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Abstract

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Letter to the Editor of the Journal of Theoretical Biology

Long-Bone Allometry of Terrestrial Mammals and the Geometric-Shape and Elastic-Force Constraints of Bone Evolution

A natural similarity in body dimensions of terrestrial animals noticed by ancient philosophers remains the main key to the problem of mammalian skeletal evolution with body mass explored in theoretical and experimental biology and tested by comparative zoologists. We discuss the long-standing problem of mammalian bone allometry commonly studied in terms of the so-called "geometric", "elastic", and "static stress" similarities by McMahon (1973, 1975a, 1975b). We revise the fundamental assumptions underlying these similarities and give new physical insights into geometric-shape and elastic-force constraints imposed on spatial evolution of mammalian long bones.

A realistic description of an animal skeletal bone might be thought in terms of a hollow, irregular, curved structural rigid beam, whose linear dimensions guarantee the avoidance of fracture caused by axial and non-axial external peak loads. Meanwhile, most mammalian skeletal bones manifest a *geometric similarity* that permits one to introduce a *cylinder-shape approximation* through the characteristic dimensions D_{is} and L_{is} related to bone diameter and length for a given bone i of a certain mammalian species s . This surmise can be verified experimentally with the help of bone allometry,

which provides data on mammalian allometric exponents d_i and l_i through the power-law scaling regressions $D_{is} = c_{is}M^{d_i}$ and $L_{is} = h_{is}M^{l_i}$, where *body mass* M ($\equiv M_s^{(body)}$) is treated as an external *mammalian* parameter and c_{is} and h_{is} are constants. The i -bone allometric exponents obey the cylindrical-shape evolution *constraint* equation $2d_i + l_i = 1$. This immediately follows from (i) the relation between *bone mass* M_{is} and its volume $D_{is}^2L_{is}$ ($M_{is} = \rho D_{is}^2L_{is}$, ρ is bone density), (ii) the aforementioned scaling regressions, and from (iii) McMahon's hypothesis that skeletal mass is linearly scaled to body mass, *i.e.*, $M_s^{(skel)} \propto M_{is} \propto M$. In what follows, we give an analysis of the bone dimension scaling in terms of the "overall-bone" (hereafter effective bone) *mammalian* allometric exponents $d = n^{-1}\sum_{i=1}^n d_i$ and $l = n^{-1}\sum_{i=1}^n l_i$, which obey the corresponding cylindrical-shape constraint $2d + l = 1$ resulting from the corresponding i -bone constraint averaged over n mammalian bones. Below we give statistical analysis for experimental data by Christiansen (1999b) on allometric exponents for mammalian long bones and show that it corroborates the cylindrical-shape approximation very accurately.

More sophisticated bone allometric studies provide information on evolution of real non-circular hollow bones with a cross section $A_{is}^{(exp)} (\propto M^{a_i})$, approximated by coaxial cylinders of length L_{is} , with external D_{is} and internal d_{is} diameters and of area $A_{is} = \pi(D_{is}^2 - d_{is}^2)/4$. As follows from Table 2 by Selker and Carter (1989) given for allometric exponents for Artiodactyl long bones, the circle-cross-section geometric similarity explicit in the constraint $a_i = 2d_i$ works well (with the accuracy amounting to 5%). Furthermore, similar to the internal bone diameter, the bone curvature, also shows a great deal of variation between different i -bones in the same animal and among different s -animals, but does not show a significant influence from animal mass (Selker and Carter, 1989). We see that geometric similarity does not depend on local deviations of bone shape from the ideal cylinder form and can therefore be castled into the cylindrical-shape evolution constraint equation. It is worth noting that the geometric similarity by McMahon (1975b) corresponds to a particular case of the *isometric solution* of the cylindrical-shape constraint given by $d_0 = l_0 = 1/3$ and $a_0 = 2/3$.

