Research Article

# Body Size, Biology and Encephalization Quotient of *Palaeoloxodon* ex gr. *P. falconeri* from Spinagallo Cave (Hyblean plateau, Sicily)

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## Abstract

During the period of 1958 and 1960, the richest sample of *Palaeoloxodon* ex gr. *P. falconeri* (104 individuals) was recovered from Spinagallo cave (Syracuse, Hyblean Plateau, SE Sicily). Subsequently, several composite skeletons were reconstructed. Four of them are today exhibited at the Paleontological Museum of Department of Earth Sciences of Sapienza University of Rome (MPUR). Three of the skeletons representing an adult male (MPUR/V n1), an adult female (MPUR/V n2) and a calf (MPUR/V n3), were analysed in order to reconstruct the physical appearance and estimate the body mass of the species. The rigorous skeletal restorations suggest that the living males approached a height of 100 cm at the shoulder and over 300 kg in body mass, whereas females were around 80 cm high and around 165 kg. The sexual dimorphism in *Palaeoloxodon* ex gr. *P. falconeri* was concluded to be comparable to that of extant elephants. The small size probably had a direct influence in the animals' physiology and biology; including a shorter life span, rapid growth, and changes in thermoregulation mechanisms. The drastic allometric size reduction experienced by Siculo-Maltese dwarf elephants, produced noticeable changes in the skull, showing some paedomorphic features that were present in young *P. antiquus* and in extant juvenile elephants, and in the axial and appendicular skeleton proportions with respect to its putative mainland ancestor *Palaeoloxodon antiquus*. Some unique traits observed in the limb bones, suggest a more agile locomotion in *P.* ex gr. *P. falconeri* than other elephantids. Nevertheless, the most noteworthy change is the positive allometric increase of the brain case. The large change in brain proportions was related to the need to maintain the minimal functional volume of the brain when the size of the skull was drastically reduced.

## Introduction

Dwarf proboscideans are prominent elements of fossil insular faunas (Ambrosetti, 1968; Roth, 1993; Caloi et al., 1996; van den Bergh, 1999; Agenbroad, 2001; Palombo, 2003, 2007; Ferretti, 2008; van der Geer et al., 2010; Herridge, 2010). Being excellent swimmers, elephants during the Pleistocene frequently colonized and became isolated on islands where they underwent significant changes in both skeletal structure and body mass. Among the different species that inhabited large and small Mediterranean islands, most originated from the mainland species *Palaeoloxodon antiquus*, and a couple from *Mammuthus* (see Palombo, 2001a, 2007; Theodorou et al., 2007; van der Geer et al., 2010, 2014; Herridge, 2010; Herridge et al., 2014). The smallest taxa recorded in the Siculo-Maltese archipelago, undoubtedly are the epitome of the insular dwarfism and the most prominent examples of the so-called "Island rule" (Foster, 1964; Van Valen, 1973).

The Sicily and Malta smallest dwarf elephants have generally been regarded during the last decades as belonging to a single species (i.e. *Palaeoloxodon falconeri*). Nonetheless, despite they likely are phylogenetically and taxonomically closely linked, it is challenging to ascertain how many species sharing nearly the same size were actually present in Malta and Sicily, as well as the chronology of each population/fauna. Any assessment of the taxonomy of the smallest Sicilian and Malta elephants is beyond the scope of this research. Therefore, 1) pending a taxonomic revision of Siculo-Maltese remains, 2) bearing in mind that dwarfism toward extremely diminutive size may have occurred in Sicily and Malta more than one time and from different ancestral population sources, and 3) considering the poorly constrained chronological range of some specimens (e.g. in Sicily those coming from Lupparello cave Vaufrey, 1929; Imbesi, 1956; Burgio and Cani, 1988; Esu and Girotti, 1991), we provisionally include the smallest Siculo-Maltese elephants in "*Palaeoloxodon* ex gr. *P. falconeri*", acknowledging that the group possibly includes multiple morphotypes or taxa.

The richest sample of *Palaeoloxodon* ex gr. *P. falconeri* (more than 3000 bones) comes from the Spinagallo cave (Syracuse, Hyblean Plateau, SE Sicily) (Ambrosetti, 1968). The low-diversity, unbalanced and strongly endemic Spinagallo mammalian fauna (*Crocidura esuae*, *Lutra trinacriae*, *Palaeoloxodon* ex gr. *P. falconeri*, *Leithia cartei*, *Leithia melitensis*, *Maltamys gollcheri*, bats associated with diversified herpetofauna and avifauna), typical of the so-called Sicilian "*Elephas falconeri* FC" (Masini et al., 2008 and references therein), was believed to be early Middle Pleistocene in age. A date of about 500 ka (based on Amino Acid Racemization of elephant tooth enamel) was proposed by Belluomini and Bada (1985) for the Spinagallo elephant.

Nonetheless, this age has to be considered with high caution not only because the uncertainties connected with the method, but especially because the authors used specimens from Isernia la Pineta (central Italy) as standard to date the remains from Spinagallo cave. The site of Isernia La Pineta was considered at that time older than 700 ka, whereas new datings have recently demonstrated that it is substantially younger (about 600 ka, Coltorti et al., 2005). Therefore, sediments con-

taining the Spinagallo fauna, were possibly deposited during the late Middle Pleistocene, as recently confirmed by U-Th ages obtained by speleothem samples above and below in situ fossil remains, and Optically Stimulated Luminescence (OSL) ages of the fossiliferous red earth (Herridge et al., 2014).

During the late Middle Pleistocene, the putative mainland ancestor of the Spinagallo elephant, *Palaeoloxodon antiquus*, was largely spread across the Italian peninsula (Palombo, 2003). Various data indicate that at that time, the size of the Italian straight-tusked elephants was particularly large, reaching in adult males a shoulder height of 4 m and a body mass of about 13 tonnes (Larramendi, 2015b).

