspect of a "living" *Palaeoloxodon*, such as the ear morphology and size, which are possibly more related to the body size and ecology than to phylogeny, or the form of the tip of the trunk. We may tentatively conjecture that the ears of *P. antiquus* were large, helping to dissipate the heat of the body, but it is impossible to estimate the appearance of the trunk tip, because its morphology seems not to be related to dietary behaviour. Extant elephants, indeed, both African and Asian, can be regarded as mixed feeders, with a complex feeding behaviour, although *L. africana* usually consumes herbs, grass, leaves, fruit and bark, as well as aquatic vegetation, while *E. maximus* generally eats more grass than African bush species. The ratio of browsing in the latter species, however, varies widely, depending on the availability of different kinds of plants and on climatic conditions, increasing during the dry season, when grass tends to wither, while during the wet season, grass consumption notably increases (Eltringham, 1992; De Boer et al., 2000). This dietary behaviour has been also reported in *P. antiquus* populations from two late Middle Pleistocene sites from Campagna Romana (central Italy), where results of microwear and isotope analysis document a different feeding behaviour (browser versus grazer-prevalent diet) in different climatic conditions (Palombo et al., 2005). The results obtained for NN1 elephants is consistent with those reported for the Italian elephant. The NN1 elephants were mixed feeders, including in their diet a lot of grasses as suggested by the large variety of plants in the wooded, humid grassland that dominated the landscape (Grübe et al., 2010). Considering these factors, it is impossible to formulate any hypothesis whit regard to the shape of the trunk tip in *P. antiquus*.

Ontogenetic growth in males and females

Extant elephants of both genera *Loxodonta* and *Elephas* rapidly increase their stature during the first ten years of life. The growth rate is higher in males than females leading to a marked difference in stature between sexes around this age (Laws, 1966; Laws et al., 1975; Sukumar et al., 1988; Lee & Moss, 1995; Arivazhagan & Sukumar, 2008). During the following five years, elephant growth rate is still quite fast, and then dramatically slows down, especially in females (the slackening is more marked in *Loxodonta* than in *Elephas*). The females of both extant genera moderately and slowly increase their size until their middle twenties. The stature of *L. africana* males may continue to increase until the age of 40-45, while *E. maximus* males stop growing earlier, at about 35-40 years (Laws, 1966; Hanks, 1972; Laws et al., 1975; Jachmann, 1988; Sukumar et al., 1988; Lindeque & Jaarsveld, 1993; Lee & Moss, 1995; Arivazhagan & Sukumar, 2008). According to Roth (1984) and Haynes (1991), the growth patterns are consistent with the time of the complete epiphyseal-diaphyseal fusion of limb bones which in living elephant males occur at about age 40, with the radius-ulna distal epiphyses and the dorsal margin of the scapula being the last to ossify. The complete epiphyseal-diaphyseal fusions of long bones, contrastingly, take place in females at age 25-30 years. Haynes (2017) reconsidered, however, the age of the complete limb bone ossification in *L. africana* males, noting that the humerus proximal epiphysis may completely fuse to the diaphysis at the an age of about 40-47. Ulna and radius distal epiphyses may fuse even later.

The pattern of the ontogenetic growth of *P. antiquus* from NN1 seems to be significantly different from that shown by the extant species. In the individual 152-E9 (male, 47 AEY), some epiphyses are not completely fused (e.g., some cranial bones, the distal epiphyses of radius and ulna, and the caput femoris), suggesting a further potential increase in stature. Clues from NN1 suggest that *P. antiquus* males may have grew up to their fifties, which is about ten years more than males of *L. africana* (Laws et al., 1975; Roth, 1984; Haynes, 1991; Lindeque & Jaarsveld, 1993; Lee & Moss, 1995; Larramendi, 2016 vs Haynes, 2017).

