

Observation of Mammalian Similarity through Allometric Scaling Laws

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ABSTRACT

We discuss the problem of observation of natural similarity in skeletal evolution of terrestrial mammals. Analysis is given by means of testing of the power scaling laws established in long bone allometry, which describe development of bones (of length L and diameter D) with body mass in terms of the growth exponents, *e.g.* $\lambda = d \log L / d \log D$. The bone-size evolution scenario given three decades ago by McMahon was quiet explicit on the geometrical-shape and mechanical-force constraints that predicted $\lambda = 2/3$. This remains too far from the mammalian allometric exponent $\lambda^{(\text{exp})} = 0.80 \pm 0.2$, recently revised by Christiansen, that is a chief puzzle in long bone allometry. We give therefore new insights into McMahon's constraints and report on the first observation of the critical-elastic-force, bending-deformation, muscle-induced mechanism that underlies the allometric law with estimated $\lambda = 0.80 \pm 0.3$. This mechanism governs the bone-size evolution with avoiding skeletal fracture caused by muscle-induced peak stresses and is expected to be unique for small and large mammals.

Keywords: allometric scaling , long bones, muscles, terrestrial mammals.

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by V.B. Kokshenev

I. INTRODUCTION

In general, biological laws do not follow from physical laws in a simple and direct way. Examples include Kleiber's allometric law known as the 3/4 power law that scales metabolic rates for animals and plants to their mass within the range of three order of magnitude. As shown by West *et al.* in Refs. [1,2] the observed metabolic rate scaling law arises from the interplay between geometric and physical constraints implicit, respectively, in space-filling fractal networks and energy dissipation*. Another famous 2/3 power law was proposed by McMahon [6] for scaling of longitudinal-to-transverse dimensions of animals and plants through physical description of geometric-shape and critical-force similarities noticed in their size evolution. Given in Ref. [6] in explicit form, the geometrical-(cylindrical-volume)-shape and mechanical-(critical-elastic-buckling)-force constraints imposed on size evolution for animals and plants with their mass yielded the 2/3 power scaling law, along with the 1/4 and 3/8 laws deduced [6], respectively, for longitudinal and transverse linear dimensions. During almost three decades, McMahon's scaling laws have been a controversial subject of intensive study and debate. As a matter of fact, McMahon's description of the geometrical-shape and mechanical-force similarities was experimentally proved for terrestrial mammals neither in body allometry [7] nor in long bone allometry [8,9,10,11,12,13,14,15,16]. Moreover, the most recent condemnation by Christiansen [15] states that no satisfactory explanation for any power-law scaling observed in mammalian allometry can be expected.

*For simple explanations of Kleiber's allometric scaling, which is shown to originate from the general features of the networks irrespective of the geometrical and dynamical details, see Refs. [3,4,5]

We will demonstrate that the failure of McMahon's constraints is due to the fact that the skeletal subsystem of animals is not mechanically isolated from their muscle subsystem, as was suggested in Ref. [6]. Also, McMahon's hypothesis that the skeletal support of weight and fast locomotion of mammals is driven solely by a gravitation contradicts to up-to-date comprehension on a role of muscle fibers and tendons in formation of maximum skeletal stresses. We therefore revisit McMahon's evolution constraint equations in Sec.II within the context of their application to long bone allometry for terrestrial mammals. These equations are modified and generalized in view of the known experimental findings in muscle fiber allometry. Experimental testing of the two distinct critical-elastic-force mechanisms that govern evolution of mammalian bones is elaborated in Sec. III. Discussion and conclusions are given in Sec. IV.

II. MCMAHON'S CONSTRAINTS IN LONG BONE ALLOMETRY

A. Elastic Similarity Model Revisited

Famous power laws by McMahon [6] for scaling of linear dimensions of animals and plants was proposed within the framework of the so-called elastic similarity model (hereafter, ESM). Application of the ESM by McMahon to the case of mammalian bone allometry was based on the *cylindric-shape* correspondence that takes place between a given skeletal bone and a cylindrical beam. A bone sample was therefore geometrically approximated by a cylinder of diameter D_{is} and length L_{is} , where index i counts different bones and s indicates mammalian specie. The *mechanical-force* correspondence to the same *rigid* cylinder is justified by observation of the universal (specie-independent) bone-stress safety factors. These are given by ratio (about 3) of yield stress to peak stress. Exploration of such a kind of mechanical correspondence by McMahon gave rise to the maximum-(elastic-buckling)-force *constraint* imposed on volume-size evolution of a given bone.

