23

ELEPHAS FALCONERI FROM SPINAGALLO CAVE
(SOUTH-EASTERN SICILY, HYBLEAN PLATEAU, SIRACUSA):
A PRELIMINARY REPORT ON BRAIN TO BODY WEIGHT COMPARISON.

Maria Rita PALOMBO & Caterina GIOVINAZZO

Resum

El crani d'*Elephas* (*Palaeoloxodon*) *falconeri* Busk 1867 de la cova de Spinagallo (Pleistocè Mitjà, sud-est de Sicília, Itàlia) forneix l'evidència de que la mida relativa del cervell d'aquest elefant va augmentar significativament degut a les condicions d'aïllament. El pes del cervell de l'espècie continental *Elephas* (*Palaeoloxodon*) *antiquus* Falconer & Cautley, 1847, del Pleistocè mitjà tardà d'Itàlia, correspon a devers 1/600 del seu pes corporal, mentre que als exemplars nans adults procedents de la cova de Spinagallo aquesta proporció és de 1/60. El canvi significatiu en les proporcions del cervell a *Elephas falconeri* està relacionat amb la necessitat de mantenir un volum mínim del cervell funcional, fins i tot quan el crani es redueix molt. A més, són particularment evidents característiques pedomòrfiques a la forma del crani d'*Elephas falconeri*, semblant al crani d'exemplars juvenils d'elefants vivents i extingits, especialment als que pertanyen als gèneres *Elephas* i *Loxodonta*.

S'ha estimat la massa corporal d'elefants nans i continentals en base a noves equacions basades en l'alçària a la creu i la circumferència de les potes, comprovades als elefants vivents. L'adult d'*Elephas falconeri* hauria d'haver tingut una alçària màxima a la creu de devers 120 cm i un pes de devers 150 kg, amb valors devers el 70% inferiors en l'altària i devers el 98,4% en pes en comparació amb les alçàries i pesos promig estimades per als espècimens italians d'*Elephas antiquus*.

Paraules clau: *Elephas falconeri*, mida corporal, mida del cervell, Pleistocè Mitjà, Sicília, Itàlia.

Abstract

The skull of *Elephas* (*Palaeoloxodon*) *falconeri* Busk, 1867 from Spinagallo Cave (Middle Pleistocene; south-eastern Sicily, Italy) provides evidence that the brain of this dwarf elephant significantly increased in relative size as a result of its geographic isolation. Indeed, the brain weight of continental *Elephas* (*Palaeoloxodon*) *antiquus* Falconer & Cautley, 1847, from the late Middle Pleistocene of Italy, corresponded to about 1/1600 of its body weight, whereas for the adult dwarf specimens from Spinagallo Cave, this ratio was about 1/60. The significant change in brain proportions in *Elephas falconeri* was linked to the need to maintain minimal functional brain volume, even when the skull was greatly reduced in dimensions. Moreover, paedomorphic features are particularly evident in *Elephas falconeri* skull shape, similar to the skull of juvenile specimens of extant and fossil elephants, especially those belonging to the *Elephas* and *Loxodonta* genera.

We have estimated the body mass of dwarfed and continental elephants on the basis of new equations based upon shoulder height and pad circumference and tested on living elephants. On the basis of our results, the adult *Elephas falconeri* should have had a maximum height at withers of about 120 cm and a weight of about 150 kg, with values of about 70 % in height and about 98.4% in weight as compared with the average height and weight estimated for Italian specimens of *Elephas antiquus*.

Key words: *Elephas falconeri*, brain and body size, Middle Pleistocene, Sicily, Italy.

INTRODUCTION

Elephas falconeri, the smallest dwarfed elephant on the Mediterranean islands, was first described by Busk (1867) on Malta. Numerous, particularly significant samples were found in Sicily, in Luparello (Vaufrey, 1929; Imbesi, 1956) and Spinagallo Cave (Siracusa; Ambrosetti, 1968), as well as in the travertine cropping out at Alcamo (Trapani; Burgio & Cani, 1988). In the Spinagallo Cave deposit, oligotypic, clearly endemic mammal fauna was recovered between 1958 and 1960 (Accordi, 1962).

Based on absolute dating (isoleucine racemisation), an age of about 500 ka has been inferred for this fauna (Belluomini & Bada, 1985; Bada *et al.*, 1991). Over 3000 elephant remains were uncovered, representing at least 104 individuals belonging to all age groups, although the abundance of young and very young specimens is noteworthy.

A remarkable feature of *E. falconeri* Busk 1867 is the allometric reduction of the cranium, axial skeleton and limb bones, proportionally shorter than in mainland *E. antiquus* Falconer & Cautley 1847. *E. falconeri* seems to be characterised by precocious stunting of ontogenetic

growth, as confirmed by skull features, tusk structure and cranium, axial skeleton and limb proportions (Palombo, 2001; 2003). Paedomorphic features are particularly evident in skull shape, characterised by extensive development of the brain case, linked to the need to maintain minimal functional brain volume, even when skull dimensions are greatly reduced. Actually, juvenile specimens of extant and fossil elephants, especially those belonging to the *Elephas* and *Loxodonta* genera, show very similar skull morphology to that of the adult skulls of *E. falconeri*.

Accordingly, we considered it of interest to evaluate how a reduction in size might affect the relationship between brain and body size, and whether the relatively larger brain size in *E. falconeri* depended more on precocious stunt of ontogenetic growth (paedomorphosys) or on changes in sense dependent (olfactory, optic, acoustic) and locomotion centres, induced by insular environmental conditions (e.g., Köhler & Moyà-Solà, 2004, and references therein). This paper illustrates the preliminary results of our ongoing research.

MATERIALS

To estimate brain versus body mass allometric reduction in *E. falconeri*, we used the samples found in the 20th and 50-60th years in Luparello (Vaufrey, 1929; Imbesi, 1956) and Spinagallo (Ambrosetti, 1968) Caves and in the travertine cropping out at Alcamo (Burgio & Cani, 1988; Fig. 1).

In particular, measurements of *E. falconeri* were taken from skulls and over 190 limb bones from Spinagallo Cave (Dipartimento di Scienze Geologiche, Catania University, and Museo di Paleontologia, "La Sapienza" University of Rome -MPUR), from Alcamo (Museo Geologico "G. G. Gemmellaro" – MGUP -, Dipartimento di Geologia e Geodesia, Palermo University) and from Luparello (MGUP and Institut de Paléontologie Humaine de Paris – IPH).