The growth pattern shown by the NN1 females is quite surprising. The chronology of ossification of the epiphyses of their long bones, indeed, differs from that of extant *Loxodonta* and *Elephas* females, but is comparable to that of *L. africana* males. According to various authors (e.g., Hanks, 1972; Laws et al., 1975; Lindeque & Jaarsveld, 1993; Shrader et al., 2006), the height at the shoulder of *L. africana* males of the same estimated age as the Crumstadt *P. antiquus* 161-E22A and E10B individuals ranges from 255 to 300 cm, falling in the range of *P. antiquus* females of the same age (Tabs 2 and 5), while the fully-grown females may have reached a size similar to that of mature *L. africana* bulls (see below; Tab. 6; Larramendi, 2016). This might suggest that female *P. antiquus* completed their epiphysis long bone fusion close to 40 AEY.

Sexual dimorphic traits in NN1 elephants

The most notable sexual dimorphic feature shown by NN1 elephants is their difference in size. Differences in body size between males and females are commonly found among many extant species, including elephants, but it is not so marked as in the *P. antiquus* from NN1. Healthy, fully-grown *E. maximus* males are about 15% taller and weigh 48% more than the females, whereas *L. africana* males are 23% taller and weigh twice as much or 100% more than females (Larramendi, 2016). The differences in size between genders are even greater in *P. antiquus* from NN1, with the fully-grown males being about one-third taller (33%) and weighing about 136% more than the females (Tab. 2).

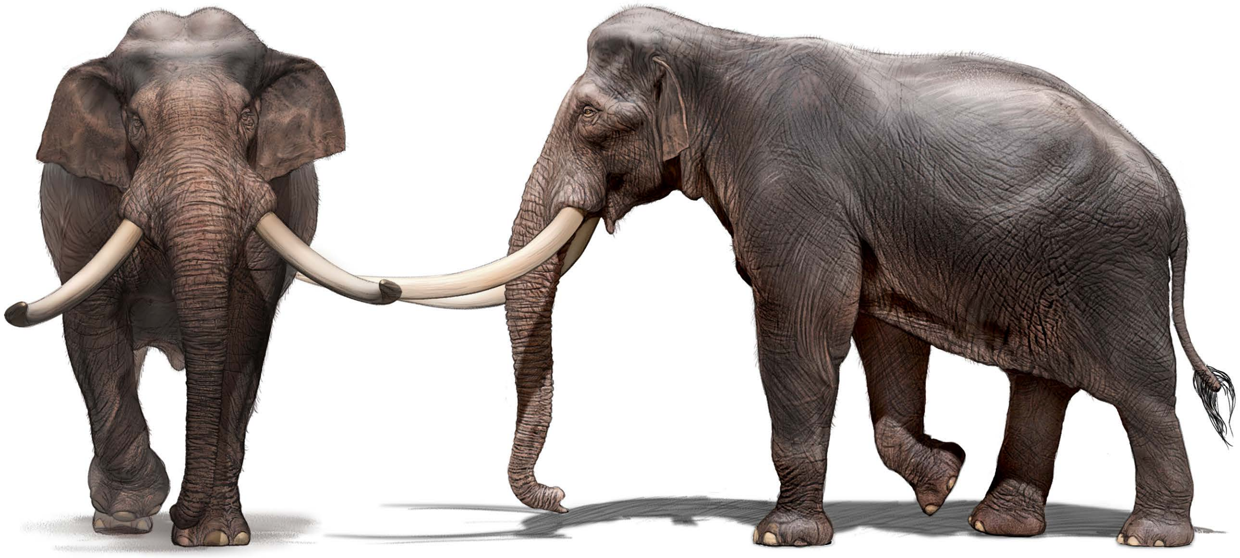

Fig. 11 - Artistic and rigorous representation of the life appearance of *Palaeoloxodon antiquus* from Neumark-Nord 1, based on 152-E9/175-E23A skeletons. Note the scarred injury on the forehead. Drawing by Shu-yu Hsu.

The great differences in body size between sexes of living elephants mainly depend on the late fusion of long bone epiphyses in males. In the NN1 males, the epiphyseal fusion of long bones occurs later than in the extant species, explaining the great differences in body size between male and female adult individuals. It is difficult to say whether the huge difference in size between *P. antiquus* males and females may have created a risk of injuries (e.g., a serious danger of breaking bones) for females during mating. Among extant elephants the oldest and largest males are most likely mates (Hollister-Smith et al., 2007; Rasmussen et al., 2008; Loizi et al., 2009). Whether the differences in size between adult females and males from NN1 may imply that *P. antiquus* may have had a social and sexual behaviour different from that of living elephants remains an open question.