The magnitude of the reduction in size of the elephant from Spinagallo cave, has been estimated by various scholars (e.g. Roth, 1990; Palombo and Giovinazzo, 2005; Moncunill-Solé et al., 2015). The difference among the obtained results, depends not only on the different equations used by each author to calculate the proboscidean body mass, but also on the difficulty to find an appropriate method for calculating the average body mass of a dramatically dwarf elephant species that changed its proportion significantly with respect to its mainland ancestor. This appears evident comparing an adult *P.* ex gr. *P. falconeri* with young extant elephants having a similar shoulder height. The Spinagallo elephant differs from both mainland and larger insular palaeoloxodonts (e.g. *Palaeoloxodon mnaidriensis* from Malta, and *Palaeoloxodon creutzburgi* from Crete) in showing paedomorphic traits (particularly evident in the skull that looks like the skull of young *P. antiquus* (see e.g. Maccagno, 1962; D'Erasmo and Moncharmont Zei, 1955)), a positive allometric reduction of cranium and teeth (that may implies biases in calculating the encephalization index), and also in the robustness index of long bones. The actual relative length of long bones of the elephant from Spinagallo cave can be only supposed based on the dimensions of stylopodium and zeugopodium elements whose articular epiphyseal surfaces are compatible (can articulate to each other). This because no articulated skeleton of *P.* ex gr. *P. falconeri* has been found to date.

This research aims to reconstruct the physical appearance, estimate the body mass of the dwarf elephant from Spinagallo cave, calculate its encephalization quotient, evaluate the allometric brain size reduction with respect to its mainland ancestor *P. antiquus*, and scrutinize the biological implications of the reduced body size of *Palaeoloxodon* ex gr. *P. falconeri*.

## Materials and methods

The sample of Spinagallo counts more than 3000 elephant remains belonging to at least 104 individuals (Ambrosetti, 1968). Six skeletons have been reconstructed based on "a statistical correlation among the various bones... carried out in the hope of at least being able to reconstruct an average individual animal." (Ambrosetti, 1968, p. 285). Four of them, well preserved composite skeletons (a male, a female, a young and a nearly newborn males), are exhibited at the Paleontological Museum of the Department of Earth Sciences of Sapienza University of Rome (MPUR).

To reconstruct the life appearance, study sex dimorphism and ontogenetic traits, estimate the body size and encephalization quotient of *P.* ex.gr. *P. falconeri* recovered from Spinagallo cave, we analysed the skeletons of the adult male (MPUR/V n1) and the female (MPUR/V n2), both with the last molariform teeth in an average wear stage, as well as the new-born (MPUR/V n3), stored at MPUR.

The best way to estimate the body size of an extinct animal, is to build an accurate skeletal reconstruction model based on the most complete and best-preserved specimens (Jerison, 1973; Paul, 1997; Hurlburt, 1999; Murray and Vickers-Rich, 2004; Larramendi, 2015a,b). Fortunately, the rich material recovered during the period between 1958 and 1960 in Spinagallo Cave (Accordi and Colacicchi, 1962; Ambrosetti, 1968), allows to perform accurate reconstructions of *P.* ex gr. *P. falconeri* individuals of different sizes and sexes.

The cranial and postcranial skeletons measurements were taken with sliding callipers or flexible tape following Göhlich (1998) and Lister (1996). The skeletal reconstructions were made bone by bone apply-

ing comparative anatomy of extant proboscideans as in Larramendi (2015b). The forelimbs position was restored somewhat more flexed than observed in extant elephants, because the articular surface of the humerus of *P.* ex gr. *P. falconeri*, is proportionally larger and more extended antero-posteriorly. Since the studied specimens are composite skeletons, and in order to provide the most plausible skeletal reconstructions, the relative proportions of bones (ratios) were checked and corrected based on a critical revision of data available in literature (e.g. Ambrosetti, 1968), on the epiphyseal fusion stage and new measurements. As a result, the humeri of the adult male (MPUR/V n1), were scaled up a 3% to fit with the ulnae and femora, and the tibiae were scaled up a 10% to fit with the overall size of the skeleton. The femora of the adult female (MPUR/V n2), were scaled up a 3% to correspond with the dimensions of the pelvis acetabulum. The total number of thoracic, lumbar and caudal vertebrae was assumed to be the same as in the mainland ancestor *P. antiquus*. Accordingly, the vertebral column consists of 7 cervical, 19 thoracic, 4 lumbar, 4/5 sacral and 25 caudal vertebrae (Schauer, 2010). The adult male (MPUR/V n1) has a total of 5 sacral vertebrae preserved; the adult female (MPUR n2) has 4 and the calf (MPUR/V n3) was restored with 4 sacral vertebrae.

Body volumes were estimated using Graphic Double Integration (GDI) (Jerison, 1973; Hurlburt, 1999; Murray and Vickers-Rich, 2004; Larramendi, 2015a,b). GDI is a volumetric method developed by Jerison (1973) for estimating the volumes of endocasts from dorsal and lateral views. Later, other authors applied it to whole animals (Hurlburt, 1999; Murray and Vickers-Rich, 2004; Larramendi, 2015a,b). To determine the volume, the body or body part of the life restoration is divided into slices, and each slice is modelled as an elliptical cylinder (Jerison, 1973). For estimating the body masses, specific gravities of 0.99 and of 1.8 were assumed to the animals' body and tusks respectively (Larramendi, 2015b). In order to compare *P.* ex gr. *P. falconeri* proportions with extant elephant calves of the same shoulder height, several silhouettes were made on the basis of photographs of newborn captives.

The endocranial volume of *P.* ex gr. *P. falconeri*, was obtained from the female MPUR/V n2 (Accordi and Palombo, 1971). To estimate the approximate brain weight, a brain-mass:endocast volume ratio of 0.8 was applied. This is because in elephants, the space occupied by the dura mater and intercranial fluids has been estimated to be about the 20% of the total endocranial volume (Osborn, 1942; Accordi and Palombo, 1971; Palombo and Giovinazzo, 2005) and because the specific gravity of brain is very close to one (Jerison, 1973; Hurlburt et al., 2013), brain volume can be equalled to mass in grams. Additionally, sources of comparative proboscidean material (extinct and extant) and data of other mammals obtained from the literature, and sometimes corrected (see below), are summarized in Tab. 1.