Generally speaking, *elastic-force* mammalian similarity suggests that there exists a unique mechanism, attributed to the natural elasticity of the bones of adult animals, that provides an escape from the critical elastic deformation (fracture) of bones under peak mechanical stresses. This similarity is ensured by a safety factor of about 2-4, independent of mammalian mass

(see Biewener, 1990 among others). Following Rashevsky (1948) and McMahon (1973), the elastic similarity can be introduced in explicit form on the basis of a mechanical analogy that takes place between a given bone (or an animal trunk) and a quasi-cylindrical, rigid beam. Elastic-force mammalian similarity, in a way, completes the geometric-shape similarity that eventually provides predictions for the dimension-growth effective bone exponents d and l tested by long bone allometry. For the case of long bones, it seems plausible to approximate the long ($D_{is} \ll L_{is}$) cylindrical beams by rigid rods for which the condition of elastic instability against *axial* loads was first established by Euler. This was given in terms of the critical *elastic-buckling* force $F_{buckl}^{(crit)} = c\pi^2 EI_{is}/L_{is}^2$ where E is the elastic modulus and $I_{is} = \pi D_{is}^4/64$ is the second cross-area moment of inertia. A numerical factor c depends on the boundary conditions, *i.e.* on the way of application of the axial external forces at the rod ends. One can show (see e.g. Landau and Lifshits, 1989) that $c = 1$ and 4 for the cases of both the non-fixed (on the hinges) ends and fixed ends, respectively. The first case was cited by Hokkanen (1986) concerning with a clarification of the elastic similarity employed by McMahon and Rashevsky. Then, Carter and Spengler (1982, cited by Selker and Carter, 1989) reported that long bones in living animals are extremely rarely fractured by axial loads. This is due to the curved structure of bones, which in the case of *in vivo* axial loading introduce *bending* moments in their diaphysis, that create stresses of a greater amplitude than those caused by pure axial loading (Selker and Carter, 1989). This real case can also be related to Euler's solution with $c = 1$. McMahon (1973) extended these conditions for the case of the limbs of trees, when a free horizontal *bending* of the top from the trunk is caused by proper weight. This results in $c = 1/4$ and permits one to summarize all the buckling-deformation cases for the critical elastic force as

$$F_{elast}^{(max)} = F_{buckl}^{(crit)} \sim E \frac{D_{is}^4}{L_{is}^2}. \quad (1)$$

McMahon (1973) suggested additionally that all bone elastic forces for terrestrial mammals are caused solely by animal weight ($F_{buckl}^{(crit)} \sim gM$, g is the gravitation constant) and therefore McMahon's elastic similarity for mammalian long bones can be introduced (see also discussion by Hokkanen, 1986) through (i) the elastic-rod, critical-force and (ii) the cylindric-shape constraints, namely

$$a) 4d - 2l = 1 \text{ and } b) 2d + l = 1. \quad (2)$$

Similarly to the aforegiven b constraint, the elastic-force a constraint in (2) follows from the allometric bone-dimension scaling applied to (1) further averaged over all long bones. The system of two equations provides the well known (McMahon, 1973) elastic model predictions for the bone diameter $d_0^{(buckl)} = 3/8$, bone length $l_0^{(buckl)} = 1/4$ exponents, along with the length-to-diameter ($l_0^{(buckl)} / d_0^{(buckl)}$) dimension-bone exponent $\lambda_0^{(buckl)} = 2/3$, related to the allometric scaling $L_{is} \sim D_{is}^{\lambda_i}$. The latter was in part corroborated by bone allometry by McMahon (1975b) who derived $\lambda_F^{(exp)} = 0.67, 0.52$ and 0.83 for *families*, respectively, Bovidae, Suids, and Cervids in the order Artiodactyla. A similar study by Alexander (1997) established $d_B^{(exp)} = 0.34$ and $l_B^{(exp)} = 0.26$, with $\lambda_B^{(exp)} = 0.76$ for the family Bovidae. When a wider variety of phylogenetically and anatomically distinct samples were analyzed within a larger body size range, experimental allometric exponents exhibited rather the isometric scenario ($\lambda_0 = 1$) than the elastic model behavior predicted by McMahon (1973, 1975a). This incompatibility with long-bone allometric observations was reported among others by Alexander *et al.* (1979a) and Biewener (1983). Furthermore, recent systematic investigations by Christiansen (1999a, 1999b) suggest that experimental observations of bone dimensions “support neither geometric nor elastic similarity, making both questionable as a means of explaining long-bone scaling in terrestrial mammals”. Moreover, according to criticism by Economos (1983) shared by Christiansen (1999b), no satisfactory explanation for any power-law scaling observed in mammalian allometry can be expected. From the physical point of view, however, there is no doubt that long bones possess simultaneously cylindrical-type-shape and elastic-critical-force similarities. We therefore revise the underlying hypotheses of the elastic model by McMahon (1973) to describe the elastic-force ($F_{elast}^{(max)} \propto M$ and $F_{buckl}^{(crit)} = F_{elast}^{(max)}$) and geometric-shape ($M_s^{(skel)} \sim M$) similarities in terms of constraints given in (2).