Fig. 12 - Artistic and rigorous representation of the life appearance of *Palaeoloxodon antiquus* from Neumark-Nord 1. Side comparison between 152-E9/175-E23A (SH: 363 cm and BM: 9.5 tonnes) and 175-E23B (SH: ~400 cm and BM: ~13 tonnes) enormous elephant; the largest individual from NN 1. Drawing by Shu-yu Hsu.

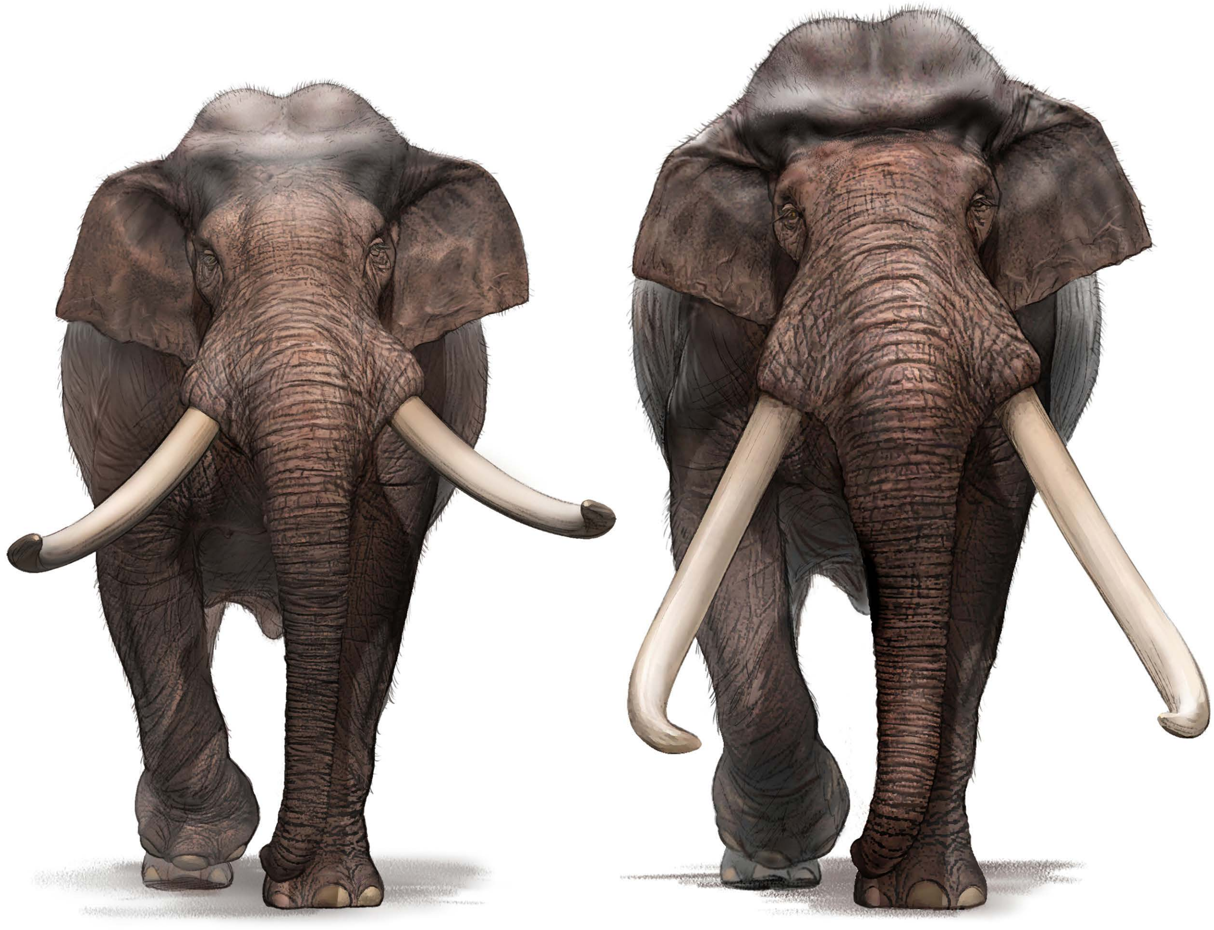

Fig. 13 - Artistic and rigorous representation of the life appearance of *Palaeoloxodon antiquus* from Neumark-Nord 1. Front view of 152-E9/175-E23A (left) and 175-E23B (right) drawn at the same scale showing the muscles on the top of the head, more developed in 175-E23B (looking like the so-called "namadicus morph") than 152-E9 (similar to the so-called "Stuttgart morph"). The tusks have been reconstructed assuming that they may be more developed and straighter in the largest animals (Palombo et al., 2010). Drawing by Shu-yu Hsu.

Were the NN1 elephants in optimal conditions in terms of body size?

Larramendi (2016), after analysing a large number of *P. antiquus* skeletons, suggested that fully grown males of this species in good health were 400 cm high at the shoulder and 13 tonnes in body mass. The same author proposed to classify proboscidean populations in five size classes (0-IV). The second class (grade I) includes the average sized animals, whose shoulder height varies by ± 5% from the average size estimated for the species. In grade I, the average shoulder height of adult male *P. antiquus* ranges from 380 to 420 cm. In a healthy population, the percentage of the complete grown adult male individuals with a height of less than 380 cm and more than 420 cm at the shoulders is expected to be low (Larremendi, 2016).

In the NN1 sample, some individuals are close to the optimal condition, whereas others are not. The size of the largest fully-grown individuals (154-E10A, 175-E23B, 167-E43A) is consistent with the grade I (see Tab. 2). In particular, 175-E23B, the largest elephant from NN1, can be considered as the epitome of a fully-grown, average-sized animal, while the sizes of 154-E10A and 167-E43A