**Table 1** – Volumes and masses of different specimens of *Palaeoloxodon* ex gr. *P. falconeri*, estimated by Graphic double integration. Masses assume a specific gravity of 1.8 for tusks and 0.99 for the rest of the body (Larramendi, 2015b) .

| Body part | **Male**<br>Volume (l) | **Female**<br>Volume (l) | **Calf**<br>Volume (l) |
|---|---|---|---|
| Tusks (pair) | 2.44 | - | - |
| Trunk | ∼ 5.4 | ∼ 2.5 | ∼ 0.06 |
| Head-Neck-Body | 281 | 157.2 | 5.9 |
| Forelimbs (pair) | 9.2 | 5.6 | 0.48 |
| Hindlimbs (pair) | 7 | 3.4 | 0.3 |
| Ears (pair) and tail | ∼ 0.5 | ∼ 0.3 | ∼ 0.05 |
| Total volume | 305.5 | 169 | 6.79 |
| **Total mass (kg)** | **304.5** | **167.3** | **6.72** |

The Encephalization Quotients were calculated using the Jerison (1973) and Hurlburt (1996) formulae. The last author reviewed and improved Jerison's methods based on much larger sample (Hurlburt, 1996; Wharton, 2002). For this work, Jerison's (1973) method was used for comparison to results of other studies. In order to discern the two methods, the abbreviation EQ (Encephalization Quotient) was

used for Jerison's (1973) formula, and MEQ (Mammal Encephalization Quotient) for Hurlburt's (1996) one. The Encephalization indexes were calculated with the following equations:

$$EQ = Brain\ mass/0.12 * (Body\ mass)^{0.667}$$

(Jerison, 1973, p. 61)

$$MEQ = Brain\ mass/0.056 * (Body\ mass)^{0.751}$$

(Hurlburt, 1996, p. 77)

where brain and body masses are in grams.

## Results and Discussion

### Body Size

#### Shoulder heights

The rigorous restorations show that the shoulder height of *P.* ex gr. *P. falconeri* from Spinagallo cave, is lower than past estimates. The large male (Fig. 1), whose femur is 410 mm long, only 17 mm less than the largest specimen recovered in Spinagallo Cave (Ambrosetti, 1968), had a shoulder height in the flesh of 96.5 cm (skeletal shoulder height = about 91.5 cm). This implies that the largest individuals of *P.* ex gr. *P. falconeri* from Spinagallo cave could reach 100 cm in height. Their stature was therefore about 20–30 cm less than previous estimates (see e.g. Palombo and Giovinazzo, 2005; Roth, 1990). The adult female (MPUR/V n2), had a shoulder height of about 80 cm in the flesh (Fig. 2). It was rather large because the maximum length of the left humerus (258 mm) is 8 mm more than female specimens and only 2 mm less than the maximum value given by Ambrosetti (1968). In the mounted skeleton, the right humeral (266 mm long) proximal epiphysis is not totally fused. Thus, it likely belonged to a subadult male. The right humerus of the digital restoration was therefore scaled to the same size of the left one. The femur length, which is scaled up to 340 mm, is 8 mm more than the average size of females (Ambrosetti, 1968). Finally, the newborn male (MPUR/V n3), was only 33 cm tall at the shoulder in the flesh (see Fig. 3, Fig. 4).

#### Body masses

The estimated body volumes and body masses of the skeletons kept at the MPUR using Graphic Double Integration, are summarized in Tab. 1. The body volume, and hence the mass, of the adult male, is calculated in 305 kg, nearly up to three times more than the body mass estimated by Palombo and Giovinazzo (2005). The so different estimates depend on the methods used by the latter authors, who estimated the body mass of fossil dwarf elephants by means of new equations based on the shoulder height and pad circumference of a large sample of young to adult living elephants. These equations give good results if tested on living elephants, but can hardly be applied to Spinagallo dwarf elephants, due the fact of the extreme differences in body proportions of these animals compared with the calves of extant forms having the same
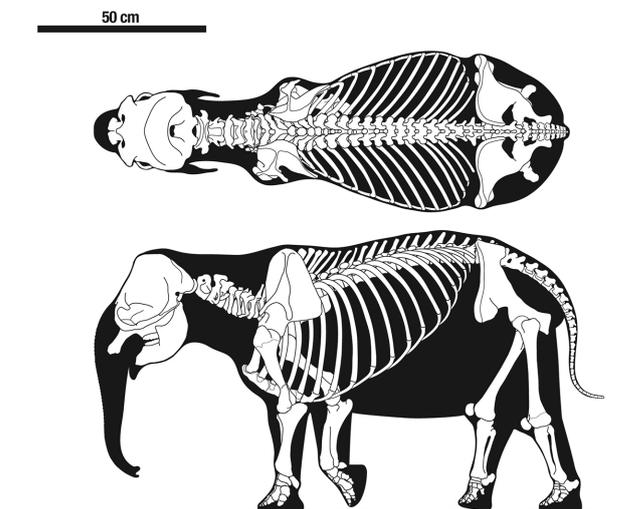


Figure 2 – Rigorous multiview skeletal restoration of adult female *Palaeoloxodon* ex gr. *P. falconeri* based on MPUR/V n2 composite skeleton. Reconstruction by Asier Larramendi.

height at the shoulder (see Fig. 5). Roth (1990) also proposed several allometric equations based on the long bone dimensions of a large number of living animals of the size range of extinct dwarf elephant species. However, nowadays, the volumetric method, provided that the reconstructed models are technically correct, is regarded as a more accurate method than the allometric one (Haynes, 1991; Paul, 1997; Hurlburt, 1999; Murray and Vickers-Rich, 2004; Larramendi, 2015b). This is because extinct species had significant differences in body mass/bone dimension relationships compared to extant species (Haynes, 1991; Paul, 1997; Larramendi, 2015b). This is illustrated by applying Roth's equations (based on the maximum length and minimum circumference of humerus and femur) on the MPUR/V n1 male, where the results varies from 151 to 321 kg in body mass.