First, under locomotion peak dynamic conditions, skeletal elastic forces of animals may exceed those driven by static body weight (Hokkanen, 1986), and therefore the peak stresses in bones are due to muscle contractions, rather than to gravity (Carter *et al.*, 1980, Biewener, 1982, Rubin and Lanyon, 1984, Selker and Carter, 1989, and Biewener, 1991). This implies that the peak elastic forces in (1) should be substituted by those of muscle subsystem (muscles, tendons and ligaments), which stores and return elastic energy (Farley

et al. 1993), *i.e.*, $F_{elast}^{(max)} = F_{musc}^{(max)}$. Furthermore, after Rubin (1984) many studies provide strong evidence that the maximum muscle strains recorded in rigorous activities of animals are independent of body mass, and thus muscle-induced bone stresses are $F_{elast}^{(max)}/A_m \propto M^0$, where A_m is the cross-section area of muscle fibers. This, in turn, exhibits scaling to body mass through the *muscle-area* allometric exponent a_m defined through the scaling law $A_m \propto M^{a_m}$. As a consequence, the elastic-buckling-force constraint should be *modified* and changed in (2) for $4d - 2l = a$, with $a = a_m$.

Second, in view of the observation by Prange *et al.* (1979) of nonlinear evolution of skeletal mass with body mass M , Hokkanen (1986) noted that the corresponding McMahon's hypothesis ($M_s^{(skel)} \sim M$) makes the b constraint inaccurate in (2). With taking into account the bone-mass-to-body-mass scaling law $M_{is} = \rho D_{is}^2 L_{is} \propto M^{b_i}$, one obtains the following *modified* cylindrical-shape bone constraint for terrestrial mammals: $2d_i + l_i = b_i$. Modified in such a way McMahon's constraint results in *a*) $4d - 2l = a$ and *b*) $2d + l = b$ that provides a new prediction due to *elastic-buckling similarity*, namely

$$d^{(buckl)} = \frac{a^{(exp)} + 2b^{(exp)}}{8} \text{ and } l^{(buckl)} = \frac{2b^{(exp)} - a^{(exp)}}{4}. \quad (3)$$

This prediction is tested below on the basis of the experimental data on muscle-area $a^{(exp)}$ and bone-mass $b^{(exp)}$ mammalian effective exponents.

Third, after Alexander *et al.* (1979b) it has been widely recognized that the external critical loads acting parallel to the axis of the bone shaft (diaphysis) are often fewer than those applied in the perpendicular direction, although the corresponding peak stresses are of the same order of magnitude (see Rubin and Lanyon, 1984). Within the context of theory of elasticity, this experimental finding can be treated in terms of the thermodynamic instability of an *i-s*-bone approximated by a convex shell of characteristic size L_{is} with fixed ends subjected to deformation of flexure H_{is} . The free energy of the shell (a difference between the elastic energy and the work of deformation produced by some uniform external peak pressure $p^{(crit)}$) shows its instability when $p^{(crit)} \approx E(H_{is}^{(max)}/L_{is})^2$ (Pogorelov, 1960). Adopting for a critical condition of bone fracture $H_{is}^{(max)} \sim D_{is}$ one has

$$p^{(crit)} \approx \frac{F_{buckl}^{(crit)}}{D_{is}^2} \approx \frac{F_{bend}^{(crit)}}{L_{is} D_{is}} \sim E \frac{D_{is}^2}{L_{is}^2}. \quad (4)$$