should be classified as low-average (height at the shoulder < 400 cm and > 380 cm). The size of 176-E24A, a fully-grown male individual, would suggest a grade 0, but the height at the shoulder is just 1 cm less than the minimum of grade 1, indicating that its health was quite good, although not optimal. The sizes of 152-E9 and 175-E23A fall in grade 0, but 152-E9, i.e. not completely fully-grown, might have reached the grade I at the final growth stage. The size variation shown by the adult males from NN1 is not significant and falls within the range of extant populations of *L. africana* and *E. maximus* (e.g., Laws et al., 1975; Kurt & Kumaransinhe, 1998; Larramendi, 2016). Overall, the stature of the *P. antiquus* adult males from NN1 indicates that they were healthy individuals at the time of their death, as it should be similarly hypothesised for the largest females of about 300 height at the shoulder and weighing about 5.5 tonnes. Although data on the body size of *P. antiquus* females available in literature are quite sparse, it is interesting to note, for instance, that the large female from Grabschütz (Jakubowski, 1996) was about 301 cm high at the shoulders with an estimated body

Locality	Crumstadt	Gröben II	Ciechanow	Grabschütz
Age (AEY)	18	Adult	Adult	Adult
Scapula max. length	-	-	-	>811
Scapula articular length	(790)	840e	-	-
Humerus max. length	920	985	1056	990
Humerus articular length	880	955	-	950
Ulna max. length	-	860	840e	865
Ulna articular length	-	730	684e	722
Radius length	650	735	722	765
Femur length	1040	1130	-	1130
Tibia length	602	660	-	666
Fibula length	-	-	-	637
Skeletal shoulder height	259	284	299e	285
Shoulder height in the flesh	273	300	315e	301
Estimated body mass	4.3	5.6	6.5	5.7

Tab. 6 - Physical parameters of some *Palaeoloxodon antiquus* females from selected European sites. The body mass (in tonnes) is calculated from shoulder height in the flesh according to Larramendi (2016) ($BM = 3.63 \times 10^{-4} \times SH^{2.903}$). Shoulder heights are given in cm; e: estimated; () estimated size including the epiphysis.