Following the method here proposed, the largest humerus and femur included in Ambrosetti's (1968) sample, which are about 4% longer than those of the adult male mounted skeleton, suggest that the body mass of the largest individuals from Spinagallo cave was about 340 kg. The average size for adult male individuals probably was about 95 cm at the shoulder height in the flesh and 280-300 kg in body mass. The body mass for the large adult female (MPUR/V n2) is estimated to be 168 kg, nearly the half of the adult male, indicating a strong sexual dimorphism as observed in extant elephants (Laws, 1966; Laws and Parker, 1968; Laws et al., 1975; Kurt and Kumarasinghe, 1998; Larramendi, 2015b). Assuming an average body mass of about 160 kg
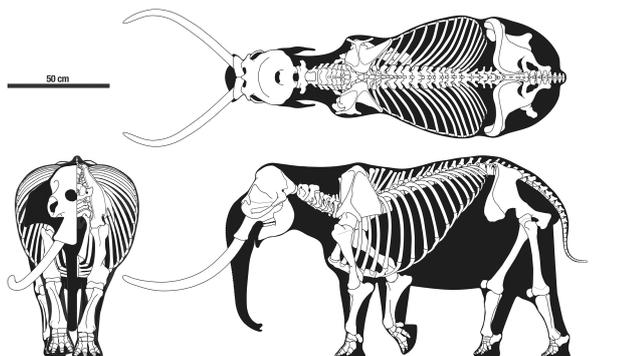


Figure 1 – Rigorous multiview skeletal restoration of adult male *Palaeoloxodon* ex gr. *P. falconeri* based on MPUR/V n1 composite skeleton. Reconstruction by Asier Larramendi.
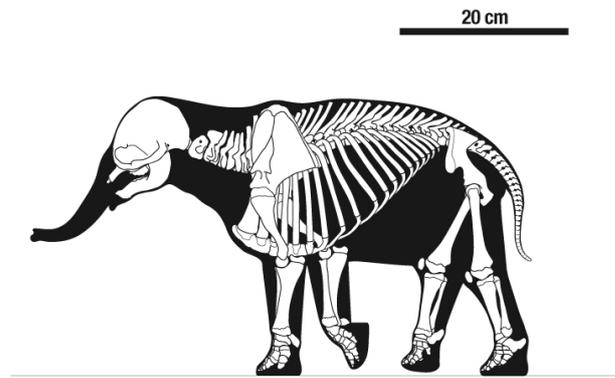


Figure 3 – Rigorous skeletal restoration of calf *Palaeoloxodon* ex gr. *P. falconeri* based on MPUR/V n3 skeleton. Reconstruction by Asier Larramendi.

for fully grown female individuals, the adult males and females of *P. ex gr. P. falconeri* from Spinagallo cave, were about 20 and 19 times lighter than *L. africana* males and females respectively, and roughly 13 and 17 times smaller than *E. maximus* of both sexes (Laws and Parker, 1968; Laws et al., 1975; Sukumar et al., 1988; Kurt and Kumarasinghe, 1998; Larramendi, 2015b). Finally, the weight of Spinagallo cave calf (6.7 kg), was about 15-17 times less than that of extant elephant calves of both sexes (see Dale, 2010).

## Body Structure and Appearance

The body structure and proportions of *P. ex gr. P. falconeri* from Sinagallo cave, clearly differs from those of its ancestor *P. antiquus* and even more from extant *Loxodonta africana* and *Elephas maximus* (Fig. 5).

### Changes in morphology

The skulls of adult individuals from Spinagallo cave show some features generally observed in continental elephant calves. The skull is fairly globular in shape, with single domed and quite flattened apex without a fronto-parietal crest, nearly plane wide forehead, long and slightly concave frontal-parietal region, external nasal choanae opening in low position, and absence of parietal swelling (Palombo, 2003). These paedomorphic morphological traits (*sensu* Gould, 1977), are confirmed by the reduced pneumatization of the parieto-frontal bones, and by the size of the brain case that in the adult elephants from Spinagallo cave is extraordinarily developed (Accordi and Palombo, 1971). The relative broad development of the brain case, is related to the need to maintain the minimal functional volume of the brain when the size of the skull is drastically reduced (Palombo, 2001b; Palombo and Giovinazzo, 2005). The allometric skull reduction, made on one hand the skull of the adult elephants from Spinagallo cave markedly different in shape to that of its putative mainland ancestor *P. antiquus*, and on the other similar to that of extant juvenile elephant species (Palombo, 2003). Moreover, the lack of the fronto-parietal crest, suggests that in *P. ex gr. P. falconeri*, as in young *P. antiquus* individuals, the additional muscle arising along splenius, known as *splenius superficialis* or *splenius capitis superficialis*, which inserts on the fronto-parietal crest, present in *E. maximus* and suggested to be present in several extinct species such as *P. antiquus* (Schauer, 2010; Larramendi, 2015b), was weakly developed. This extra muscle might give additional strength for supporting the load of tusks and may increase its size as the tusks become more and more robust (see Marchant and Shoshani, 2007; Larramendi, 2015b). Accordingly, the hypothesis that that the muscles linked to the head movements were less developed in *P. ex gr. P. falconeri*, than in *P. antiquus* cannot be discounted.

The postcranial skeleton of *P. ex gr. P. falconeri* shows some unique characteristics related to the dwarfism and possibly to locomotory adaptations. The adult of *P. ex gr. P. falconeri*, had synostosis of ulna and radius, and tibia and fibula (Ambrosetti, 1968). Moreover, in the tibiae of MPUR/V n1 male and MPUR/V n2 female, the minimum diaphyseal latero-medial width, is less than the antero-posterior minimum thickness. This morphological trait has never been observed in any Elephantimorpha and the proportion matches that observed in curs-

orial animals (Christiansen, 2007). It has also been suggested that in the Spinagallo elephant, the smaller size and the reduced weight, possibly favour the development of joints, which bring the limbs closer to the sagittal plane, with respect to the mainland ancestor, and facilitate anterior-posterior oscillation of limbs (Palombo, 1996). These modifications may be related not only to the lighter body weight, but also to the need of more secure movements on relatively uneven ground and climbing rather steep slopes (see Sondaar, 1977), as supported by the supposed more digitigrade structure of Spinagallo feet (Palombo, 2003 and reference therein, Palombo and Giovinazzo, 2005; Scarborough et al., 2014). Although the hypothesis that *P. ex gr. P. falconeri* had a more agile locomotion than other elephantids may be quite reasonable, this does not imply that *P. ex gr. P. falconeri* was able to perform true running with a suspended phase, because of the great similarities of the appendicular skeleton proportions to that of the extant species and its columnar stance (Larramendi, 2015b).