A scaling of the critical elastic-buckling force to bone dimensions, that follows from (4), is given in (1), and that for the elastic-bending case is

$$F_{elast}^{(max)} = F_{bend}^{(crit)} \sim F_{tors}^{(crit)} \sim E \frac{D_{is}^3}{L_{is}} \gg F_{buckl}^{(crit)} \text{ for } L_{is} \gg D_{is}. \quad (5)$$

Besides the critical force $F_{bend}^{(crit)}$ due to a perpendicular load that a rigid beam can withstand without breaking that was already cited by Hokkanen (1986) and by Selker and Carter (1989, see (11) and (4), respectively), we have included a corresponding torsional force $F_{tors}^{(crit)}$. An estimate for the latter immediately follows from the critical torsional angle of a slightly bent and twirled rod considered by Landau and Lifshits (1989). For the critical torsional moment along the rod axis, one therefore has $F_{tors}^{(crit)} D_{is} = 8.98 E I_{is} / L_{is}$ that results in the scaling given in (5).

Although the importance of *bending* and *torsional* critical loads in the production of peak bone stresses is well established (Rubin and Lanyon, 1982, Biewener, 1982, Biewener and Taylor, 1986, Selker and Carter 1989), we have demonstrated a natural property of elasticity of bones, similar to the geometric-shape similarity, in a certain way does not depend on details of the local bone geometry and bone-end boundary conditions, *i.e.* all possible elastic-force scaling (similarities) follow from (4). The elastic-force *bending-torsional* scaling given in (5) provides the corresponding critical-force constraint $3d - l = a$, that in combination with the modified cylindrical-shape constraint $2d + l = b$ results in the relevant *bending-torsional* criterium for effective-bone evolution, namely

$$d^{(bend)} = \frac{a^{(exp)} + b^{(exp)}}{5} \text{ and } l^{(bend)} = \frac{3b^{(exp)} - 2a^{(exp)}}{5}. \quad (6)$$

As seen from (6), within the context of the hypotheses adopted by McMahon (1973) one has $d_0^{(bend)} = 2/5$, $l_0^{(bend)} = 1/5$, and $\lambda_0^{(bend)} = 1/2$ that was denominated as a static stress similarity (McMahon (1975b)). Remarkable that both the elastic-force criteria, given in (3) and (6) show a consistence with the isometric solution. For this specific case, the muscle subsystem develops independently ($b_0 = 1$) and isometrically ($a_0 = 2/3$) and both the critical elastic forces scale to mass as $F_0^{(max)} \propto M^{2/3}$ regardless of the underlying bone-structure protecting mechanism against critical buckling, bending or torsion deformations (see similar discussion by Selker and Carter, 1989).