More specifically, the ESM is based on the fact that the mechanical failure of a bone

is prevented through its linear dimensions D_{is} and L_{is} , adjusted to bear critical *buckling deformations*, related to peak stresses through the maximum elastic forces: $F_{elast}^{(\max)} = F_{buckl}^{(crit)}$. The latter is describes an elastic instability caused by critical bending deformations that was specified by the Euler critical estimate $F_{buckl}^{(crit)} = \pi^2 EI/L^2$ for a given cylinder (of length L and of diameter D , with the moment of inertia $I = \pi D^4/64$ and the elastic modulus E , see *e.g.* Cap.IV in Ref. [17]). Thus the ESM constraint equations attributed by McMahon to the cylindric-shape and elastic-force similar skeletal bones can be introduced through (a) the elastic-buckling critical force $F_{is}^{(crit)}$ and (b) the cylindric-bone volume $V_{is}^{(bone)}$, namely

$$F_{is}^{(crit)} = \frac{\pi}{64} E \frac{D_{is}^4}{L_{is}^2} \quad (1a)$$

$$V_{is} = D_{is}^2 L_{is}. \quad (1b)$$

In long-bone allometry, the observation of evolution of limb bones across mammalian species is discussed though the bone-size linear-dimension scaling to body mass M_s . This is given in terms of the bone-diameter and the bone-length allometric exponents, respectively, d_i and l_i , or of the i -bone-dimension *growth exponents*, introduced by the following scaling differential relations, namely

$$d_i = \frac{d \log D_{is}}{d \log M_s}, \quad l_i = \frac{d \log L_{is}}{d \log M_s}, \quad \text{and} \quad (2)$$

$$\lambda_i = \frac{d \log L_{is}}{d \log D_{is}} \equiv \frac{l_i}{d_i}. \quad (3)$$

The *reduced dimension* exponent λ_i , related to the longitudinal-to-transverse scaling, is also defined. As seen, Eqs.(2),(3) are equivalent to the corresponding differential equations $dD_{is}/dM_s = d_i D_{is}/M_s$, etc., which solutions are commonly derived in bone allometry through regression equations $D_{is} = c_{is} M^{d_i}$, where M is treated as an external mammalian parameter and c_{is} are constants. A notable feature of the introduced scaling differential relations is independence of the i -bone exponents on mammalian specie s . This corroborates the bone allometry observations and Eqs.(2),(3) are therefore treated as the allometric *scaling laws*. This implies a universal fashion in evolution of any linear dimension of bones, as well as bone *volume* $V_{is} = D_{is}^2 L_{is}$, with body mass that in a certain way reflects similarity

of mammals with their size evolution. With taking into account that $\rho V_{is} = M_{is}$ (ρ is bone density), and adopting additionally McMahon's hypotheses that (a) effective skeletal growth is driven by gravitation, *i.e.*, $F_{is}^{(crit)} \sim gM_{is}$ (g is the gravity constant) and that (b) bone mass M_{is} linearly scales to body mass M_s , the following *i*-bone-evolution equations, namely

$$\begin{cases} 4d_i - 2l_i = 1, \\ 2d_i + l_i = 1 \end{cases} \quad (4)$$

result from, respectively, Eqs.(1a) and (1b) with the help of the scaling relations given in Eq.(2). In turn, Eqs.(4) and (3) provide the well known ESM predictions: $d_0^{(buckl)} = 3/8$, $l_0^{(buckl)} = 1/4$, and $\lambda_0^{(buckl)} = 2/3$, including a trivial *isometric* solution $d_0 = l_0 = 1/3$ and $\lambda_0 = 1$. As mentioned in the Introduction, these predictions were not experimentally proved even when a statistical dispersion of allometric data was taken into account (for recent criticism of the ESM predictions for the allometric exponents d , l and λ see analyses given in Table 5 in Refs. [14] and Table 3 in Ref. [15], respectively).

B. Elastic-Buckling-Force Criterium

Skeletal evolution of animals cannot be studied independently of their muscle fibers and tendons. Moreover, the peak skeletal stresses are generated rather by muscle contractions than by gravitation. These both statements follow from studies of muscle design and bone strains during locomotion [18,19,20,21]. We infer therefore that the maximum elastic forces exerted by long bones are originated from the *maximum* muscle forces, *i.e.*, $F_{elast}^{(\max)} = F_{musc}^{(\max)}$. The same studies provide strong evidence that the maximum muscle stresses are independent of body mass, and thus $F_{musc}^{(\max)}/A_{musc}^{(\max)} \propto M^0$, where $A_{musc}^{(\max)}$ is the maximum cross-section area of muscle fibers. The critical-force constraint, justified through the aforementioned bone-stress safety factors, can be therefore formally introduced into consideration by the "overall-bone" *critical-force exponent* a_c , namely

$$a_c = \frac{d \log F_{musc}^{(crit)}}{d \log M_s} = a_{cm} = \frac{d \log A_{musc}^{(\max)}}{d \log M} \quad (5)$$

and the corresponding *critical muscle-area* exponent a_{cm} . These should be distinguished from the exponents

$$a_{ci} = \frac{d \log F_{is}^{(crit)}}{d \log M_s} \text{ and } a_m = \frac{d \log A_{musc}}{d \log M} \quad (6)$$

where $F_{is}^{(crit)}$ is given in Eq.(1a). The muscle-area exponent a_m is known in muscle allometry [10,20,22] as the muscle-fiber, cross-section-area exponent and can be exemplified by data $a_m^{(exp)} = 0.69 - 0.91$ derived by Pollock and Shadwick for four distinct groups of muscles in mammalian hindlimbs (see Fig.3 in Ref. [22]). The maximum muscle force is commonly associated [10] with the *leg group* of muscles of animals, *i.e.*, $A_{musc}^{(\max)} = A_{musc}^{(leg)}$. With adopting of the latter in Eq.(5), the "leg-muscle" *critical* exponent $a_{cm}^{(exp)} = 0.81 - 0.83$ was obtained [22] (on the bases of data [10] for six groups of mammalian leg muscles by Alexander *et al.*) and reported by Pollock and Shadwick in Ref. [22]. As seen, the means $\bar{a}_m^{(exp)} = 0.80$ and $\bar{a}_{cm}^{(exp)} = 0.82$ are different but not distinguished within the experimental error.