### Change in proportion (positive versus negative allometric size reduction)

A remarkable feature of *P. ex gr. P. falconeri*, is the allometric size reduction of the cranium and appendicular skeleton. The forelimb bones, for instance, were proportionally shorter than in the mainland *P. antiquus*, whereas in the axial skeleton, the torso was longer and wider (due the relatively broader pelvis) than that of its ancestor (see Larramendi, 2015b, Appendix 3, Fig. 4). Moreover, the hindlimbs were relatively longer and the proportions of thoracic neural spines were different, producing slightly concave shaped backs. The elongated hindlimbs make the hip region higher than the shoulder. This may be interpreted as paedomorphic feature because in extant elephant calves, this feature is commonly present, contrary to adult individuals. Nonetheless, it is worth noting that in the skeleton of the new-born elephant from Spinagallo cave mounted at MPUR, the shoulder is higher than the hip (Fig. 3), similar to adult *P. antiquus* and extant species.

It is a challenging task to explain the inferred lengthening of the hindlimbs in *P. ex gr. P. falconeri* during the ontogenetic growth. Whether calves experienced drastic changes in body size and structure during their growth, and whether this would have influenced on the distribution of body mass and of the location of the centre of mass, it is difficult
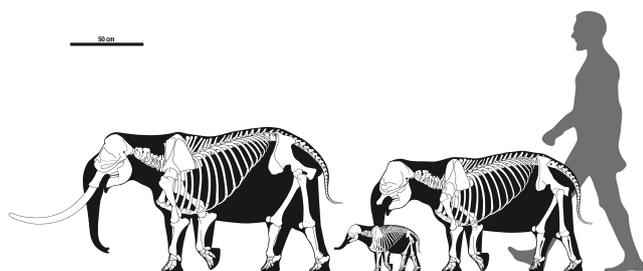


**Figure 4** – Comparative skeletal restorations of *Palaeoloxodon* ex gr. *P. falconeri*, Male, Calf and Female, to the same scale. The human silhouette is 180 cm tall. Reconstructions by Asier Larramendi.
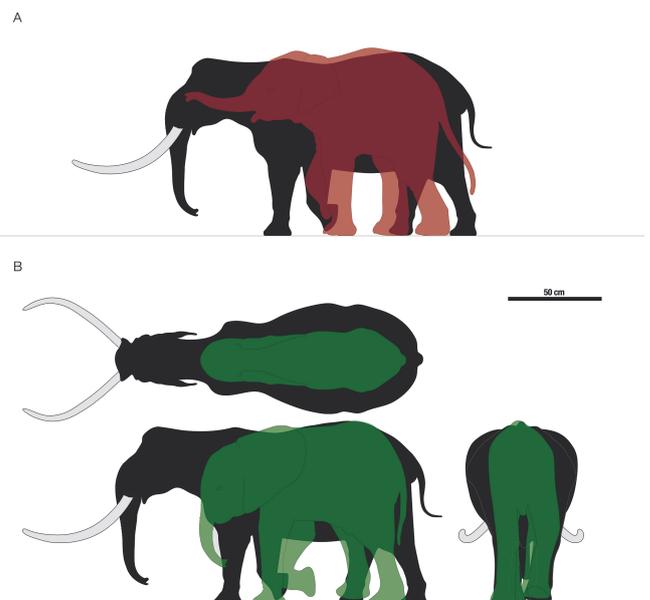


**Figure 5** – Comparative silhouettes of *Palaeoloxodon* ex gr. *P. falconeri* average sized adult bull (black), Asian elephant calf (light red) and African elephant calf (light green). The 3 species are shown at the same shoulder height of 95 cm. Note the great body volume differences. Illustrations by Asier Larramendi. A. Lateral comparative view of 290 kg adult bull *P. ex gr. P. falconeri* and 120 kg calf *E. maximus*. B. Lateral, dorsal and rear comparative views of 290 kg adult bull *P. ex gr. P. falconeri* and 120 kg calf *L. africana*.

to ascertain. In extant elephants about the 60% of the weight is supported by forelimbs (Henderson, 2006; Miller et al., 2008). Based on the reconstructions, it would be suggested that in young *P.* ex gr. *P. falconeri* the centre of mass was similarly positioned as in adult *Elephas maximus*, whereas in adult individuals it was placed more posteriorly because of their more elongated body, wider pelvis, and therefore much more massive rear part. If so, the hindlimbs were expected to have supported more mass than the forelimbs. Assuming this hypothesis as reasonable, the differences in proportions inferred for young and adult *P.* ex gr. *P. falconeri* would be related to an efficient body mass distribution, loading the extra weight of the rear part to the front, and this way balance the body's centre of gravity. Therefore, the tall hip would not be a paedomorphic feature. Nonetheless, more data is needed to make the hypothesis less speculative.

Another peculiar feature of *P.* ex gr. *P. falconeri* resulting from the reconstruction of skeletons from Spinagallo cave material, is a negative allometric reduction of the neck, that is relatively longer than in its putative ancestor. Adult males appear to have had a neck about 10% shorter than the females, maybe in order to balance out the extra weight of the tusks. A proportionally long neck may have influenced the length of proboscis; assuming that in the dwarf elephants (as in all animals) body parts develop harmoniously for a high performance in terms of energy conservation (Shoshani and Foley, 2000; Larramendi, 2015b), it may be suggested that a long neck and proportionally shorter forelimbs, would lead the mouth being closer to the ground and therefore a relative shorter proboscis than extant forms would be expected. Whether the neck allometry of *P.* ex gr. *P. falconeri* with respect to its putative ancestor depends on the strong body size reduction of *P.* ex gr. *P. falconeri* or to biomechanical requirements is difficult to explain.

