

## Scaling of proximal limb bones between *Elephas antiquus* and its insular descendant *Elephas falconeri*

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**SUMMARY:** In this study we have calculated allometric equations for the scaling of linear dimensions (length and diameter) of the proximal elements of limbs in *Elephas antiquus* and of its insular descendant *Elephas falconeri*. We have found that the legs of these closely-related elephants species of the Middle and the Late Pleistocene scale according to the geometric similarity model. According to this model, all linear dimensions scale proportionally to the mass raised to the 1/3 power, so the relationship between them is independent of mass. By the same token, our results contradict other theoretical models such as elastic similarity. Some mechanical consequences of geometric similarity are discussed.

### 1. INTRODUCTION

Due to the scaling of physical, ecological and metabolic factors, large mammals are rather different from those of small size. Since Kleiber (1932) showed that the metabolic demands of mammals scale according to  $M^{3/4}$ , where  $M$  is the body mass, a number of studies have been devoted to the effects of scaling or allometry. The surface area of the body, and the cross-sectional area of bones, muscles and tendons, all scale with the square of linear dimensions, while the mass scales with the cube. Because of this simple relationship, large mammals have, in addition, a smaller mass-specific resting metabolism, while life span or age of first reproduction, are increased (Alexander 1992; Biewener 1989, 1990; Calder 1996; Damuth 2001; Gould 1975; Hildebrand 1995; Norris 1998; Pollock *et al.* 1994; Promislow & Harvey 1990; Sinervo *et al.* 2000; Stearns 1983, West *et al.* 1997). The purpose of this study is to examine scaling in linear dimensions (length and diameter) in the proximal limb bones of the extinct European elephant *Elephas antiquus*, Middle to Late Pleistocene

in age. We concentrate on the notable size reduction that has occurred in the evolution of *E. antiquus* in Sicily, where it is recognised to have given rise to a separate species, the dwarf elephant, *Elephas falconeri*.

### 2. MATERIALS AND METHODS

We have collected, in part from the literature (Maccagno 1962, and references therein; Ambrosetti 1968), up to 51 measurements of the length and the cross-sectional diameter at the midshaft of humeri and femurs of *E. antiquus* and its insular descendant *E. falconeri*. Measurements of the latter are on specimens from the Spinagallo caves (Sicily, Italy) previously described by Ambrosetti (1968). We have re-measured bones of *E. falconeri*, now held at the University of Catania (Sicily). One of us (M.C.) has taken further measurements from limb bones of *Elephas antiquus* recovered from the lacustrine basin of Mercure (Lucania, Italy). Professor Paul Mazza, University of Florence, kindly gave us further measurements. We have reported exclusively data regarding adult individuals, i.e. we restricted our sample

to long bones with fused epiphyses. This avoids the confounding effect of differential growth during ontogeny.

We transformed our data to logarithms and performed least squares regressions, plotting bone midshaft diameter versus total length. The exponents of the allometric equations have been appraised in comparison with the expectations of common scaling models (Alexander *et al.* 1979; MacMahon 1973, 1975). Because the data of Alexander *et al.* (1979) were obtained with mass as the dependent variable, we devised a simple arithmetic transformation, by dividing Alexander *et al.*'s general equations by each other. This allows direct comparison to our equations, which were obtained using two linear dimensions.

### 3. SOURCES OF ERROR

Fossil bones are not fresh bones. Since we rely upon linear measures, we need to consider whether taphonomic processes could have altered bone proportions. We have not found any mention in the literature that the diameters

of bones are somehow more or less easily weathered than their lengths. Indeed, diaphyses are formed from lamellar bone, whereas epiphyses are formed from trabecular bone. To avoid the possibility that the different responses of those tissues to diagenetic stresses may have influenced our equations, we have chosen to limit ourselves to data from well-preserved bones. Unfortunately, this slightly limits our sample, especially concerning *E. antiquus* specimens. Many studies suggest allometric equations are valid even within a single genus (e.g. Woodhead & Reiss 1991). Moreover, since the data cover a large size span (*E. falconeri* was close to  $10^{-2}$  times the mass of *E. antiquus* according to the estimates made by Roth 1990), we consider our equations to be reliable (Calde 1996). Nonetheless, the biological interpretation of allometric relationships is still the subject of debate (Kozlowsky & Weiner 1997; West *et al.* 1997). And since we have taken some data from the literature, we have repeated possible authors' errors in measuring and/or reporting bone dimensions.