In order to establish the critical muscle-area exponent $a_{cm}^{(exp)}$ defined in Eq.(5), we have reanalyzed the experimental data by Pollock and Shadwick on muscle fiber area A_{musc} in hindlimbs of 35 quadrupedal mammals as a function of body mass represented in **Fig.1** from Fig.3 in Ref. [22]. In general, the *gastrocnemius* group of muscles (shown by diamonds in Fig.1 for points $A_m^{(G)}$ adjusted [22] with $a_m^{(G)} = 0.77$), unlike the *common digital extensors* group (shown by crosses for points $A_m^{(C)}$ with [22] $a_m^{(C)} = 0.69$), plays a principal role in formation of maximum bone stresses. This is due to the fact that for small and large species of animals $A_m^{(G)} > A_m^{(D)}$. Other two groups of muscles exhibit a crossover from the almost isotropic evolution with $a_0 = 2/3$ to somewhat given by the exponent a_{cm} and driven by the maximum muscle areas controlled by the *gastrocnemius* group, *i.e.* by A_{cm} established by maximum points of $A_{musc}^{(G)}$. First the highest 5 points (shown by arrows in Fig.1) are fitted by $A_{cm}^{(1)} = 428 * M^{0.80}$. Next nearest-neighbors (16 points indicated as solid symbols below the line A_{cm} in Fig.1) are fitted with $A_{cm}^{(2)} = 304 * M^{0.83}$. Regression elaborated within all the field of a maximum muscle area, defined by the highest 21points, provides $a_{cm}^{(1,2)} = 0.82 \pm 0.01$ (with correlation coefficient $r = 0.996$). Remarkably, this finding matches well the aforegiven

data for the "leg-muscle" exponent by Alexander *et al.* reported in Ref. [22] and can be therefore treated as a reliable data.

Eqs.(5) and (6) provide the following definition for the "overall-bone" averaged exponents, namely

$$a_c = \langle a_{ci} \rangle \equiv \frac{1}{n} \sum_{i=1}^n a_{ci} = a_{cm}, \text{ with } a_{cm}^{(\text{exp})} = 0.82 \pm 0.01, \quad (7)$$

where summation is limited by bones which do play a *principal* role in effective support and fast locomotion of body mass of animals. Eq.(7) can be also treated as an extension of a similar definition of the *mammalian* principal-bone-averaged exponents d , l and λ introduced with the help of Eqs.(2),(3), *e.g.*, $d = \langle d_i \rangle$. Thereby, revision of McMahon's a -hypothesis provides a new a -constraint equation imposed on the exponents: $4d - 2l = a_c$.

In view of the fact that neither skeletal mass [12] nor bone mass [16] are linear with mammalian body mass, McMahon's revised b -constraint equation given in Eq.(4) for i -bone is also modified as $2d_i + l_i = b_i$. Here the i -bone-mass exponent, namely

$$b_i = \frac{d \log M_{is}}{d \log M_s}. \quad (8)$$

is introduced through the relevant power scaling law. Thus, McMahon's critical-force and cylindric-shape constraints given in Eq.(4) result in the following *modified* ESM constraints, namely

$$\begin{cases} 4d - 2l = a_c, \\ 2d + l = b. \end{cases} \quad (9)$$

In turn, this yields new predictions for the mammalian overall-bone dimension and reduced-dimension exponents, or the *elastic-buckling-criterium* predictions, namely

$$d^{(buckl)} = \frac{a_c + 2b}{8}, \quad l^{(buckl)} = \frac{2b - a_c}{4} \text{ and} \quad (10)$$

$$\lambda^{(buckl)} = 8 < \frac{b_i}{a_{ci} + 2b_i} > -2. \quad (11)$$

The latter prediction follows from the definition for the reduced-dimension exponent $\lambda_i = l_i/d_i$ given in Eq.(3) and presented here in the form $\lambda_i = b_i/d_i - 2$, with the help of the b -constraint equation.