All in all, the main trait *P.* ex gr. *P. falconeri*, is the marked difference in body proportions and body volume among an adult male *P.* ex gr. *P. falconeri* and young elephants of extant species having a similar shoulder height. According to Dale (2010) data, *E. maximus* and *L. africana* calves 95 cm high at the shoulder, are expected to weigh about 118 kg. Consistently, the body mass of the *Loxodonta africana* calf silhouette (Fig. 5), calculated by GDI, is about 119 kg, confirming the accuracy of the *L. africana* silhouette proportions. At the same shoulder height, the body volume of a *P.* ex gr. *P. falconeri* male individual, is over 240% greater, suggesting for the Spinagallo elephant a body about 80% broader and 65% longer than *E. maximus* and 50% than *L. africana* (see Fig. 5).

### Biological implications of small body size

It might be speculated that the small size of the Siculo-Maltse dwarf elephants could have had some impact on the animals' thermoregulation mechanism. Larger animals have increased difficulty dissipating heat due the high body volume to surface ratio (when an animal increases in size, its volume increases at a faster ratio than its surface area), and accordingly there is a negative correlation between hair density and body size in mammals as hair density represents a thermoregulatory adaptation (Schwartz and Rosenblum, 1981; Myhrvold et al., 2012; Sandel, 2013; Larramendi, 2015b). Larramendi (2015b) showed that extant land mammals above 1500 kg are "hairless", below this weight, all land mammals have a high density of hair regardless climatic conditions, although must be noted that there are a very few exceptions including humans, which the real reasons of our "nakedness", still without satisfactory explanations (see Rantala, 2007; Sandel, 2013). The only land mammal (with non-aquatic habits) without an appreciable amount of hair comparable to that of extant elephants, and with a similar body weight of that of *P.* ex gr. *P. falconeri*, is the Buru babirusa, *Babyrousa babyrussa* (probably due to a combination of a very high average annual temperatures of its tropical habitat, Maluku islands, and the absence of use of thermal sweat glands for cooling as some pigs Powell, 2004). The rest of the total terrestrial mammals of the size range of *P.* ex gr. *P. falconeri*, have a visible and considerably high density of hair. Concerning the extant proboscideans, they have low hair densities. The sparse hair of living elephants increases heat loss, unlikely any other mammal known (Myhrvold et al., 2012). This mechanism is a response to the big heat transfer problem due the very

large body size of elephants (Myhrvold et al., 2012). Whether this peculiar mechanism was present in *P.* ex gr. *P. falconeri* it is difficult to ascertain. Nonetheless the low value of the body volume to surface ratio, may suggest that such a mechanism may have been unsuitable for the dwarf elephant physiology. Hence, as it would be expected for an animal of the body size of *P.* ex gr. *P. falconeri*, let us to hypothesize that *P.* ex gr. *P. falconeri* was covered by some amount of hair that might help to keep the body temperature constant and also protect the skin. Assuming that they did not have functional sweat glands as modern elephants (Wright and Luck, 1984; Myhrvold et al., 2012), the hairs were probably quite short and relatively sparse. Also, in the same way, the ears probably experienced a drastic allometric reduction as a system to save heat, unlike today big elephants' ears do. Thus, the ears might have been proportionally smaller than in larger elephants (Fig. 6).
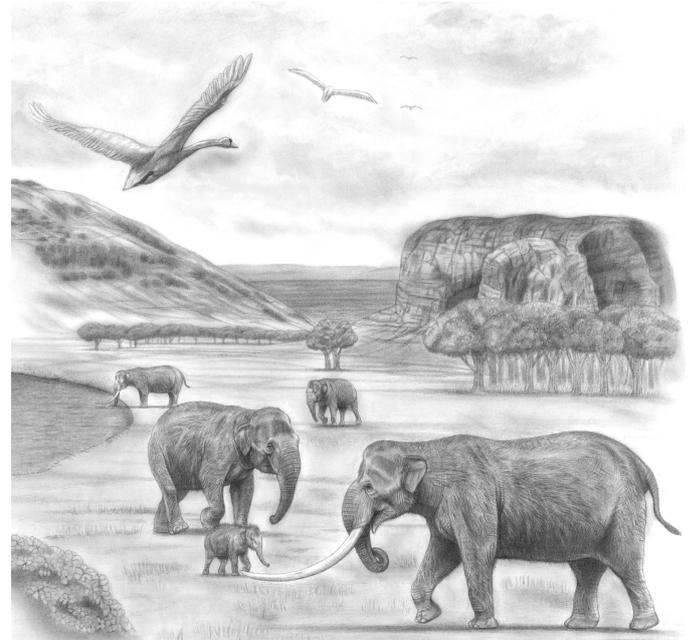


**Figure 6** – Artistic reconstruction of the environment of Spinagallo Cave showing *Palaeoloxodon* ex gr. *P. falconeri*. The swan is *Cygnus falconeri*. Drawing by Shuhei Tamura.

## Sexual Dimorphism and Longevity

*P.* ex gr. *P. falconeri* from Spinagallo cave shows a marked dimorphism that related on both dimensions; proportions and morphology. The sexual dimorphism in size, roughly matches to that observed in *L. africana*; the dwarf adult males being about 20% taller and over 85% heavier than females (Laws, 1966; Laws and Parker, 1968; Laws et al., 1975; Kurt and Kumarasinghe, 1998; Larramendi, 2015b), whereas the differences in height at the shoulder and body mass in *E. maximus* are about of 15% and 50% respectively (Laws and Parker, 1968; Laws et al., 1975; Kurt and Kumarasinghe, 1998; Larramendi, 2015b).

The pelvic morphology provides the best information for determining the gender of elephants (Lister, 1996). The MPRV-15 fully grown pelvis, was used for the restoration of the MPURV/ n2 specimen. According to Marano and Palombo (2014), this pelvis belongs to a male individual. However, the ratio of the minimum width of the ilium shaft to the maximum horizontal width of the MPRV-15 pelvis, generally regarded as the best indicator of gender in elephants (Lister, 1996), is 0.116, a value comparable with that of female mammoths (0.113 - 0.132; Lister, 1996), and very low with respect to the value (1.38) obtained for the MPURV/ n1 male. Moreover, the pelvis size is too small for an adult male individual. The MPRV-15 pelvis may therefore belong to a female individual.