Moreover, measurements of *Elephas mnadriensis* Adams 1874 were taken from 7 skulls and 31 limb bones from Puntali Cave (MGUP, Museo di Paleontologia,
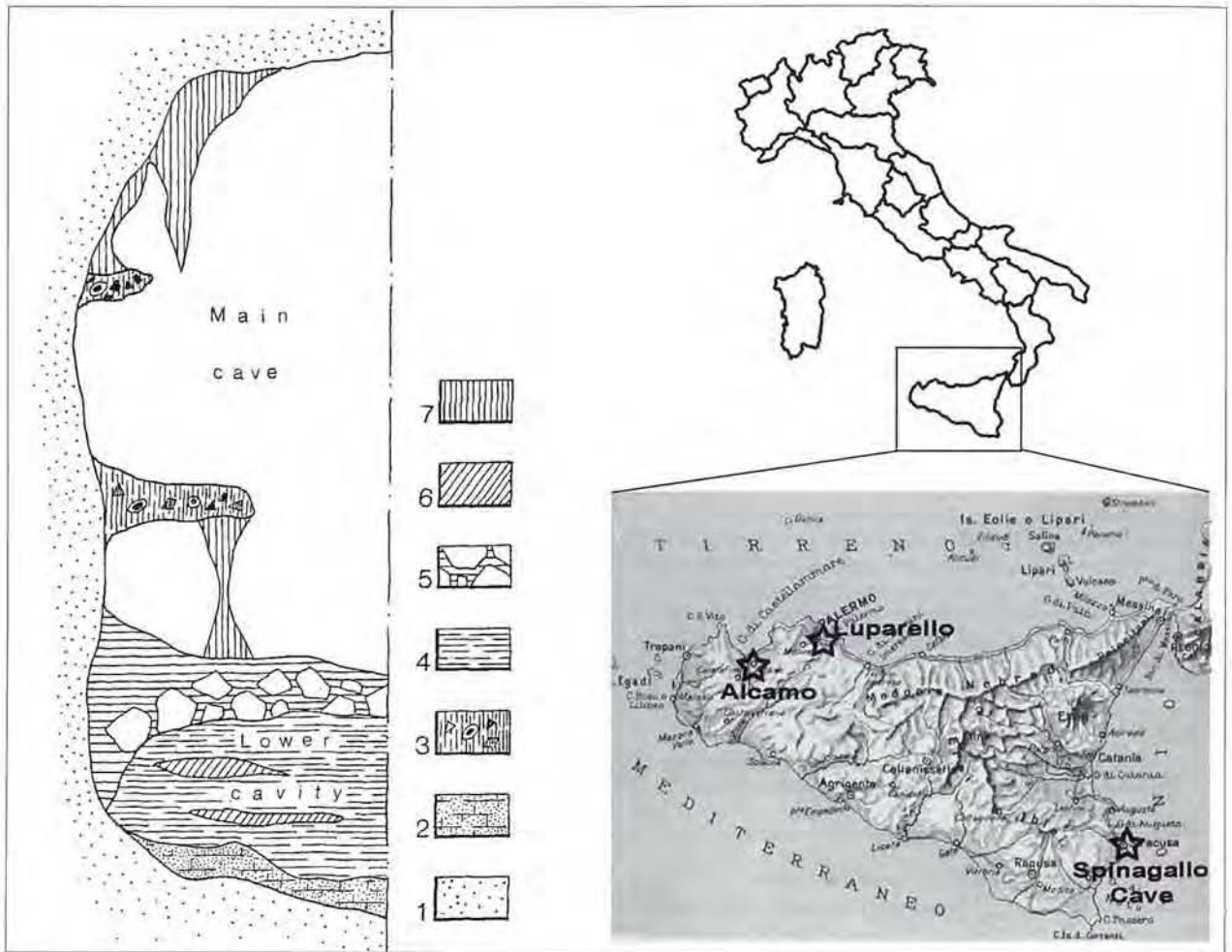

Fig. 1. Location of the most important Middle Pleistocene sites containing *E. falconeri* specimens. On the left, a schematic section of the Spinagallo Cave main cavity: 1 = Miocene limestone; 2 = "Milazzian" fossiliferous levels; 3 = bone breccia with *Elephas mnaidriensis* Adams, 1924 and *Hippopotamus pentlandi* Meyer, 1832 remains; 4 = calcareous sands with *E. falconeri* remains; 5 = floor of cemented blocks; 6 = stalagmitic levels that partly include the elephant bones; 7 = recent stalactite and stalagmite.

Fig. 1. Localització de les localitats del Pleistocè mitjà més importants amb E. falconeri. *A l'esquerra, secció esquemàtica de la part principal de la Cova de Spinagallo. 1: Calcàries del Miocè. 2: Nivells fossilífers del "Milazzià". 3: Bretxa ossífera amb restes d'*E. *mnaidriensis Adams, 1924 i* Hippopotamus pentlandi *Meyer, 1832. 4: Arenes calcàries amb restes d'*E. *falconeri. 5: Pis de blocs cimentats. 6: Nivells estalagmítics que inclouen en part ossos d'elefants. 7: Estalactites i estalagmites recents.*

Fig 2. *Elephas falconeri* Busk, 1867; Spinagallo cave (Syracuse, South-Eastern Sicily), *E. falconeri* faunal complex, early Middle Pleistocene. Reconstructed skeletons of a male (on the right), a female (left) and two young males (Museo di Paleontologia, "La Sapienza" University, Rome).
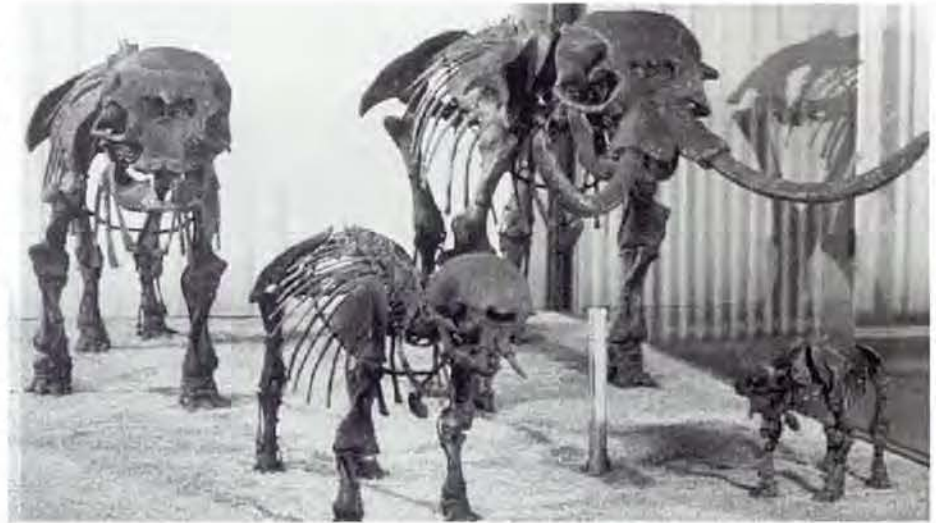
Fig. 2. Elephas falconeri *Busk, 1867; Cova de Spinagallo (Syracusa, sud-est de Sicilia), complex faunistic* E. falconeri. *Pleistocè Mitjà primerenc. Esquelets reconstruïts d'un mascle (a la dreta), una femella (esquerra) i dos mascles joves (Museu de Paleontologia, Universitat de "La Sapienza", Roma).*

Padova University - MPUP) and from some limb bones from San Teodoro Cave (MGUP, IPH).

Skull and bone measurements of *E. antiquus* were taken from 2 complete skeletons from Grotte Santo Stefano (MPUR = speciment 'B' and Museo Civico "Andrea Doria", Genova = specimen "A" as in Palombo & Villa, 2003), and one nearly-complete skeleton from Riano 'Il Crocifisso'(MPUR; Maccagno, 1962); skull measurements were also taken from specimens from Pian dell'Olmo (MPUR; Maccagno, 1962), Pignataro Interamna (Museo di Paleontologia, Napoli -MPN; Osborn, 1942, D'Erasmo & Moncharmont Zei, 1955) and Val di Chiana (Museo di Paleontologia, Florence – IGF).