Let us test the predictions for the bone-diameter $d^{(pred)}$ and $l^{(pred)}$ growth exponents given in (3) and (6) with those known from the one-scale (overall small and large mammals) bone allometry and those available in the literature data on $a^{(exp)}$ and $b^{(exp)}$. For the case of a constraint, an estimate for the overall mammalian data, including birds, on muscle-area allometric exponent obtained among others by Alexander (1977), Alexander *et al.*, (1981), and Pollock and Shadwick (1994), *i.e.*, $a_m^{(exp)} = 0.77 - 0.83$, was proposed by Garcia (2001). The most recent data on the i -bone-mass allometric mammalian exponents $b_i^{(exp)}$ by Christiansen (2002) are presented in the last column of **Table 1**, and the relevant long-bone mammalian exponent $b^{(exp)}$ ($= \sum_{i=1}^4 b_i^{(exp)} / 4$) can be introduced with accounting for statistical error due to distinct regressions, approximately, by $b^{(exp)} = 1.0 - 1.1$. In **Fig.1** we give a comparative analysis for the distinct bone-evolution scenarios predicted by the elastic-force buckling (area 1) and bending-torsional criteria (area 2), on the basis of (3) and (6), respectively, with the help of the aforementioned experimental data $a^{(exp)} = a_m^{(exp)}$ and $b^{(exp)}$. The modified and improved cylindrical-shape and elastic-force constraints are shown by solid lines for the limiting data $a^{(exp)}$ and $b^{(exp)}$ and the dashed lines and open points correspond to the simplified constraints by McMahon. In general, one can see that the long-bone allometry data on mammalian effective (all-bone-averaged) exponents by Biewener (1983), Bertram and Biewener (1992, reestimated by Garcia, 2001), and Christiansen (1999a) are close to both the elastic-force criteria. An exception although should be made for the pioneering data by Alexander *et al.* (1979a), where dispersion due to phylogenetic spectrum of terrestrial mammals was not reduced (see discussion by Christiansen, 1999b).

Besides the effective-bone mammalian evolution observed from Fig.1, we give a *statistical analysis* of the similarity constraints in Table 1 with the help of the one-scale¹ i -bone allometric data on the dimension exponents $d_i^{(exp)}$, $l_i^{(exp)}$ and the i -bone-mass exponents $b_i^{(exp)}$ derived by Christiansen (1999a, 1999b and 2002, respectively) within four decades of mammalian mass ($1-10^5 kg$) through the two different one-scale regressions. As seen from Table 1, the cylindrical-shape approximation for the geometric-shape similarity through the constraint $2d_i^{(exp)} + l_i^{(exp)} = b_i^{(exp)}$ is experimentally justified with a good level of accuracy by the data on $b_i^{(exp)}$ derived by both the methods for all $n = 1, 2...6$ long bones, except for the case of the *ulna*. A high

¹Extended statistical analysis of the long-bone allometric data scaled for small and large mammals by Christiansen (1999a, 1999b) was given by Kokshenev (2003).

precision is established for the bone-mass allometric exponent $b^{(\text{exp})} = 1.0\text{-}1.1$ predicted on the basis of the cylindrical-shape constraint $b^{(\text{pred})} = 2 d^{(\text{exp})} + l^{(\text{exp})}$ within 4-bone averaging, with $b^{(\text{pred})} = 1.03\text{-}1.06$.

The elastic-force similarities are tested through the predicted effective-bone mammalian exponents $a^{(\text{pred})}$, related to the muscle-area exponents, found as certain predictions given by the elastic-force buckling and bending-torsional constraints, respectively: $a^{(\text{buckl})} = 4d^{(\text{exp})} - 2l^{(\text{exp})}$ and $a^{(\text{bend})} = 3d^{(\text{exp})} - l^{(\text{exp})}$. As follows from the analysis elaborated in Table 1, the overall-bone predictions for $a^{(\text{buckl})}$ and $a^{(\text{bend})}$ are, respectively, wedged between 0.89-0.97 and 0.81-0.87. With taking into account that $a_m^{(\text{exp})}$ is limited by 0.83, we infer that the predicted data based on (i) that the elastic buckling force given in (1) and those for (ii) long bones *fibula* and *ulna* (treated by the *RMA* regression method) contradict to muscle-area allometry and therefore should be excluded from the critical-force evolution scenario. The first statement is discussed in (4) and the second is in line with the notes by Christiansen (1999a, 1999b) that “too thin *ulna*” and greatly reduced *fibula*” do not have “any importance in support of body mass”. In the special case of carnivore’s *ulna*, however, provides a substantial forelimb support (Christiansen, 1999a).