One among the most evident dimorphic traits shown by the dwarf elephants from Spinagallo cave, is the tusklessness observed in both young and adult females (Palombo, unpublished data). A congenital bilateral tusklessness is present in females of *E. maximus*, but also oc-

**Table 2** – Body mass, brain mass, EQ (after Jerison, 1973), MEQ (after Hurlburt, 1996) and Brain mass *vs.* Body mass ratio in selected proboscideans and other mammals.

| Taxon | Specimen/Locality | Sex | Body mass (kg) | Brain mass (g) | EQ | MEQ | Brain-body mass ratio | Brain and body mass reference |
|---|---|---|---|---|---|---|---|---|
| **PROBOSCIDEA** | | | | | | | | |
| *Palaeoloxodon* ex gr. *P. falconeri* | MPUR n2 | F | 168 | 1440 | **3.94** | **3.06** | 1:117 | This paper |
| *Palaeoloxodon antiquus* | Pian dell'Olmo | M | ~11000[1] | 7200 | 1.21 | 0.66 | 1:1528 | This paper |
| *Mammut americanum* | MCZ 11106 | F | ~4000[2] | 3680[3] | 1.22 | 0.72 | 1:1087 | This paper |
| *Elephas maximus* | Iki | F | 2200 | 4550 | 2.24 | 1.4 | 1:484 | Shoshani et al. (1982) |
| *Loxodonta africana* | Kenia | M | 1793 | 4050 | 2.29 | 1.45 | 1:443 | Shoshani et al. (2006) |
| *Loxodonta africana* | Ngaruka | M | 6654 | 5712 | 1.35 | 0.77 | 1:1165 | Crile and Quiring (1940) |
| *Moeritherium lyonsi* | BM 9176 | - | ~150[4] | 192[3] | 0.57 | 0.44 | 1:781 | This paper |
| **OTHER MAMMALS** | | | | | | | | |
| Human | - | M | 75[5] | 1336 | **6.26** | **5.21** | 1.56 | Hartmann et al. (1994) |
| Human | - | F | 60[5] | 1198 | **6.51** | **5.52** | 1.50 | Hartmann et al. (1994) |
| Chimpanzee | Budonga Forest | M | 56.7 | 440 | **2.48** | **2.12** | 1:129 | Crile and Quiring (1940) |
| Chimpanzee | Zoo specimen | - | 44.5 | 347.4 | **2.31** | **2** | 1:128 | Shoshani et al. (2006) |

[1] Approximate body mass calculated from the skull size.
[2] Body mass calculated from the estimated shoulder height in the flesh (~ 230 cm) of this specimen on the basis of the data given by Larramendi (2015b).
[3] Jerison (1973) translated the endocast volumes to brain grams. Here, a factor of 0.8 was applied to the endocast volumes to get more reliable results.
[4] *Moeritherium* body mass calculated from the C. 7867 skull (from which the brain endocast was made). This young specimen represents an individual about 15% smaller than the restored by Larramendi (2015b). The 1000 kg of body mass estimated for this specimen by Jerison (1973) is clearly exaggerated.
[5] Approximate average body masses for different gender human beings.

casionally reported in females of *L. africana*. In African isolated populations, e.g. that from Addo Elephant National Park (South Africa), the high percentage of bilateral tusklesseness has been considered as due to either a non-selective genetic drift resulting from a high frequency of inbreeding, or from an augmented resource allocation to reproductive efforts (see e.g. Seydack et al., 2000; Whitehouse, 2002; Steenkamp et al., 2007 for discussion). Assuming as true the hypothesis that bilateral tusklessness in females from Spinagallo cave relates to an increase in the reproduction rate of endemic elephants, a rapid increase might contribute to avoid an extinction risk related to the small size of the pioneer population (Raia et al., 2003; Palombo, 2007). This hypothesis is at least partially supported by the small body size of *P.* ex gr. *P. falconeri* that suggests a shorter life span and pregnancy duration compared with extant forms. Applying the Blueweiss et al.'s (1978) formula to infer the longevity and gestation time of *P.* ex gr. *P. falconeri* (longevity in days proportional to body mass in grams$^{0.17}$ and gestation time in days proportional to body mass in grams$^{0.26}$) and assuming a longevity of 60 years, a time of gestation of 660 days, and a body mass of 6 tonnes for *L. africana*, a longevity of 36 years, and a gestation time of 314 days can be hypothesized for *P.* ex gr. *P. falconeri* from Spinagallo cave. This estimate is considerably higher than the proposed by Raia et al. (2003) because these authors estimated the longevity and time of gestation of *P.* ex gr. *P. falconeri* species, assuming a body weight of 100 kg.

A shorter life span likely implies a more rapid growth, which in turn may enhance the allometric differences between young and adult individuals that were particularly remarkable in *P.* ex gr. *P. falconeri*. The calves differ from adults in having a narrower and shorter body and a convex back shape (Fig. 5). The body become more robust with age, as observed in extant species.

## Brain Size and Encephalization Quotient

Despite the small size of *P.* ex gr. *P. falconeri*, it had an extremely large brain. This peculiar feature depends on the allometric growth of the neuro and splanchno-cranium that markedly differs from those of mainland elephants. In *P. antiquus*, for instance, during the ontogenetic growth the thickness of frontal and parietal bones greatly increases, the forehead changes its curvature, the respiratory axis rotates upward and backward, condyles and auditive meatus move to a higher position because of the positive allometric growing of the posterior part of maxillary bones. As a result, the brain case volume proportionally reduces considerably. Conversely, in *P.* ex gr. *P. falconeri* from Spinagallo cave, the thickness of frontal and parietal bones is not remarkable, the rotation of the respiratory axis is modest, and the negative allometric growth of the braincase is nearly insignificant (see Palombo, 2001b, 2003).

Thus, the adult skull of the Spinagallo specimens maintains a very large cerebral mass. The estimated weight of the brain in the adult female (MPUR/V n2), weighting only 168 kg, is of about 1440 g (a brain mass comparable to that of *Homo sapiens*) (Tab. 2). On the contrary, the much larger *P. antiquus* adult male from Pian dell'Olmo (Fiano Romano, Italy) (Maccagno, 1962), with an estimated body mass of about 11 tonnes, had a brain weighting about 7200 g. As a result, the brain mass vs body mass ratio is about 1/115 in *P.* ex gr. *P. falconeri* and 1/1500 in *P. antiquus* (Tab. 2; Fig. 7).