As far as extant species are concerned, we examined adult specimens of *Loxodonta africana* (Blumenbach, 1797) and an *Elephas maximus indicus* Cuvier, 1798 calf (Museo Civico di Zoologia, Rome); other data are courtesy of: Kruger National Park, Tulsa Zoological Park, Chester Zoo, Knoxville Zoological Garden, Indianapolis Zoo for *L. africana* and Honolulu Zoo for *E. maximus* Linnaeus, 1758.

Directly-examined brain casts come from: *E. falconeri*, two specimens from Spinagallo Cave (Accordi & Palombo, 1971) and two natural casts from Alcamo (Burgio & Cani, 1988; MGUP); *E. manaidriensis*, four more or less incomplete casts belonging to specimens kept in the MPUP (Piccoli *et al.*, 1970; Palombo, unpublished data); *E. antiquus* from Pian dell'Olmo (MPUR).

Additional data for extant and fossil taxa were obtained from Heynes (1991), Osborn (1942) and Dechaseaux (1959) respectively.

METHODS

Body mass estimation

A correct estimation of body mass of dwarfed *Elephas falconeri* constitutes the most important basis for evaluating relative brain size changes undergone by this dwarfed species after its geographic and reproductive isolation from its continental ancestor. This is not a simple task, due to the peculiar proportions of the *E. falconeri* body, thus far determined only from compiled skeletons (Fig. 2).

The characteristic dentition of the elephant makes it imperative to focus on long bone dimensions, whose size and proportions change during growth, when estimating body mass (Maglio, 1972). Moreover, as far as dwarfed mammals are concerned, due the disproportion in tooth dimension characterising insular species (see e.g. Maglio, 1972; Gould, 1975; Azzaroli, 1982; Wayne, 1986; Demetrius, 2000; Alba *et al.*, 2001), it is widely accepted that limb bone parameters and shoulder height are the most reliable body mass predictors (e.g., Damuth, 1990; Roth, 1990; Scott, 1990; Köhler, 1993).

Some authors have suggested using maximum humerus and femur length for estimating body mass in specimens smaller than 2000 kg (see Roth, 1990). As far as body size estimation of dwarfed elephants is concerned, Roth (1990) employed long bone dimensions (length and circumference of humerus and femur) as, in her opinion, they "consistently provided the best mass estimated" (Roth, 1990, p.158). The above-mentioned author applied some established formulas for testing the relationships between long bone dimensions and body mass in animals of similar size and structure to dwarfed elephants (static interspecific model). Moreover, the same author estimated body mass of dwarfed elephants also using regressions of mass over shoulder height (ontogenetic model; Roth, 1990, p. 158); the author pointed out that estimated body weights were greater than those obtained using bone length. Notably, the limbs of dwarfed elephants are more slender than those of continental ones, probably in response to a different anatomical structure required by reduced body size, changing in turn the static and dynamic equilibrium (Palombo, 1996). On the other hand, the size of the largest *E. falconeri* was nearly the same as that of an African elephant about three years old, in spite of eventual differences in overall build. Moreover, according to our data, the "height at the shoulder / body weight" ratio in a calf averages one-fourth that of an adult African elephant.

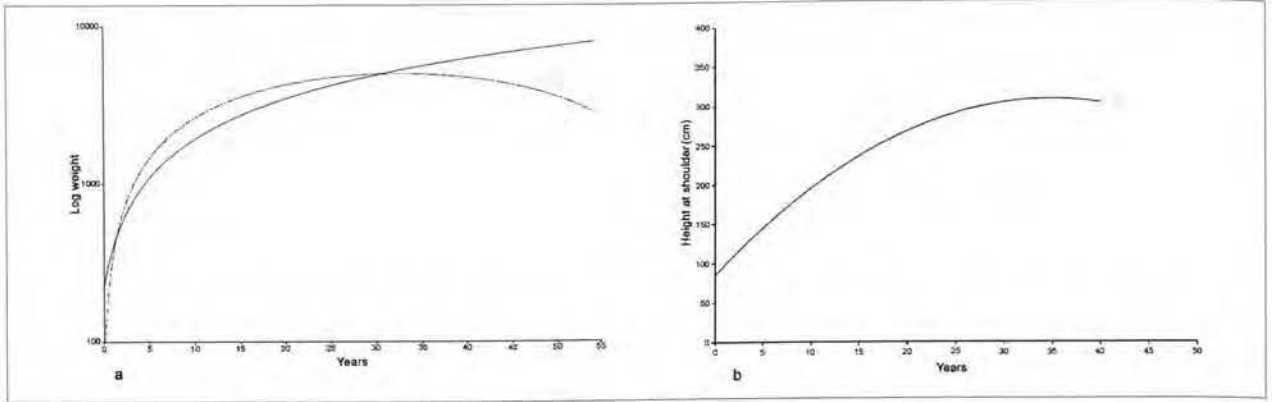Indeed, in accordance with the paedomorphic cha-

Fig. 3. Increase in body mass of African elephants during growth: poly-
nomial line of second order (dotted) and logarithmic line (con-
tinuous), (a). Shoulder height plotted against age (b).

*Fig. 3. Increment en massa corporal dels elefants africans durant el seu
creixement: línia polinòmica de segon ordre (puntejat) i línia
logarítmica (contínua), (a). Alçària a la creu respecte l'edat (b).*

racteristics of *E. falconeri*, in order to estimate the average
weight of an adult individual belonging to this species, we
have to discern the allometric relationships between bone
dimensions and body mass at different growth stages.

In keeping with the fact that mass can only be esti-
mated approximately for fossil taxa, we tried to predict
the body mass of *E. falconeri* by computing regressions of
mass over shoulder height on the basis of a new data set
obtained, along with associated body mass, from extant
elephant individuals belonging to different age groups,
as well as by estimating the allometric relationships bet-
ween body mass and long bone dimensions during the
ontogenetic growth of single individuals. This makes it
possible to test the reliability of the estimated body mass
using different equations.

According to our data, body mass in extant Indian
and African elephants increases rapidly from birth up to
8 years, after which the increase is not so significant.
Weight remains quite stable from age 40 to old age,
when it slightly decreases (Fig. 3a). It is worth noting
that shoulder height and body size are closely correlated
(Fig. 3b).

Moreover, taking into account the columnar limb
and graviportal structure of elephants (Biewener, 2000),
we have estimated the body size of living individuals
(whose weight was known) on the basis of hand and foot
circumferences, on which body weight is nearly equally
distributed. We tested the validity of methods on extant
specimens using pad circumferences and shoulder
height, comparing our estimated weights with the actual
body weight known for each individual examined. Our
data pointed to a strong correlation between both body
mass and pad circumferences, and body mass and
shoulder height (Fig. 4, Tab. 1).

Accordingly, we have estimated the body size of *E.
falconeri* from Spinagallo Cave using our equations
based on pad circumference and shoulder height, as well
as the equations based on femora and humeri length, as
proposed in Roth (1990).

Brain Mass Estimation

We measured cranial capacities on the basis of casts
of the brain case, both in fossils and extant individuals.
However, in keeping with the fact that endocranial volu-
me is not equivalent to brain volume, due the space
occupied by the *dura mater*, arachnoid and *pia mater*, as
well as by cranial nerves and blood vessels (note that
meninxes are particularly thick in elephants), we plotted
cranial capacities directly against body mass and com-
pared the results with those obtained converting cranial
capacities to brain mass. The volume of brain case casts
(cranial capacities) of specimens was transformed into
brain mass, calculating brain volume from cranial capa-
city and then converting brain volume to brain mass. To
compute brain mass, we used the following equation:
brain mass (g) = brain volume (cm^3) W 1.036 (specific
weight of brain substance; g/cm^3; Ebinger, 1974; Röhrs &
Ebinger, 2001; Köhler & Moyà Solà, 2004).