As follows from analysis given in Table 1, the overall-bone (*LSR* method) prediction for the muscle-area exponent is $a^{(\text{bend})} = 0.81\text{-}0.83$, which coincides with the *critical-muscle-force* exponent $a_{cm}^{(\text{exp})} = 0.81\text{-}0.83$ provided by muscle-fiber allometry data by Pollock and Shadwick (1994) reanalyzed recently by Kokshenev (2003). This finding implies that the statistical analysis of the elastic-force criteria based on the equation $F_{\text{elast}}^{(\text{max})} = F_{\text{musc}}^{(\text{max})}$ is related to the peak-area muscles and should therefore exclude muscle fibers with relatively small cross-sections. This can be exemplified by *common digital extensors* which have the lowest “maximum” area and exhibit isotropic evolution with $a_m^{(\text{exp})} \approx a_0 = 2/3$, as shown in Fig.1 by Kokshenev (2003). Finally, let us estimate the aforementioned length-to-diameter effective bone exponent $\lambda^{(\text{bend})} = (3b^{(\text{pred})} - 2a^{(\text{pred})}) / (b^{(\text{pred})} + a^{(\text{pred})})$ predicted with 4-bone exponents $b^{(\text{pred})} = 1.03\text{-}1.06$ and $a^{(\text{pred})} = 0.81\text{-}0.83$ obtained in Table 1. This provides $\lambda^{(\text{bend})} = 0.77\text{-}0.83$ that corroborates the allometry exponent $\lambda^{(\text{exp})} = 0.781\text{-}0.810$ derived by Kokshenev (2003) from the relevant data by Christiansen (1999b).

To summarize, we have revised McMahon’s elastic similarities that have long been a controversial subject of intensive study in the last three decades, especially in the long-bone allometry for terrestrial mammals. The elastic-

force and cylindrical-shape bone evolution constraint equations were not supported experimentally, and we have therefore reconsidered the basic hypotheses of the approach by McMahon (1973). As a matter of fact, exploration of the long bone allometric data was commonly given within the framework of model simplifications such as (i) the skeletal subsystem of animals operates separately from the muscle subsystem and (ii) the bone stresses are induced solely by gravity (Rashevsky, 1948, McMahon, 1973). These contradict to the observed evolution of bone mass and ignores a role of muscle contractions in formation of peak skeletal stresses. McMahon's description of the cylindrical-shape and elastic-force similarities implicit in the bone dimensional constraints is revised, modified and extended in view of the up-to-date knowledge on the bone-mass and muscle-area scalings and on domination of the bending-induced deformations.

Unlike the case of McMahon's (1973) elastic similarity model, the elastic-force (buckling-deformation) and cylindrical-shape similarities modified by muscle-area and bone-mass evolution (shown by shaded area 1 in Fig.1) become closer to almost all cited experimental data. At the same time, the most accurate data by Christiansen (1999a, 1999b) conflicts with the modified elastic-buckling bone evolution scenario. Further improvement of the elastic-force similarity by critical bending and torsional deformations made it eventually observable (see shaded area 2 in Fig.1). Statistical analysis of the allometric data by Christiansen (1999b, 2002) corroborates, at least in the case of the standard *LSR* method, the proposed description of the geometric-shape and elastic-force mammalian similarities given in terms of the corresponding constraints within the cylindrical-shape and elastic-rod model approximations.

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	methods	LSR	LSR	buckl	bend	cylind	cylind
i	Bones	$d_i^{(\text{exp})}$	$l_i^{(\text{exp})}$	a_i	a_i	b_i	b_i^*
1	humerus	.3816	.2996	0.93	0.85	1.06	1.07
2	femur	.3548	.3014	0.82	0.76	1.01	1.06
3	tibia	.3600	.2571	0.93	0.82	0.98	0.98
4	radius	.3868	.2995	0.95	0.86	1.07	1.08
5	fibula	.3379	.2250	0.90	0.79	0.90	—
6	ulna	.3551	.3016	0.82	0.76	1.01	1.08
n	Averaged	$\bar{d}^{(\text{exp})}$	$\bar{l}^{(\text{exp})}$	a	a	b	b^*
4	- bone	.3708	.2894	0.90	0.82	1.03	1.05
5	- bone	.3642	.2765	0.90	0.82	1.00	—
6	- bone	.3627	.2807	0.89	0.81	1.01	—