The encephalization quotient, sometimes employed as a measure of the relative cognitive abilities, is defined as the ratio between actual brain mass and predicted brain mass for an animal of a given size (Jerison, 1973). An encephalization quotient equal to 1.0 is considered as average. Therefore, animals having a lower and a higher value than 1.0, would be regarded as having a lower or higher cognitive abilities than the average. Humans, for example, have an EQ around 7.0 and MEQ close to 5.5 (Tab. 2; Jerison, 1973; Hurlburt, 1996), chimpanzees up to 2.5 and 2.0 respectively (Tab. 2). The EQ in extant elephants range from 1.3 to 2.3 and the MEQ from 0.77 to 1.45 depending on the sex (Tab. 2; Shoshani et al., 2006). The EQ=3.94 obtained for *P.* ex gr. *P. falconeri* is very high, similar to the values observed in delphinids (Marino, 2004). This value is much more reliable than the 6.62 value,

nearly equal of that of humans, calculated by Palombo and Giovinazzo (2005) for the *P.* ex gr. *P. falconeri* female MPUR/V n2, whose body mass was estimated by those authors to be only 91 kg.
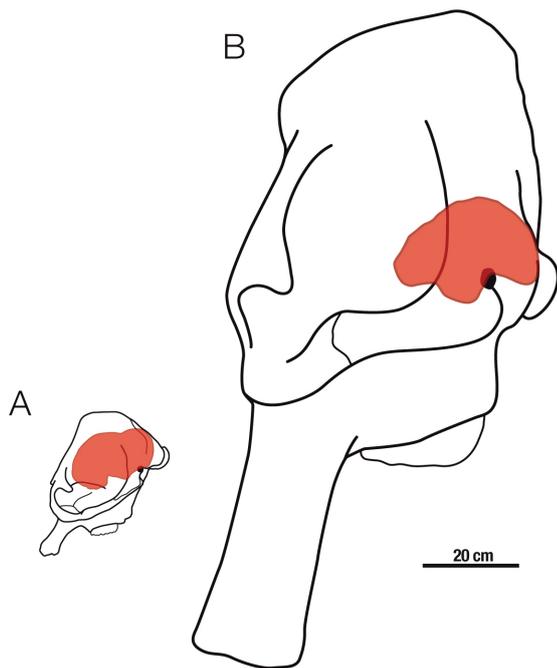


**Figure 7** – Comparison between the brain case of *Palaeoloxodon* ex. gr. *P. falconeri* (female from Spinagallo Cave, south-esatern Sicily) (a) and *Palaeoloxodon antiquus* (Pian dell'Olmo, Central Italy) (b). Reconstructions by Asier Larramendi.

The EQ = 1.21 and MEQ = 0.66 obtained for *P. antiquus* from Pian dell'Olmo, although considerably lower than that obtained for *P.* ex gr. *P. falconeri*, are similar to the values of 1.35 and 0.77 obtained for a huge extant *L. africana* male from Ngaruka (the largest elephant ever weighed according to Wood (1982)), and nearly equal to the results calculated for an adult female *M. americanum* (Tab. 2). Primitive proboscideans had sensible inferior Encephalization quotients. For instance, the values of 0.57 – 0.44 calculated here for *Moeritherium lyonsi*, are nearly 7 times less than that of *P.* ex gr. *P. falconeri* (3.94 – 3.06) and indicates that Encephalization quotient increased about 4 times from *Moeritherium* to the extant elephants.

## Remarks

*P.* ex gr. *P. falconeri*, with an estimated average weight of 300 kg for adult males and 160 kg for fully grown females, and a maximum shoulder height in the flesh of 100 cm, was probably the smallest Elephantidae thus far known, maybe with the exception of *Mammuthus creticus*, whose skeleton proportions are however unknown (Larramendi, 2015b).

The Siculo-Maltese elephants experienced a drastic size reduction of about 75% in shoulder height and 97.7% in body mass compared with the average estimated body size of its mainland ancestors *P. antiquus*. The extreme size reduction on *P.* ex gr. *P. falconeri*, led to a new body structure that made the aspect of Spinagallo dwarf elephant different from that of its young and adult relatives, having a comparatively longer neck and body trunk, proportionally longer hindlimbs and probably more digitigrade feet.

Considering that in animals having a similar body structure, the body volume augments more than the surface area as the size grows (Galileo, 1638; Schmidt-Nielsen, 1984; McGowan, 1991; Larramendi, 2015b), can be hypothesized that *P.* ex gr. *P. falconeri* had proportionally more slender limbs than its putative ancestor because the stress suffered by limb bones in the dwarf palaeoloxodonts, was proportionally smaller than in larger species. The proportions of the appendicular skeleton and

the higher digitigrade degree, suggest that the locomotion of an adult *P.* ex gr. *P. falconeri*, probably was more cursorial and agile than in extant elephants. Nonetheless, the ontogenetic changes in body proportions inferred for the Spinagallo dwarf elephants, leaves open the question if very young individuals and adults shared the same type of locomotion.

The drastic allometric size reduction experienced by Siculo-Maltese dwarf elephants, produced noticeable changes in the skull, which shows some paedomorphic features that were present in young *P. antiquus* and in extant juvenile elephants. As in young palaeoloxodonts, in the skull of the adult dwarf elephant, the parieto frontal crest is absent. As a result, the insertion for the *splenius capitis superficialis* muscles, was remarkably less extended than in *P. antiquus*, possibly because a proportionally much lighter skull, implies smaller acceleration and deceleration forces needed for head movements (see Schmidt-Nielsen, 1984). Among the paedomorphic features retained by *P.* ex gr. *P. falconeri*, the most notable is the large brain. The positive allometric increase of the braincase, resulting in a notably high EQ, was related to the need to maintain the minimal functional volume of the brain when the size of the skull was drastically reduced.

Finally, it may be speculated that the small body size of *P.* ex gr. *P. falconeri* had some biological implications that affected its physiology, and behaviour. In particular, the small size may imply a life span shorter than that of its mainland ancestor, a more rapid growth, a shorter gestation period and maybe changes in thermoregulation mechanisms.

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