The Encephalisation Quotient (EQ) is defined as the
ratio of the actual brain mass (Mbrain) to the expected
brain mass given body size. Thus: EQ = Mbrain / Ebrain.
Ebrain is the expected brain mass (in grams) for a mam-
mal with body mass Mbody (also in grams). We have cal-
culated Ebrain with the following formulas:

Ebrain = 0,12Mbody$^{2/3}$ (Jerison, 1973)
Ebrain = 0,059Mbody$^{0.76}$ (Martin, 1984)

Regression	R^2	SEE	F	Sig.
logBM =3.2039logHS - 4.096	0.93651817	0.07478	103.27	p<0.00002
logBM =3.3221logPC - 3.388	0.96625034	0.05732	143.15	p<0.00007
BM = Body mass (g); HW = height at shoulder (cm); PC = Pad circumference (cm)				

Table 1. Regression equations used in the estimating of body mass in
extant and fossil elephants.

*Taula 1. Equacions de regressió emprades per a estimar la massa corpo-
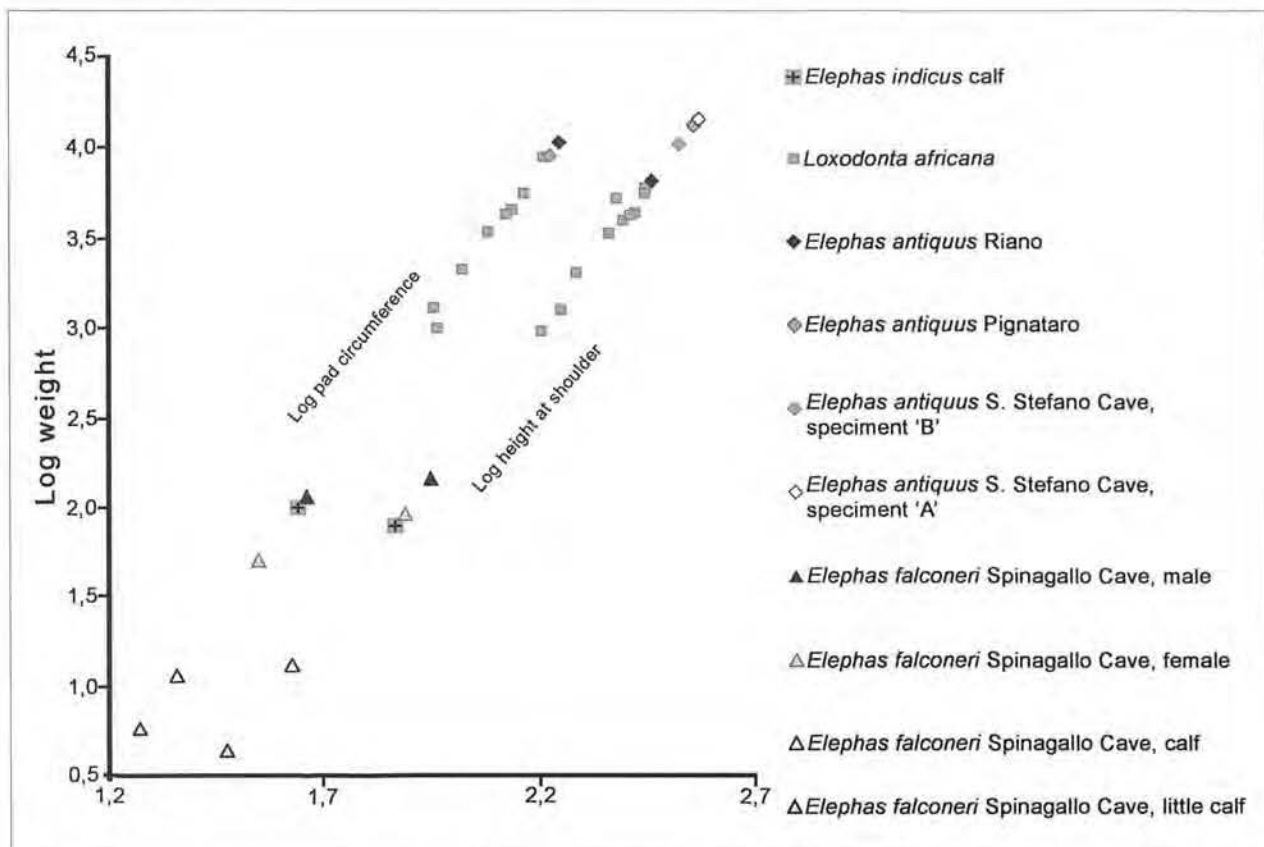ral d'elefants fòssils i actuals.*

Fig. 4. Log$_{10}$ body mass (kg) plotted against log$_{10}$ of pad circumference (mm) and log$_{10}$ of height at shoulder (mm) in extant elephant, *Elephas antiquus* Falconer & Cautley, 1847 and *Elephas falconeri* Busk, 1867.

Fig. 4. Log$_{10}$ de la massa corporal (kg) respecte el log$_{10}$ de la circumferència de les potes (mm) i el log$_{10}$ de l'alçària a nivell de la creu (mm) als elefants actuals, Elephas antiquus Falconer & Cautley, 1847 i Elephas falconeri Busk, 1867.

RESULTS

Body mass of *E. falconeri*

In Tab. 2 the body masses estimated for *E. falconeri* skeletons kept at the MPUR are reported. In particular, according to our equations, we estimated a weight of 91.1 kg for the adult female specimen (MPUR n 2), using shoulder height, and 51 kg with regression based on pad circumference; body weights calculated on the basis of

Elephas falconeri specimens	BM-HS	BM-PC
male	141.14	114.2
female	91.12	51.07
calf	12.87	11.79
little calf	4.33	6.16
BM-HS = Body mass (kg) estimated from height at shoulder regression equation from Table 1; BM-PC = Body mass (kg) estimated from pad circumference regression equation from Table 1		

Table 2. Body mass estimation for *Elephas falconeri* Busk, 1867.

Taula 2. Estimes de la massa corporal per a Elephas falconeri Busk, 1867.

humerus and femur dimensions (length -circumference) are, on the contrary, 79.8 kg - 240.2 kg and 81.3 kg -189.2 kg respectively. In addition, using the same equations, the estimated weight of E. *falconeri* (MPUR, DDG, MGUP and IPH specimens) ranges from 59.5 kg to 174.1 kg and from 183.4 kg to 520 kg on the basis of humerus length and circumference, and from 81.4 kg to 151.52 kg and from 166 kg to 517 kg on the basis of femur length and circumference. Moreover, according to the largest specimen (DDG, specimen S1) found in Spinagallo Cave, the maximal body mass obtained using femur length should be 298.27 kg.

It is worth noting that the height value obtained using humerus and femur circumferences confirms that these regression equations are not available for elephants, as we also verified on extant adult African individuals, whose weight calculated on this basis was about 40% overestimated.

In conclusion, our preliminary analysis lead us to affirm that weights estimated on the basis of the regression of shoulder height are the most consistent with the expected values for elephants of a size similar to that of *E. falconeri*. The *E. falconeri* weights, estimated on the basis of pad circumference, are underestimated and overestimated respectively for adults and young individuals.