C. Elastic-Bending-Force Criterium

After Alexander *et al.* [23] it has been widely recognized (for recent references see Ref. [16]) that the elastic *bending* deformations play a crucial role in the overall peak stresses of long bones instead of a simple axial compression discussed [6] by McMahon in terms of the critical buckling deformations. The corresponding critical force $F_{elas}^{(\max)} = F_{bend}^{(crit)}$ applied normally to the bone before fracture was already discussed in long-bone allometry in Refs. [12,20]. In view of the elastic nature common for both kind of deformations, the force $F_{bend}^{(crit)}$ in a certain way extends the ESM given in Eq.(1) for the case of the bending critical deformations, namely

$$F_{is}^{(crit)} \sim E \frac{D_{is}^3}{L_{is}}, \quad (12a)$$

$$\rho D_{is}^2 L_{is} = M_{is}. \quad (12b)$$

Straightforward application of the scaling differential relations introduced in Eqs.(2),(3), with accounting of the critical-force and the bone-mass growth exponents given in, respectively, Eqs.(5),(8) and (9), results in the following new constraint equations:

$$\begin{cases} 3d - l = a_c, \\ 2d + l = b. \end{cases} \quad (13)$$

This provides the *elastic-bending criterium* expressed in terms of the following predictions for the mammalian bone-dimension growth exponents, namely

$$d^{(bend)} = \frac{a_c + b}{5}, \quad l^{(bend)} = \frac{3b - 2a_c}{5} \text{ and} \quad (14)$$

$$\lambda^{(bend)} = 5 < \frac{b_i}{a_{ci} + b_i} > -2. \quad (15)$$

Notably that both the elastic-force criteria given in Eqs.(10) and (14) are consistent with the isometric solution ($d_0 = l_0 = 1/3$ and $\lambda_0 = 1$), which is found under conditions that the mammalian muscle-area subsystem develops isometrically ($a_0 = 2/3$) and independently of the skeletal subsystem ($b_0 = 1$). The observed allometric scaling laws with $d^{(\exp)} > 0.33$, $l^{(\exp)} < 0.33$, and $\lambda^{(\exp)} < 1$ corroborate that this simplified geometric scenario is avoided by the nature.

III. OBSERVATION OF BONE EVOLUTION SIMILARITIES THROUGH EXPERIMENTAL TESTING OF THE CONSTRAINT EQUATIONS

All predictions given by the original ESM [6] and the revised ESM are analyzed in the bone growth diagram in **Fig.2**. As seen, the available experimental data matches neither the isometric nor the original ESM solutions (shown by crosses), even in case when dispersion effects of the experimental data (shown by error bars) are taken into account. Note that this large dispersion is not caused by error measurements of bone dimensions or body mass of animals, but is resulted from a large phylogenetic spectrum of terrestrial mammals[†]. Unlike the case of the pioneer data [9] by Alexander *et al.*, all species which have multiple specimens, were additionally averaged [15] within a certain mammalian subfamily before to be documented. The most accurate allometric data with the systematically reduced phylogenetic statistical error was given [14,15,16] by Christiansen.

Predictions of the modified ESM and the extended ESM are shown in Fig.2 by the shaded areas, which correspond, respectively, to Eqs.(9) and (13) estimated with account of the reliable domain for the critical-force exponent $a_c^{(\text{exp})} = 0.81 - 0.83$ and of that for the bone-mass exponent $b^{(\text{exp})} = 1.0 - 1.1$ (that approximately covers error scatter of the experimental data on $b_i^{(\text{exp})}$ (given in Table 2 in Ref. [16])). The shaded areas indicate the critical-force constraints given by the a -constraint lines $4d - 2l = 0.82$ and $3d - l = 0.82$ extended by cylindric-volume constraints implicit in the form of the elastic-buckling-force and elastic-bending-force criteria, respectively. As seen from Fig.2, the elastic-*buckling* criterium seems to be observable within the range of the unreduced phylogenetic statistical error. After reduction of this error, only the elastic-*bending* criterium corroborates.

Besides the case of the 6-long-bone-averaged allometric data [14] given in Fig.2 for the

[†]In fact, there exist a certain error due to deviation of bone shape from the ideal cylinder. Also, not all body mass were really measured but taken as an average from the literature data (see discussion in Ref. [15]).

one-scale least-square regression (*LSR*), we have also elaborated analysis of the double set of the allometric exponents (taken from Table 5 in Ref. [14]) derived within the *two-scale* regressions made for small ($M < 50\text{kg}$) and large ($M > 50\text{kg}$) mammals. But no definitive conclusions on domination of any elastic-force criteria can be inferred. Indeed, in the case of the overall-(6 -bone)-average analysis, the data for small and large animals is far to be fitted by any of the dashed areas in Fig.2. When the *ulna* and the *fibula* are excluded, the principal-(4-bone)-averaged *LSR* data justifies the elastic-bending and the elastic-buckling criteria for the cases of small and large mammals, respectively. However, unlike the case of the one-scale data, experimental accuracy of the two-scale analysis is marginal that makes doubtful any inference on observation of both the distinct critical-force constraints. We have therefore restricted our analysis by one-scale allometric data for the four principal mammalian long bones listed in **Table 1**.