RMA	RMA	buckl	bend	cylind	cylind
$d_i^{(\text{exp})}$	$l_i^{(\text{exp})}$	a_i	a_i	b_i	$b_i^{(\text{exp})}$
.3860	.3109	0.92	0.85	1.08	1.083
.3599	.3089	0.82	0.77	1.03	1.071
.3654	.2767	0.91	0.82	1.01	0.998
.4014	.3210	0.96	0.88	1.12	1.101
.3681	.2430	0.99	0.86	0.98	—
.4579	.3177	1.20	1.06	1.23	1.101
$\bar{d}^{(\text{exp})}$	$\bar{l}^{(\text{exp})}$	a	a	b	$b^{(\text{exp})}$
.3782	.3044	0.90	0.83	1.06	1.063
.3762	.2921	0.92	0.84	1.04	—
.3898	.2964	0.97	0.87	1.08	—

Table 1. Analysis of the bone evolution mechanism through observation of the mammalian long-bone similarity on the basis of the elastic-force and cylindrical-shape evolution constraint equations. Experimental data on the mammalian bone diameter $d_i^{(\text{exp})}$, length $l_i^{(\text{exp})}$ allometric exponents for 6 long bones obtained by the least square regression (*LSR*) and the reduced major axis (*RMA*) methods are taken from Table 2 by Christiansen (1999a). The *RMA* data for the bone-mass allometry exponent $b_i^{(\text{exp})}$ ($= b_i^{(RMA)}$) is taken from Table 2 by Christiansen (2002). The *LSR* data is estimated here, approximately, through the relation $b_i^* = r_i^{(RMA)} b_i^{(RMA)}$, where $r_i^{(RMA)}$ is the

corresponding correlation coefficient by Christiansen (2002). The muscle-area a_i and the bone-mass b_i exponents are predicted with the help of the elastic-force *buckling*-deformation ($a_i = 4d_i - 2l_i$) and *bending*-deformation ($a_i = 3d_i - l_i$) constraint equations, and cylindrical-shape constraint equation ($b_i = 2d_i + l_i$). The effective n -bone mammalian allometric exponents are given through the mean values of n corresponding exponents, *e.g.*, $a = n^{-1} \sum_{i=1}^n a_i$.

FIGURE CAPTURES

Fig.1. Mammalian bone-dimension evolution diagram: diameter against length. *Solid lines* are given by the elastic-force a -constraint *buckling* ($4d - 2l = a$) and *bending* ($3d - l = a$) equations, and for the cylindrical-shape constraint ($2d + l = b$) equation. *Dashed lines* - the same for the case of $a = b = 1$. *Points*: (*open squares*) 0, 1 and 2 correspond, respectively, to the isometric (1/3, 1/3), the elastic similarity (3/8, 1/4), and to the stress similarity (2/5, 1/5) models by McMahon (1975b); *closed circles* symbolized by A'79, B'83, B'92 and C'99 are due to one-scale, overall-bone-averaged, least-square-regression data on the mammalian long-bone allometry by Alexander *et al.* (1979a), Biewener (1983), Bertram & Biewener (1992, reestimated by Garcia, 2001), and Christiansen (1999a), respectively. Statistical error is shown by bars. *Dashes areas* 1 and 2 correspond to the proposed criteria given by the predictions $d^{(buckl)}$, $l^{(buckl)}$ and $d^{(bend)}$, $l^{(bend)}$ in, respectively, (3) and (6) for the case of the overall muscle areas with $a_m^{(exp)} = 0.77 - 0.83$ (by Garcia, 2001) and bone masses with $b^{(exp)} = 1.0 - 1.1$ (from Table 1).