Indeed, an *E. maximus indicus* calf, 4 cm shorter than the *E. falconeri* female, weighs 14 kg less. On the contrary, the *E. falconeri* female had a foot circumference 7 cm smaller than the *E. maximus indicus* calf; this dif-

ference can be translated into a reduction in the estimated weight of 49 kg. In reality, the feet of adult *E. falconeri* were more digitigraded than *E. antiquus* ones, probably in keeping with the decrease in body mass, a more agile gait and the need for more secure movements on relatively uneven ground and in climbing rather steep slopes (Palombo, 1996). On the contrary, the 9% difference in weight estimated for the *E. falconeri* calf (MPUR, 3), on the basis of pad circumference and shoulder height, falls within the confidence interval, confirming allometric growth.

Morphology of the brain-case endocast

Compared to those of *E. antiquus*, *E. falconeri* endocasts are more globular in shape, with a less dorsally-flattened outline. The lateral and Sylvian fissures are narrower, the temporal lobes less protrusive, the frontal lobes more curved, the olfactory bulbs larger and in an almost ventral position and the cerebellum higher and extending less at the rear. The overall shape of the brain of Spinagallo elephants is also more compact with respect to both *E. maximus* and *L. africana* (Fig. 6); however, it does not seem related to the noticeable allometric augmentation in relative brain mass, as shown by the morphology of brains belonging to young individuals of extant *L. africana* (Fig. 7).

The sense-dependent parts of the *E. falconeri* brain show a development unlike that of E. *antiquus* and extant elephants: the olfactory bulbs are not only proportionally larger, but they also have a more extensive system of nervous terminations; the impression area of the petrosal, even if not clearly delimited, does not seem to have changed significantly; the *area striata* is wide, suggesting great functionality of the vision centre, in accordance with the large orbit size (Fig. 6a).

The shape and position of the cerebellum is quite different from that of fossil and extant adult elephants:
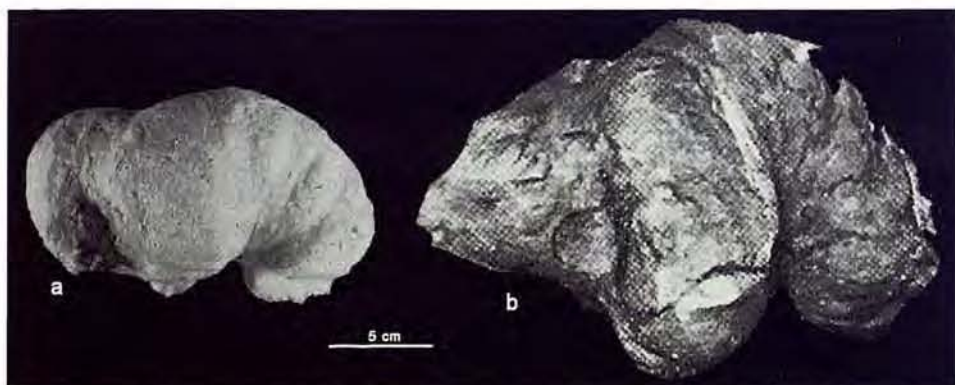

Fig . 5. Lateral view of cerebral cavity casts of *Elephas falconeri* Busk, 1867 (Spinagallo, female MPUR sn2; a) and *Elephas antiquus* Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b).

*Fig. 5. Vista lateral dels motlles de la cavitat cerebral d'*Elephas falconeri *Busk, 1867 (Spinagallo, femella MPUR sn2; a) i* Elephas antiquus *Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b).*
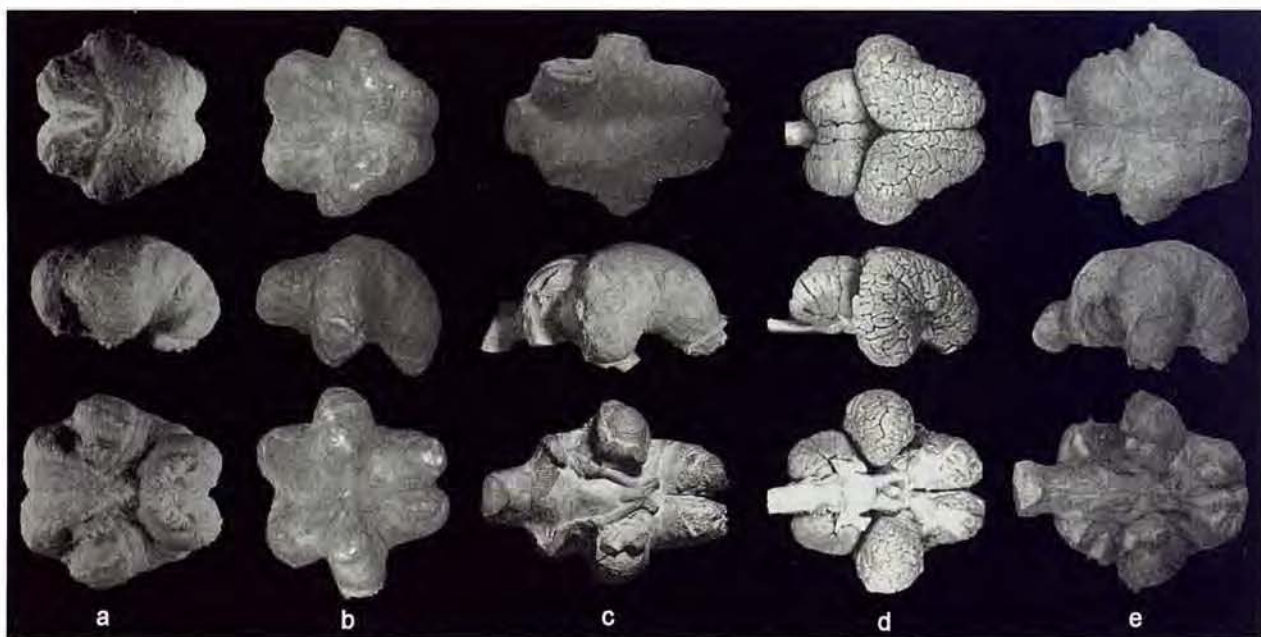

Fig. 6. Dorsal (top) lateral (middle) and ventral (bottom) views of cerebral cavity casts *Elephas falconeri* Busk, 1867 (Spinagallo, female MPUR sn2; a); *Elephas antiquus* Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b); *Mammuthus meridionalis* (Nesti, 1825; according to Dechaseaux, 1959, modified; c); *Loxodonta africana* (Blumenbach, 1797) (d); *Elephas maximus* Linnaeus, 1758 (after Osborn, 1942, modified; e). Not in scale.