mass of about 5.7 tonnes (Tab. 6). The size of the large pelvic girdle from Binsfeld (Göhlich, 2000), suggests an animal about 335 cm high and weighing about 7.5 tonnes (Larramendi, 2016, SOM: Tab. 2). The incomplete skeleton from Chiechanów (Jakubowski, 1996) indicates a very large individual, herein tentatively regarded as a female because the dentition indicates an adult animal and the postcranial bones are considerably smaller than those of males. The maximum length of the humerus (1056 mm) (Jakubowski, 1996) suggests that the elephant had a shoulder height of about 315 cm and a body mass of about 6.5 tonnes (Tab. 6). The *P. antiquus* female from Gröben had a shoulders height of about 300 cm, as suggested by the dimensions of its forelimb bones (Kroll, 1991); contrastingly, the shoulder height of the female from Crumstadt (Kroll, 1991) was a little smaller, close to 273 cm, but it represents a young individual, about 18 AEY as suggested by dentition and bone ossification. It may have reached the stature of about 300 cm or more when fully grown. Based on available data, the size of the largest *P. antiquus* females from NN1 (e.g. 161-E22A, 154-E10B and other partial skeletons) falls in the range of the fully-grown European females. Nonetheless, we are mostly dealing with young individuals, in their twenties when they died, with many non-fused epiphyses, which if fully grown, may have reached the size of the large female from Chiechanów, comparable to that of an extant fully grown African male (Larramendi, 2016). Conversely to these healthy females, the adult fully-grown female 151-E8 was fairly small, possibly because she suffered osteological pathologies (Palombo et al., 2010; Marano & Palombo, 2011), although it should be noted that the healthy adult female 171-E34 was relatively small and slender.

CONCLUSION

The elephant remains collected at NN1 provide significant information about *P. antiquus* physical parameters, and this allows a better understanding of its life history. The abundant material available has allowed for an accurate reconstruction of the species' appearance and body size.

P. antiquus was an extraordinary elephant, among the most astonishing and powerful elephants that ever lived, and the most robust and broad of the Elephantinae species. The fully-grown males were likely particularly impressive due to their towering height of more than 4 metres, their massive torso, their extraordinarily wide and high double-domed heads, carrying superbly long tusks, and a body mass three times greater than that of living male Asian elephants, and twice to that of extant African bush elephants.

NN1 males had the potential to grow up to 400 cm at the shoulders and weigh 13 tonnes, while females generally did not exceed 300 cm at the shoulders or weigh more than 5.5 tonnes, suggesting a marked sexual dimorphism in size. Several young female individuals would have surpassed these numbers had they completed their growth, reaching a size comparable to that of fully-grown male African elephants, but other adult healthy specimens (176-E24 and 171-E34) were close to the above-mentioned numbers.

The large size of NN1 males and the observed long bone ossification sequence account for their peculiar ontogenetic growth pattern. The epiphyseal fusion process and the increase in shoulder height even after the age of 50 years suggests a growth process about 10 and 15 years longer than that generally reported for *L. africana* and *E. maximus* respectively. Conversely, the growth rate of NN1 females, *P. antiquus* was possibly comparable to that of *L. africana* males.

The unique physical characteristics and proportions of *P. antiquus* (e.g., the skull and tusk morphology, the vertebral spine configuration, the relative proportion of long bones) make it different from its Elephantinae relatives, although it shares some similarities with several species. *P. antiquus*, for instance, had elongated forelimbs, similar to the forelimbs of large mammoth species, possibly in response to a scaling factor related to the need to support and balance the huge-tusked heads. Moreover, the presence of rather well preserved skulls of adult individuals showing a different development of the parieto-occipital crest, provides interesting hints toward the debate about the meaning of these peculiar morphological traits and their variation within the *Palaeoloxodon* clade.

SUPPLEMENTARY ONLINE MATERIAL

All the Supplementary data of this work are available on the BSPI website at http://paleoitalia.org/archives/bollettino-spi/

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