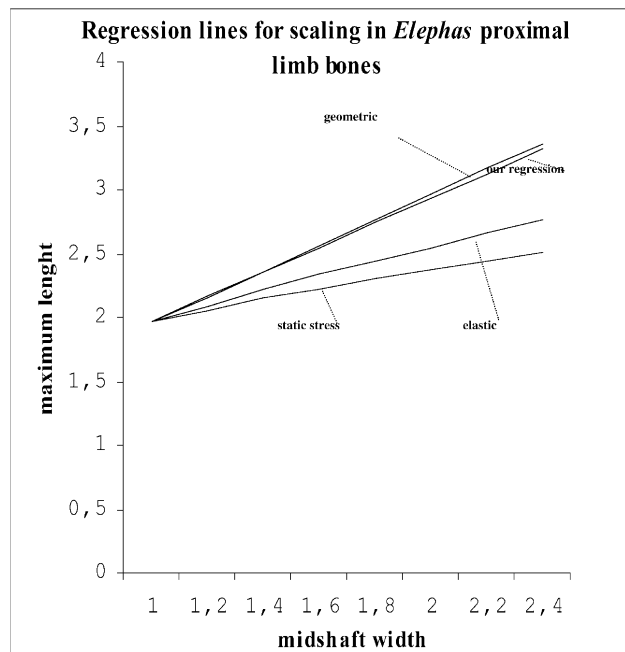


Fig.1 - Logarithmic plot of our general equation (see text for explanations) for proximal limb bone width at midshaft versus bone total length for the species *Elephas falconeri* and *Elephas antiquus*. Regression lines predicted by common scaling models are also plotted for comparison.

#### 4. RESULTS

For the humerus, we have found  $l = 5.11 d^{1.115}$ ,  $r = 0.981$ ,  $n=24$ ; for the femur;  $l = 13.97 d^{0.889}$ ,  $r = 0.972$ ,  $n = 27$ ; and overall (adding humerus to femur data)  $l = 9.183 d^{0.979}$ ,  $r = 0.958$ ,  $n = 51$ . In these equations,  $l$  is the length of the bone and  $d$  the diameter, in millimeters. The exponents are all very close to 1, that is, length and diameter scale isometrically.

The slight differences between the humerus and femur exponents are hardly significant, and may be due only to sample bias. Most significantly, they differ markedly from exponents predicted by models other than geometric similarity (see below). At first glance, this result is amazing. If the model of geometric similarity is valid, the linear dimensions both scale to the 1/3 power of the mass. Thus, dividing between them, we get:  $l/d \propto M^0$ , that is, the ratio of length to diameter scales independently of mass. Alexander *et al.* (1979) obtained a very similar result. From their equations, we calculate  $l/d \propto M^{0.01}$ , for limb bones across all mammals. This corresponds to our  $l \propto d^{0.979}$ . However, as is easily seen, body weight loads limb bone cross-sectional area in direct proportion to mass (i.e. to mass to the power of one), whence cross-sectional area itself scales to the 2/3 power of the mass, and expected stress scales to  $M^1/M^{2/3} = M^{1/3}$ .

#### 5. DISCUSSION

McMahon (1973, 1975) proposed that, to respond elastically with similar deformations, limb bones (and the whole limb) had to scale according to the relationship  $d \propto l^{3/2}$ , a model named elastic similarity. Since we have calculated around a fourfold difference between lengths and diameters of humeri and femurs of *Elephas antiquus* and *E. falconeri*, the observed midshaft widths of the latter are up to two times greater than expected under the elastic similarity model, (see appendix 1).

As shown by Biewener (1989), large mammals tend to compensate for the increase in relative stress loading their limb bones with postural adaptations. Large mammals have more

erect legs, so that the body weight is more vertically loaded upon them. A better moment arm advantage is thereby provided for the leg muscles. This is expected to produce a rather conservative average stress on bones (Biewener 1989, 1990). Lower body weight allows small mammals to adopt a more crouched posture (Alexander 1992). Biewener (1989, 1990) demonstrated that these adaptations are sufficient up to around 300 kg, and that above this limit large animals adapt by sacrificing a large part of their cursorial performance to the needs of support. Moreover, for the heaviest mammals, such as rhinos, Biewener (1990) found limbs to follow an allometric relationship named static stress similarity, in which  $l \propto d^{1/2}$ . Hildebrand (1994) further indicated 900 kg as a critical limit, beyond which limbs become columnar. Examining our data in the light of these models, the width of proximal limb bones of *E. falconeri* appears increased even if compared to the predictions of static stress similarity, which supposedly governs scaling in both extant elephants and *Elephas antiquus*. But *E. falconeri* limbs do not appear stouter than those of extant mammals of comparable size (see, for example, data reported in McMahon 1975 and Scott, 1990). Our results suggest that elastic similarity does not occur in the evolution of limbs from *E. antiquus* to *E. falconeri* during the Middle Pleistocene of Sicily (Fig. 1; Belluomini & Bada 1985). Indeed, elastic similarity seems not to apply if one deals with any mammals other than bovids (Hildebrand 1994). Since only postural changes have occurred in limbs, despite the great size reduction in the evolution of *E. antiquus* to *E. falconeri* (diameter/length ratios remain constant, at least for humerus and femur), we suggest that *E. falconeri* could move in more agile manner (maybe through less constrained articular movements) than *E. antiquus*. It is worth noticing that this suggestion agrees with the findings of Caloi & Palombo (1994) and Palombo (1996) for the elephants of Spinagallo. In keeping with this, Calder (1996, p.166) shows that in mammals, the angle in the sagittal plane covered by the legs during movement, decreases with size.

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APPENDIX 1 – CALCULATED STATISTICS (all measurements are in millimeters).

	Femur (length/diameter)			Humerus (length/diameter)		
	n	mean	coeff. of var	n	mean	coeff. of var.
<i>Elephas antiquus</i>	3	1482/182.7	4.93/3.85	4	1230/138.1	5,86/20.87
<i>Elephas falconeri</i>	2	1345/37.2	12.4/15.3	23	286/38.4	12,8/17.9