*Fig. 6. Vistes dorsal (a dalt), lateral (enmig) i ventral (a sota) dels motlles de la cavitat del cervell d'*Elephas falconeri *Busk, 1867 (Spinagallo, femella MPUR sn2; a);* Elephas antiquus *Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b);* Mammuthus meridionalis *(Nesti, 1825; d'acord amb Dechaseaux, 1959, modificat; c);* Loxodonta africana *(Blumenbach, 1797) (d);* Elephas maximus *Linnaeus, 1758 (segons Osborn, 1942, modificated; e). No a escala.*
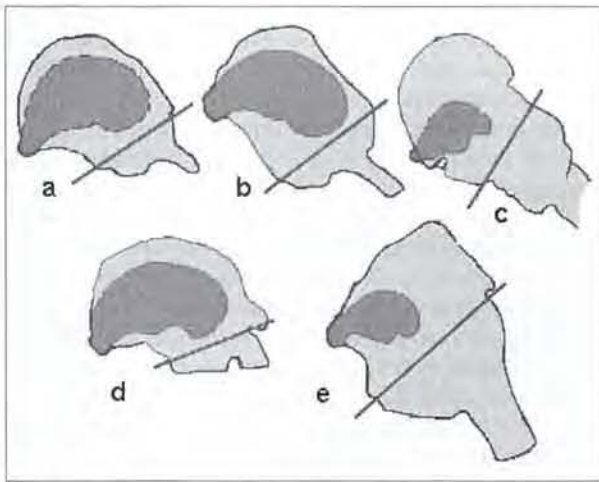
Fig. 7. Cerebral cavity and respiratory axis in: a-b = *Elephas falconeri* Busk, 1867 from Spinagallo cave, a = juvenile, b = adult female; c = *Elephas antiquus* Falconer & Cautley, 1847; d-e = *Loxodonta africana* (Blumenbach, 1797), e = foetal individual, f = adult individual. Not in scale.

Fig. 7. Cavitat del cervell i eix respiratori a: a-b = Elephas falconeri *Busk, 1867 de la cova de Spinagallo, a = juvenil, b = femella adulta; c =* Elephas antiquus *Falconer & Cautley, 1847; d-e =* Loxodonta africana *(Blumenbach, 1797), e = fetus, f = adult. No a escala.*

the cerebellum of *E. falconeri* is proportionally higher and shorter, whereas the middle lobe is enlarged towards the back and seems to partially cover it (Fig. 5).

In addition, it is worth noting that the elongated *M. meridionalis* brain shows quite archaic features in comparison with both *E. antiquus* and extant taxa (Fig. 6 c).

Brain versus body mass proportion

The proportion between cranial capacity/brain mass and body mass confirms, as already observed by Accordi & Palombo (1971), that brain mass in *E. falconeri* is noticeably greater than in continental adult elephants of the same age.

The encephalisation index in the adult female of *E. falconeri* is 6.62 (Jerison, 1973) and 4.30 (Martin, 1984), whereas for *E. antiquus* we have obtained an index value of 1.30 (Jerison, 1973) and 0.52 (Martin, 1984). Accordingly, the *E. falconeri* brain case is from 50% (Jerison, 1973) to 17% (Martin, 1984) larger than in its continental ancestor, surpassing the values given for primates (Sellers, 2002). Moreover, the brain to body mass proportion falls within the range of modern man and Phocenidae (Fig. 8).

The *foramen magnum*, as well as the orbit, are also proportionally larger than in *E. antiquus* (Maccagno,
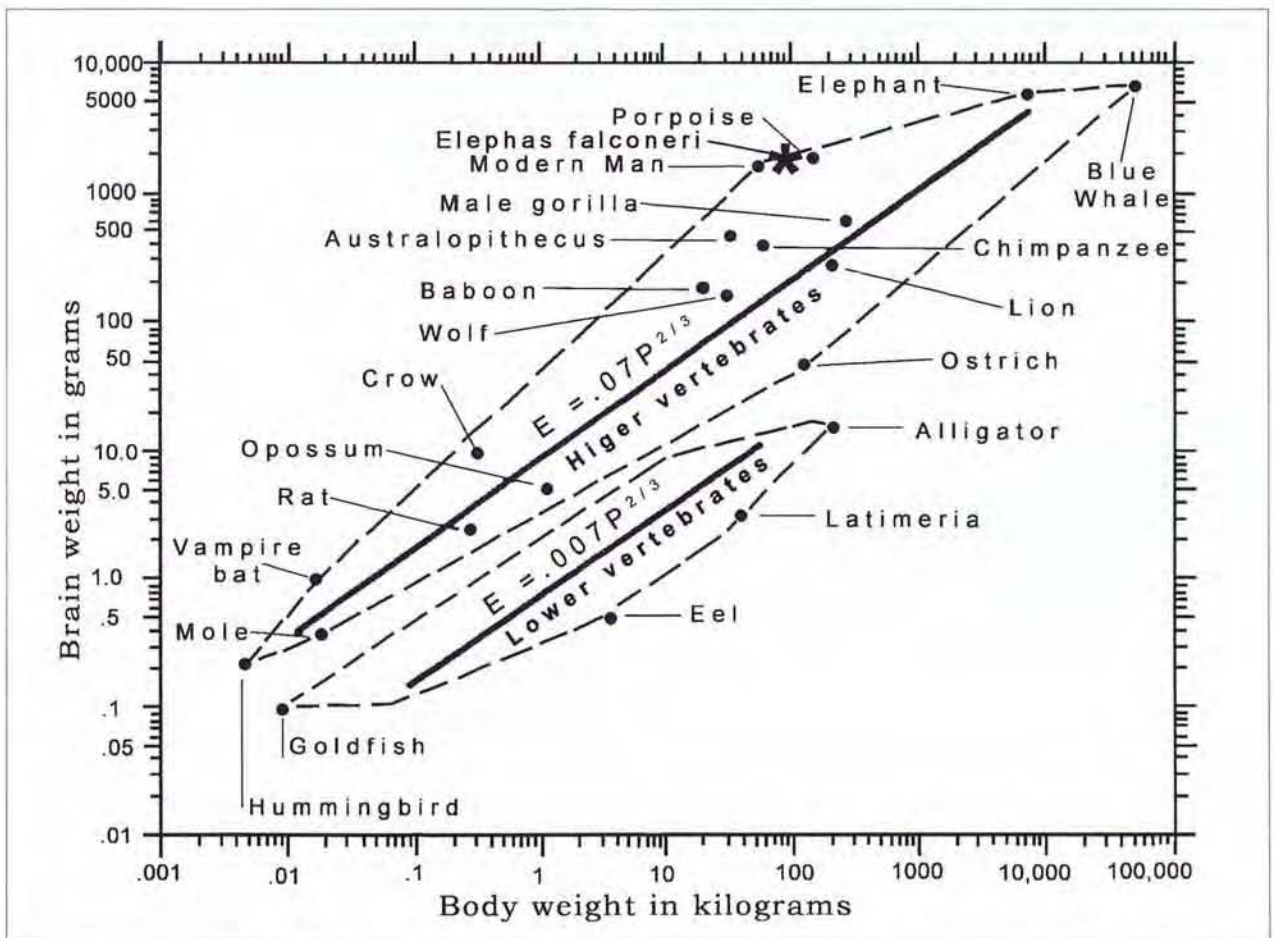

Fig. 8. Logarithm of brain weight plotted against logarithm of body weight in lower and higher vertebrates (according to Jerison, 1973, modified). It is worth noting that *Elephas falconeri* Busk, 1867 falls between modern man and Phocenidae.