First, we check a *self-consistency* of experimental data on the dimension ($l_i^{(\text{exp})}, d_i^{(\text{exp})}$) [14] and reduced-dimension ($\lambda_i^{(\text{exp})}$) [15] allometric exponents obtained independently and presented in first and second columns of Table 1, respectively. As seen, when the bone-averaged data is compared between the two regression methods, it obeys the relation $d^{(\text{exp})}/l^{(\text{exp})} = \lambda^{(\text{exp})}$ with accuracy that is much higher than that for the case of partial i -bone relations $d_i^{(\text{exp})}/l_i^{(\text{exp})} = \lambda_i^{(\text{exp})}$ compared within the same method. Then, the geometrical mammalian similarity is tested on the basis of the b -constraint equation $2d_i^{(\text{exp})} + l_i^{(\text{exp})} = b_i^{(\text{exp})}$ in second and third columns of Table 1. Again, the cylindric-shape constraints, given in terms of the bone-averaged data, are justified[‡] with a good precision. We infer that observation of the mammalian similarity through the allometric power laws can be realized only "on the average", but not for a given type of "mammalian" bone as it widely adopted in allometric studies. Examples are analyses of the original ESM predictions elaborated for a given i -bone,

[‡]Exclusion should be given for the case of the exponent b^* , which data obtained by the square regression (*LSR*) method is not available.

instead of the overall-bone data, and given in Table 5 in Ref. [14], Table 3 in Ref. [15], and Table 3.11 in Ref. [24].

The problem of validation of the bone-evolution a -constraint equation for the case of the bending loads, *i.e.*, $3d - l = a$, where a is treated as a free parameter, was first discussed [20] by Selker and Carter in terms of the bone strength index. On the basis of the mammalian data [11] by Biewener (shown in Fig.2) and their own data for *artiodactyls*, the overall-bone-averaged equation $3d^{(\exp)} - l^{(\exp)} = a$ provided [20] estimates $a = 0.77$ and 0.82 , respectively. By generalization of these findings to the overall mammalian case, allometric exponent $a_m^{(\exp)} = 0.77 - 0.82$ was adopted [20] for testing of the bending or torsion deformations in mammalian long bones due to muscle contractions. The same analysis made on the basis of other available in the biological literature allometric data, including the particular case of birds[§], has been recently given by Garcia (see Table 3.12 in Ref. [24]). As the result, the allometric muscle-area exponent was suggested $a_m^{(\exp)} = 0.77 - 0.83$, with the mean $\bar{a}_m^{(\exp)} = 0.80$, as a suitable data for experimental testing of the bending-force constraint equation (see analysis in Table 3.11 in Ref. [24]). This suggestion is not true.

Indeed, as follows from the pioneer work [6] by McMahon, revisited in the previous section, the force-constraint equation is driven by the *critical* force and therefore given as $3d - l = a_c$ where the critical-force exponent, according to Eqs.(5),(7), is established by the data on maximum-muscle-area allometry, *i.e.*, $a_c = a_{cm}^{(\exp)} = 0.81 - 0.83$, with $\bar{a}_{cm}^{(\exp)} = 0.82$ that should be distinguished from the suggested [24] data on $\bar{a}_m^{(\exp)} = 0.80$. We have therefore reconsidered analysis given in Table 3.11 in Ref. [24] and found [25] that no definite conclusions can be made on validation** on the principal-bone averaged equation $3d^{(\exp)} - l^{(\exp)} = a_{cm}^{(\exp)}$ on the bases of the *two-scale RMA* and *LSR* data [14]. Conversely, the *critical*-bending-force constraint equation $3d - l = a_c$ is strongly supported by the *one-scale* data

[§]Application of the ESM for birds remains questionable.

**Again, the marginal estimate $a_{cm} = 0.829$ is obtained in the case of the small-animal *LSR* data.

[14] by Christiansen deduced through both the different (*LSR* and *RMA*) regressions. This follows from the bone-dimension predictions $a_c = 0.82$ and 0.83 (obtained [25], respectively, for both the methods with the help of data given in first column in Table 1).

In the current study we put emphasis on observation of the mammalian similarity through the critical muscle allometry exponent $a_{cm}^{(exp)}$ established in Fig.1 along with the one-scale long-bone allometric data on the reduced-dimension exponent $\lambda_i^{(exp)}$ obtained in Ref. [15]. Therefore, we have reformulated the elastic-buckling and the elastic-bending criteria given in Eqs.(11) and (15) in terms of the observable λ_i . This provides the following predictions for the critical-force exponents, namely

$$a_c^{(buckl)} = 2 < \frac{2 - \lambda_i}{2 + \lambda_i} b_i > \text{ and } a_c^{(bend)} = < \frac{3 - \lambda_i}{2 + \lambda_i} b_i > \quad (16)$$

obtained with the help of Eq.(7) and estimated in last column of Fig.1. As seen, the elastic-force bone-*buckling*-deformation mechanism, proposed by McMahon in Ref. [6] suggests an estimate $a_c^{(buckl)} = 0.90$ for both the regression methods that is not justified by Eq.(7). In contrast, the elastic-force bone-*bending*-deformation mechanism predicted by $a_c^{(bend)} = 0.81$ (and 0.83) within the *LSR* (and *RMA* regression) methods is proved by the reduced-dimension and self-consistent linear-dimension allometry data reported by Christiansen in Refs. [15] and Ref. [14], respectively. Again, analysis, similar to that given in Table 1, extended to the case of the *two-scale* principal-bone data [14,15], corroborates the same bending-force mechanism only for the data derived for *small* mammals within the *LSR* method. No conclusions can be inferred in the case of small mammals treated by the *RMA* regression, as well as in the case of large mammals treated by both the methods.