Fig. 8. Logaritme del pes del cervell respecte el logaritme del pes corporal a vertebrats superior i inferiors (d'acord amb Jerison, 1973, modificat). És notable veure com Elephas falconeri *Busk, 1867 cau entre els humans moderns i els focènids.*

1962; Ambrosetti, 1968), confirming the great functionality of sense organs in the endemic dwarf elephant of Sicily. According to Köhler & Moyà-Solà (2004), body size, orbit and *foramen magnum* size are consistently correlated in extant and fossil wild bovids. In *Elephas falconeri*, the proportion of orbit size (log $\sqrt[4]{}$ height X width) to body mass (log $\sqrt[4]{3}$ body mass) and the proportion of *foramen magnum* size (log $\sqrt[4]{}$ height X width) to body mass (log $\sqrt[4]{3}$ body mass) are about 10% and 12% greater than in *E. antiquus*.

Moreover, Köhler & Moyà-Solà (2004) hypothesised that under altered conditions in predator free insular environments, functional demands on neural performance are reduced, allowing a reduction in brain structures and associated sense organs, as suggested, for example, by the small orbits and reduced visual brain structures of *Myotragus*. Nevertheless, our preliminary analysis performed on very young specimens of *Loxodonta africana*, similar in size to *E. falconeri*, shows that the proportion between brain mass and body mass does not vary to a great extent (Fig. 7).

DISCUSSION

The results thus far obtained from our analysis clearly demonstrate that the brain volume of *E. falconeri* was greater than that of its possible ancestor, *E. antiquus*, and, in any case, that its brain is significantly larger than that of adult individuals of extant elephants. This apparently runs counter to the fact that large insular mammals are characterised by a proportional decrease in the volume and efficiency of the central nervous system, especially as far as the functionality of the sense organs is concerned.

As clearly demonstrated by Köhler & Moyà-Solà (2004), the endemic bovid *Myotragus*, from the Plio-Pleistocene deposits of Mallorca, underwent a significant reduction in relative brain size, especially affecting the vision and locomotion centers. These changes, which parallel those shown by domesticated animals, have been interpreted as an adaptive response to insular environmental conditions, in particular to a lack of competitors and predators. As in the strongly endemic and unbalanced Balearic faunas, *E. falconeri* was also the only large Spinagallo mammal. Consequently, we would expect this species to have undergone changes in the relative size of the brain and sense organs similar to those of taxa living in anthropogenic environments or without any predation pressure, such as domesticated or endemic dwarfed mammals. However, it is worth noting that the most remarkable feature of *E. falconeri* is the peculiar shape and proportions of its skull (due to the allometric growth of the maxillary and occipital bones with respect to other cranial bones) and the steeply-inclined respiratory axis. Indeed, the skull is characterized by extensive development of the brain case, linked to the need to maintain minimal functional brain volume, even when skull dimensions are greatly reduced. Tusk structure and the proportions of the cranium, axial skeleton and limbs are consistent with such a paedomorphic feature (Palombo, 2004 and references therein).

Accordingly, *E. falconeri* seems to be characterized by precocious stunting of ontogenetic growth. Actually, juvenile and subadult specimens of extant and fossil elephants, especially those belonging to *Elephas* and *Loxodonta* genera, show very similar skull morphology to that of adult skulls of *E. falconeri* (Palombo, 2001). However, as suggested by several authors (e.g. Sondaar, 1977; Roth 1990; 1992; Damuth, 1993; Grant, 1998; Köhler & Moyà-Solà, 2004.), the lack of predators in insular environmental conditions noticeably increased population density, leading to an increase in intraspecific competition for limited food resources. On the other hand, it appears that in an insular environment and in the absence of competition factors, large herbivores reached the minimum body size required depending on their trophic level and metabolic rate, in accordance with the niche available on the island (Palombo, 2004). Accordingly, the hypothesis that the paedomorphic allometric growth of *E. falconeri*, as well as an increase in the reproductive rate (Raia *et al.*, 2003), best contributed to maintaining the optimum biomass during resource allocation shifts cannot be ruled out.

Extensive development of the areas assigned to sight, which in turn affect total brain size, can be correlated with relatively large orbits, slightly shifted to a more frontal position than in the skulls of adult elephants. On the other hand, it not easy to interpret the different proportion of the cerebellum; it seems to be higher but less elongated than the cerebellum of *E. antiquus* and extant elephants. In keeping with the more agile, faster walking gait characterising the dwarfed elephant from Spinagallo with the respect to its ancestor (Palombo, 1996), the shape and extension of the cerebellum could be inferred as depending on increased energy required for locomotion.

In any case, more data are needed to clarify the meaning and importance of extension changes in each area, affecting the entire shape of the central nervous system.

CONCLUSIVE REMARKS

The relative larger size of the brain of Spinagallo specimens in respect to their ancestor is primarily due to the impossibility of proper brain function below a critical volume, as well as to the great reduction in the pneumatisation of parietal and fontal bones. Actually, the positive increased allometric size of the skull affects the posterior region of maxillary bones (which increase in height to the edge of tooth alveoli) more than the neural and facial region of the skull. Consequently, the whole architecture of the adult skull is modified and exhibits some paedomorphic features, such as an overall globose shape, similar to that of young animals. According to Gould (1977), a large brain, "by its own mechanical pressure, causes correlated features" such as a short face, a vaulted cranium and a low *foramen magnum*. The absence of the latter characteristic in the Spinagallo skull is consistent with the persistence of positive allometric heightening of the posterior maxillary region.

The brain/body proportion of *E. falconeri* is contrary to the pattern reported for insular taxa, such as

Myotragus, as well as domesticated animals. As far as *E. falconeri* is concerned, an increase in brain size seems to be related more to a precocious stunt in growth than to the special environmental conditions of the insular ecosystem. In fact, the increase in relative brain size seems to be related to the evident paedomorphic features characterising the Spinagallo elephant. Moreover, changes in shape and proportions shown with respect to the *E. antiquus* ancestor could be interpreted as an adaptive strategy for increased fitness and efficient exploitation of energy related to reduced body dimensions and, possibly, faster metabolic activity. For instance, the smallest mammals, such as rodents, which have a brief life, a high reproductive rate and an accelerated metabolism, have a proportionally large brain.

Our ongoing research, dedicated to defining the allometric growth of brain and body size in extant and fossil elephants, should highlight the actual meaning of the apparently-advanced features of the central nervous system of *E. falconeri*.

REFERENCES

Accordi, B. 1962. La grotta ad elefanti nani di Spinagallo (Siracusa). *Atti Acc. Sc.Ferrara*, 37: 9-15.

Accordi, F.S. & Palombo, M.R. 1971. Morfologia endocranica degli elefanti nani pleistocenici di Spinagallo (Siracusa) e comparazione con l'endocranio di *Elephas antiquus*. *Rend. Accad. Naz. Lincei*, s. 8, 51: 111-124.

Alba, D.M., Moyà-Solà, S., Köhler, M. & Rook, L. 2001. Heterochrony and the cranial anatomy of *Oreopithecus*: some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. *In* De Bonis, L., Koufos, G. & Andrews, P. (eds.), *Hominoid Evolution and Climatic Change Vol 2 Phylogeny of the Neogene Hominoid Primates of Eurasia*: 284-315. Cambridge University Press. Cambridge.

Ambrosetti, P. 1968. The Pleistocene dwarf elephants of Spinagallo (Siracusa, south-eastern Sicily). *Geolologica Romana*, 7: 277-398.

Azzaroli, A. 1982. Insularity and its Effects on Terrestrial Vertebrates: Evolutionary and Biogeographic Aspects. *In* Montanaro Galitelli, E. (ed.), *Palaeontology Essential of Historical Geology*: 18-23. Modena.