IV. DISCUSSION AND CONCLUSIONS

We have discussed the problem of observation of natural similarity in evolution of terrestrial mammals. Testing of the two conceivable underlying mechanisms that drive the bone size development with body mass of animals is given on the basis of experimental data on

the reduced dimension ($\lambda_i = l_i / d_i$), longitudinal dimension (l_i), and transverse dimension (d_i) allometric exponents established through the scaling laws commonly discussed in the mammalian long-bone allometry.

Since Galilei it was repeatedly recognized that the isometric skeletal evolution prescribed by the overall-bone exponent $\lambda_0 = 1$ is not observed in the nature because the small mammals are not geometrically overbuilt and the large species do not operate very close to their mechanical failure limit, that it would be expected from the isometric scenario. This figurative, widely cited description given by Biewener [26] is in agreement with the simplified version ($\lambda_0 = 1$) of the more sophisticated scenario ($\lambda_0^{(buckl)} = 0.667$) proposed [6] by McMahon. Within the ESM, the mammalian similarity was introduced [6] on the basis of realistic geometrical-shape and mechanical-force correspondence that takes place between a given skeletal bone and a rigid cylinder. As mentioned in the Introduction and illustrated in Fig.2, predictions for evolution of bone dimensions with body mass given by the ESM were disapproved in long bone allometry. This, in particular, implies that the ESM exponent $\lambda_0^{(buckl)} = 0.667$ was not justified in long-bone allometric experiments, including the most systematic data with $\lambda^{(\exp)} = 0.78 - 0.82$ (that follows from Table 1 as the mean between the *LSR* and *RMA* bone-averaged data).

A good deal effort has been undertaking in long bone allometry to learn experimental conditions for observation of the critical-force (elastic-*buckling*-deformation and *gravity*-induced) mechanism suggested by McMahon for explanation of anatomical adaptation of skeletal bones through their linear dimensions. The first objection [7] by Economos was as follows. McMahon's mechanical-failure mechanism should not be expected as a unique for all species, but would more suitable for *large* mammals. This stimulated a careful search for additional scaling laws related to small and large mammals. Such kind of new scaling laws were established in terms of the double sets of allometric exponents introduced [14,15,16] by Christiansen through the *two-scale* regressions distinguished by $M_c = 50\text{kg}$ adopted as a boundary mass common for all species. Furthermore, it was speculated that the revealed inadequate description of the scaling laws is due to inaccuracy of the methods of regres-

sion and, as a result, the *RMA* regression was suggested [14] as well-chosen instead of the traditional *LSR*. The second objection [7] by Economos refers to the *linearity* of the logarithmic scaling laws given in Eq.(2), which was not expected to be a sole across the three order of magnitudes of body mass. Experimental verification of this idea by Christiansen revealed [14] that an application of the polynomial type of regressions in bone allometry does not improve the correlations established within the traditional linear logarithmic scaling. Finally, thorough numerical analyses [14,15] of the reasons of the ESM failure brought Christiansen to a conclusion that "many factors contribute to maintaining skeletal stress at uniform level", including the factor of bending-deformation-induced stresses, which are more important [14] than the bone stresses illuminated [6] by McMahon.

We have demonstrated how the factors of muscle fiber contractions, bone mass evolution, and of bending bone deformations can be incorporated into the ESM constraint equations. As a result, the *modified* (by bone-mass and muscle-contraction factors) ESM becomes observable (see shaded area that extends *a*-buckling line in Fig.2) under condition that the unreduced phylogenetic statistical dispersion of the allometric data [9,11,13] is taken into account. Otherwise, the *extended* (additionally by the *bending*-deformation factor) ESM agrees with experiment (see Fig.2). Another analysis (given in Table 1) yields the observation of the mammalian similarity within the *principal*-long-bone allometric data [14,15,16] with systematically reduced statistical error by Christiansen. As demonstrated, this observation is realized in terms of the bone-*averaged* allometric exponents, restricted by the *principal* bones that are involved into the evolution-constraint equations. Example is the volume-constraint equation, which should be valid for any conceivable bone-evolution mechanism. As seen from analysis given in columns 2 and 3 in Table 1, the volume-constraint equation is much better "observed" in the "bone-averaged" form $2d^{(\exp)} + l^{(\exp)} = b^{(\exp)}$ than in the form presented for a given *i*-bone. We guess that the observation of the geometric-shape similarity through experimental justification of exact Eq.(12b) should depend on neither the number of scales nor on methods chosen for regression of the bone-dimension allometric data. Our additional verification of the cylindric-shape similarity given on the basis of the *two-scale principal*

long-bone allometric data (taken from Table 3 in Ref. [14]) corroborates this statement for both small and large mammals. We infer therefore that both the methods and both the scales are equivalent in observation of the "bone-averaged" geometrical-shape mammalian similarity, at least for the principal^{††} bones.

As highlighted by Christiansen, the principal bones play a crucial role in primarily support the body mass. He noted [15] that greatly reduced *ulna* and too thin *fibula* do not play of much importance in support of body mass. They are therefore not suitable for testing of the critical-force constraints and should be excluded from the principal bone set. As follows from our analyses given in Fig.1, qualitatively the same should be referred to some muscle fiber groups such as *common digital extensors* which eventually do not produce peak bone stresses. Meanwhile, as seen from Fig.9 in Ref. [15] and Fig.1, *tibia* and *plantaris* show a crossover behavior between principal and non-principal sets, where the principle bone-set and the principle muscle-group set are presented by small and large mammals, respectively. As the reliable *critical* principal-muscle-area exponent a_{cm} ($= a_c$), which enters the critical-force a -equations, the data $a_{cm}^{(exp)} = 0.82 \pm 0.01$ is proposed in Eq.(7). This finding is derived in Fig.1 from the *maximum* muscle-area gastrocnemius group of leg muscles and should be distinguished from the *overall* muscle-area data $a_m^{(exp)} = 0.80 \pm 0.03$ that was groundlessly used, instead of $a_{cm}^{(exp)}$, in establishing of experimental validation [20,24] of the critical-*bending*-force constraint $3d^{(exp)} - l^{(exp)} = a_{cm}^{(exp)}$. As shown, this equation, unlike the case of the critical-*buckling*-force constraint $4d^{(exp)} - 2l^{(exp)} = a_{cm}^{(exp)}$ related to the original ESM, is observable directly and indirectly through, respectively, the a -constraint equation and Eq.(16) (analyzed in the last column of Table 1). Again, we infer that the observation of the *bending*-force criterium does not depend on the method chosen within the *one-scale* regression.

^{††}Extended statistical analysis of both the constraint equations, with including all available bone allometric data will be discussed elsewhere [25].

This is not the case for the *two-scale* data on bone-dimension allometric exponents reported [14] by Christiansen. Indeed, as follows from our many-sided analysis, the elastic-bending criterium is definitely supported for *small* and large mammals within the (principal-bone-averaged) *LSR* data and *RMA*, respectively. With accounting of the observation of the same criterium though the *one-scale* (principal-bone-averaged) *LSR* data, we see that correlations established by the traditional *LSR* method, unlike suggestion given in Ref. [14], show their self-consistency. But no certain conclusions can be inferred within the observation windows for small and large mammals in the cases of, respectively, *RMA* regression and *LSR*. We guess that the revealed discrepancy of the two equal in rights regression methods signals on failure of definition of the observation windows employed for the analysis of the critical-force constraints. In other words, unlike the case of the cylindric-shape similarity, these windows are not expected to be universal for observation of the elastic-force mechanisms, and cannot be therefore introduced by the unique boundary mass M_c .

Thereby we have demonstrated that the mammalian similarity, observable through experimental validation of the bone-evolution constraint equations, is described in terms of the *one-scale principal-bone-averaged* characteristics, which show independence on the regression methods. Within this context, the observed in nature long-bone mammalian evolution can be described through longitudinal-to-transverse bone-dimension scaling law, with the aforegiven "method-averaged" exponent $\lambda^{(\text{exp})} = 0.80 \pm 0.02$. Assuming a high enough accuracy for the i -bone experimental data on the exponents $a_{ci}^{(\text{exp})}$ and $b_i^{(\text{exp})}$, both the discussed evolution-mechanism criteria are approximated in the following forms, namely

$$\lambda^{(buckl)} = 2 \frac{2b - a_{cm}}{2b + a_{cm}} \text{ and } \lambda^{(bend)} = \frac{3b - 2a_{cm}}{b + a_{cm}} \quad (17)$$

that follows from Eqs.(11) and (15), respectively. With accounting of $a_{cm}^{(\text{exp})} = 0.81 - 0.83$, and adopting for the bone-mass mammalian allometric exponent $b^{(\text{exp})} = 1.03 - 1.06$ (see column 3 in Table 1) one has the following reduced-error estimates for the longitudinal-to-transverse scaling allometric exponents:

$$\lambda^{(buckl)} = 0.87 \pm 0.02 \text{ and } \lambda^{(bend)} = 0.80 \pm 0.03, \text{ with } \lambda^{(\text{exp})} = 0.80 \pm 0.02. \quad (18)$$

One can see that solely the elastic-bending criterium is validated. This implies corroboration the bone evolution mechanism, which provides avoidance of mechanical failure of mammalian bones caused by critical *elastic bending* deformations induced by *maximum-area* muscle contractions achieved in long bones during peak stresses.

From the physical point of view, the fact that the bending (but not buckling) elastic deformations are crucial for mechanical failure of *long* rigid bones should be expected, under condition that the inequality $L_{is} \gg D_{is}$ (but not $L_{is} \gtrsim D_{is}$) is fulfilled for animals of arbitrary mass. Meanwhile, this fact was not corroborated in the one-scale long-bone allometry, and we therefore report on the first observation of the bending-critical-force bone-evolution mechanism, which is suggested to be universal regardless of small and large mammals. Finally, after McMahon, we have demonstrated how the scaling laws established in mammalian allometry arise from a natural similarity of animals and how they can be quite explicit on the evolution constraints through simple geometrical and clear physical conceptions.