Bada, J.L., Belluomini, G., Bonfiglio, L., Branca, M., Burgio, E. & Delital, L.M. 1991. Isoleucine epimerization ages of Quaternary mammals from Sicily. *Il Quaternario*, 4(1a): 49-54.

Belluomini, G. & Bada, J.L. 1985. Isoleucene epimerization ages of the dwarf elephants of Sicily. *Geology*, 13: 451-452.

Biewener, A.A. 2000. Scaling of terrestrial support: differing solutions of mechanical constraints of size. *In* Brown, J.H. & West, G.B. (eds.), *Scaling in Biology*: 51-66. Oxford Unversity Press. Oxford.

Burgio, E. & Cani, M. 1988. Sul ritrovamento di Elefanti fossili ad Alcamo (Trapani, Sicilia). *Naturalista Siciliano*, 12: 87-97.

Busk, G. 1897. Description of the remains of three extinct species of elephant, collected by Capt. Spratt, C.B., R.N., in the ossiferous cavern of Zebbung, in the island of Malta; partly from the notes of the late H. Falconer. *Trans. Zool. Soc.*, 6 (5): 227-306.

D'Erasmo, G. & Moncharmont Zei, M. 1955. Il cranio giovanile di *Elephas antiquus italicus* di Pignataro Interamna, nella valle del Liri. *Accad. Sci. fis. e mat. (Soc. Naz. Sci. Napoli), Rend. s*. 4, 22: 261 pp.

Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements. *In* Damuth, J. & MacFadden. B.J. (eds.), *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*: 207-228. Cambridge University Press. Cambridge.

Damuth, J. 1993. Cope's rule, the island rule and the scaling of mammalian population density. *Nature*, 365: 748-750.

Dechaseaux, C. 1959. L'encephale d'*Elephas meridionalis*. *Annales de Paleontologie. Invertebres*, 44: 267-278.

Demetrius, L. 2000. Directionality theory and the evolution of body size. *Proc. Royal. Society London, B*, 267: 2385-2391.

Ebinger, P. 1974. A cytarquitectonic volumetric comparison of brains in wild and domestic sheep. *Z. Anat. Entwickl-Gesch*, 144: 267-302.

Gould, S.J. 1975. On the scaling of tooth size in mammals. *Am. Zool.*, 15: 351-362.

Gould, S.J. 1977. *Ontogeny and Phylogeny*. Belknap Press. Harward. 499 pp.

Grant, P.R. 1998. Patterns on islands and microevolution. *In* Grant, P.R. (ed.), *Evolution on Islands*: 1-17. Princeton University Press. Princeton.

Haynes, G. 1991. *Mammoths, mastodonts, and elephants: biology, behavior, and the fossil record*. Cambridge University Press. Cambridge.

Imbesi, M. 1956. Sugli elefanti nani della grotta di Luparello (Palermo). *Atti Congr.INQUA Rome-Pise*, 195: 443-447.

Jerison, H.J. 1973. *Evolution of the brain and intelligence*. Academic Press. New York.

Köhler, M. 1993. Skeleton and habitat of recent and fossil ruminants. *Münch. Geow. Abh.*, 25:1 –88.

Köhler, M. & Moyà-Solà, S. 2004. Reduction of Brain and Sense Organs in the Fossil Insular Bovid *Myotragus*. *Brain Behav*. 63: 125-140.

Maccagno, A.M. 1962. Gli elefanti fossili di Riano (Roma). *Geol. Romana*, 1: 33-131.

Maglio, V.J. 1972. Evolution of mastication in the Elephantidae. *Evolution*, 26: 638-658.

Martin, R.D. 1984. Body size, brain size and feeding strategies. *In* Chivers, D., Wood, B. & Bilsborough, A. (eds.), *Food acquisition and processing in primates*: 73-104. Plenum Press. New York.

Osborn, H.F. 1942. *Proboscidea Vol. 2*. The American Mus. Press. New York. 1675 pp.

Palombo, M.R. 1996. Large Pleistocene mammals of the Mediterranean islands. *Vie et Milieu*, 46 (3/4): 365-374.

Palombo, M.R. 2001. Paedomorphic features and allometric growth in *Elephas falconeri* skull from Spinagallo (Middle Pleistocene, Sicily). *In* Cavaretta, G., Gioia, P., Mussi, M. & Palombo, M.R. (eds.), *The World of Elephants*: 492-496. CNR. Roma.

Palombo, M.R. 2003. *Elephas*? *Mammuthus*? *Loxodonta*? The question of the true ancestor of the smallest dwarfed elephant of Sicily. *In* Reumer, J.W.F., de Vos, J. & Mol, D. (eds.), *Advances in Mammoth Research (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999)*. *Deinsea*, 9: 273-291.

Palombo, M.R. 2004. Dwarfing in insular mammals: the endemic elephants of Mediterranean islands. *In:* Baquedano, E., Rubio, S. (eds.), *Homenaje a Emiliano Aguirre, Zona Archeologica 4 (2 Paleontologia)*: 354-371. Museo Arqueológico Regional. Madrid

Palombo, M.R. & Villa, P. 2003. Sexually dimorphic characters of *Elephas (Palaeoloxodon) antiquus* from Grotte Santo Stefano (Viterbo, Central Italy). *In* Reumer, J.W.F., de Vos, J. & Mol, D. (eds.), *Advances in Mammoth Research (Proceedings of the Second International Mammoth Conference, Rotterdam, May 16-20 1999)*. *Deinsea*, 9: 293-315.

Piccoli, G., Laddaga Formentin, O., Winkler del Pup, G. & Zanferrari Visentin, M.E. 1970. Studi su resti di crani di *Elephas mnaidriensis* Adams del Pleistocene di Sicilia. *Memorie degli Istituti di Geologia e Mineralogia dell' Universita di Padova*, 27: 33 pp.

Raia, P., Barbera, C. & Conte, M. 2003. The fast life of a dwarfed giant. *Evolutionary Ecology*, 17:293-312.

Röhrs, M. & Ebinger, P. 2001. Welche quantitativen Beziehungen bestehen bei Säugetieren zwischen Schädelkapazität und Hirnvolumen?. *Mamm Biol.*, 66: 102-110.

Roth, V.L. 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference. *In* Damuth, J. & MacFadden. B.J. (eds.), *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*: 151-179. Cambridge University Press. Cambridge.

Roth, V.L. 1992. Inferences from allometry and fossils: dwarfing of elephants on islands. *In* Futuyma, D. & Antonovics, J. (eds.), *Oxford surveys in evolutionary biology*, 8: 259-288. Oxford University Press. Oxford.

Scott, K.M. 1990. Postcranial dimensions of ungulates as predictors of body mass. *In* Damuth, J. & MacFadden, B.J. (eds.), *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*: 301-336. Cambridge University Press. Cambridge.

Sellers, W.I. 2002. *Lecture Notes. Primate brains.* 16 pp. http://mac-huwis.lut.ac.uk/~wis/lectures/

Sondaar, P.Y. 1977. Insularity and its effect on mammal evolution. *In* Hecht, M.K, Goody, P.C. & Hecht, B.M. (eds.), *Major patterns in vertebrate evolution*: 671-707. Plenum. New York.

Vaufrey, R. 1929. Les Eléphants nains des îles meditérranéennes et la question des Isthmes Pléistocène. *Archiv. Inst. Paléont. Hum.*, 6: 1-220.

Wayne, R.K. 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution*, 40: 243-261.