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| Bone | dimensions | | reduced dimensions | | | bone mass | | muscle area | |
|-----------------|------------|-------|--------------------|-------------|-----------------|--------------|---------|--------------------|-------------------|
| <i>LSR</i> data | d_i | l_i | l_i/d_i | λ_i | $b_i^*/d_i - 2$ | $2d_i + l_i$ | b_i^* | buckling | bending |
| humerus | .3816 | .2996 | 0.785 | 0.763 | 0.804 | 1.063 | 1.070 | 0.927 | 0.838 |
| radius | .3868 | .2995 | 0.774 | 0.753 | 0.802 | 1.073 | 1.084 | 0.948 | 0.850 |
| femur | .3548 | .3014 | 0.849 | 0.843 | 0.988 | 1.011 | 1.060 | 0.816 | 0.714 |
| tibia | .3600 | .2571 | 0.714 | 0.764 | 0.717 | 0.977 | 0.978 | 0.926 | 0.822 |
| Averaged | .3708 | .2894 | 0.781 | 0.781 | 0.828 | 1.031 | 1.048 | 0.904 | 0.806 |
| <i>RMA</i> data | d_i | l_i | l_i/d_i | λ_i | $b_i/d_i - 2$ | $2d_i + l_i$ | b_i | $a_{ci}^{(buckl)}$ | $a_{ci}^{(bend)}$ |
| humerus | .3860 | .3109 | 0.805 | 0.784 | 0.806 | 1.083 | 1.083 | 0.947 | 0.862 |
| radius | .4014 | .3210 | 0.800 | 0.787 | 0.743 | 1.124 | 1.101 | 0.959 | 0.874 |
| femur | .3599 | .3089 | 0.858 | 0.864 | 0.976 | 1.029 | 1.071 | 0.850 | 0.799 |
| tibia | .3654 | .2767 | 0.757 | 0.804 | 0.731 | 1.008 | 0.998 | 0.851 | 0.781 |
| Averaged | .3782 | .3044 | 0.805 | 0.810 | 0.814 | 1.061 | 1.063 | 0.901 | 0.829 |

Table 1. Testing of the mammalian long-bone similarity through the elastic-buckling and elastic-bending criteria. Experimental data by Christiansen on the mammalian dimension allometric exponents for i -bone diameter exponent d_i , length exponent l_i , reduced dimension exponent λ_i , and bone mass exponent b_i obtained by the least square regression (*LSR*) and the reduced major axis (*RMA*) regression methods. These are taken from Tables 2 in Refs. [14], [15] and [16], respectively. The *LSR* data on b_i^* are estimated here with the help of relation $b_i^* = r_i b_i$, where r_i (correlation coefficient) and b_i are corresponding data obtained by *RMA* regression. Predictions for the muscle-area critical exponents are given with the help of Eq.(16). Bone-averaged magnitudes are found as the mean values of the corresponding mammalian allometric exponents, *e.g.*, $d = \sum_{i=1} d_i / 4$.

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Figure Captures

Fig. 1. Evolution of the cross-section area for muscle fibers with body mass in the mammalian hindlimbs. *Points*: diamonds, circles, squares and crosses are experimental data taken from Fig.3 in Ref. [22] for, respectively, gastrocnemius, plantaris, deep digital flexors and common digital extensors. *Arrows* indicate the maximum muscle-area points achieved for a given mass. *Solid line* corresponds to regression A_{cm} of these points along with their nearest neighbors, with $A_{cm} = 366 * M^{0.82}$. *Dashes line* is given for the isotropic scenario description with $A_0 = 29 * M^{2/3}$.

Fig. 2. Mammalian bone-dimension diagram: bone diameter against bone length. *Points*: A'79, B'83, B'92 and C'99 correspond to the overall-bone-averaged allometric data derived through the least square regression method by Alexander *et al.*, Biewener, Bertran & Biewener, and Christiansen and reported, respectively, in Refs. [9,11,13] and [14]. *Crosses* correspond to the ESM [6] ($d_0^{(buckl)} = 3/8$, $l_0^{(buckl)} = 1/4$, $a_0 = b_0 = 1$) and isometric scenario ($d_0 = l_0 = 1/3$, $a_0 = 2/3$, $b_0 = 1$) predictions; *a-lines* are due to the elastic-bucking and elastic-bending *a*-constraints given in, respectively, Eqs. (9) and (13) and estimated for the case of the critical-force exponent $a_c = 0.82$ derived in Fig.1. The dashed areas indicate the elastic-bucking and elastic-bending *criteria* given, respectively, in Eqs.(10) and (14). These areas extend the corresponding *a*-lines by accounting of the *b*-constraint equations within the experimental error for $a_{cm}^{(\exp)} = 0.82 \pm 0.01$ and $b^{(\exp)} = 1.05 \pm 0.05$ taken, respectively, from Fig.1 and Table 1.

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