

On the hidden physical dimensions of the allometric equation

Acerca de las dimensiones físicas ocultas
en la ecuación alométrica

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The aim of the present study was to submit Huxley's allometric equation ($Y = aM^b$) to a dimensional analysis; in this equation Y is any biological variable, a is the mass-coefficient, M represents body mass, and b the mass-exponent. The dimensions of each of its components is thoroughly analyzed by means of the MLT-system of physics, as is the dimensionality of the whole equation. The relationship between the dimensional analysis and the postulates of some theories of biological similarity is discussed. In conclusion, parameter a of the allometric equation is always dimensionless, while the physical dimensions of the dependent variable Y can be defined by means of the power function M^b .

Comparative physiometry and morphometry deal with empirical values obtained from living beings of different sizes. These numerical values are then submitted to the pertinent statistical procedure provided that the correlation between the dependent and independent variable is linear. However, if the original data are not linearly correlated, it is possible to apply a log-log transformation in order to obtain the required linear relationship. With the latter procedure the experimental data can be conveniently expressed by means of Huxley's (1932) allometric equation ($Y = aM^b$), where Y is the dependent variable; M is the independent variable, generally the body mass; and a and b are two parameters. The apparent simplicity of the allometric equation may explain the preference of biologists for this type of mathematical treatment.

Due to the fact that the allometric power formula is an equation, its dimensional homogeneity is mandatory when the physical characteristics of living beings are studied (lengths, area, volumes, pressures, compliances, concentrations, flows, resistances, elasticities, among others).

The present study deals with the dimensional analysis of the allometric equation and its possible interpretations. Never-

theless, the whole dimensional problem can be neglected when one considers:

- a) that the allometric equation has an empirical and statistical origin. In this case, the equation does not necessarily have to obey the required dimensional homogeneity which is obligatory in the physical sciences, and
- b) because logarithms are always pure numbers, the logarithmic transformation of the empirical data, which are then expressed in allometric form, annihilate the physical nature of these data; and
- c) that the physical dimensions can be eliminated from the allometric equation through the use of "dimensionless ratios" of the primary physical units, i.e., the length ratio between prototype (p) and model (m)*, which yield $L_p/L_m = \lambda$, or the ratio of time functions ($T_p/T_m = \tau$), and finally of two masses ($M_p/M_m = \mu$). In these three instances we are dealing with dimensionless numbers ($M^\circ L^\circ T^\circ$) because then corresponding physical dimensions are absent.

* *Prototype* (p) means a large or a small scale organism to which a *model organism* (m) is geometrically, chemically, or physically related.

The other alternative is to try to investigate the conditions under which the physical dimensions of the allometric equation are of importance.

First, dimensional analysis is basic when different theories of biological similarity are postulated (reviewed by Günther, 1975a, b), since in these cases it must be assumed *a priori*:

- a) that body *density* is constant; and
- b) that several exogenous or endogeneous characteristics are invariant, as for instance: i) the *acceleration* of gravity (mechanical similarity); ii) the *velocity* of certain functions (biological similarity); and iii) the *transfer* of matter or energy (transport similarity).

Second, in order to ascertain whether or not the allometric equation is physically homogeneous, dimensional analysis can be applied to the allometric equation as a whole ($Y = aM^b$), or to its different components (Y , a , M^b).

Third, the allometric equation only deals with two variables at a time, despite the fact that all biological processes are more likely to be of multivariate nature, and non-physical factors may influence the physical variables which are investigated.

Due to the general applicability of the allometric equation in the biological sciences, it seemed worth studying the physico-mathematical aspects of this equation, particularly its relationship with various theories of biological similarity, which are commonly based on the dimensional analysis of the different biological variables.

The aim of the present study is to submit the allometric equation as well as its components to the dimensional analysis, i.e., the dependent variable Y , the proportionality coefficient a (the intercept at unity mass), body mass (M), and finally, exponent b (the slope of the regression line).

A) *The allometric equation*

The relationship between any physical variable (Y) and body mass (M) can be described conveniently by means of the allometric equation which was largely developed by J.S. Huxley (1932). Since both

variables (Y and M) increase at different rates, this power equation is often defined as "allometric". When the relative sizes of Y and M are compared, the allometric equation assumes the general form

$$Y = aM^b \quad (1)$$

where Y is any physiological, morphological, or ecological variable that can be correlated in most cases with body mass (M). It should be noted that in Eq. 1 both a and b are parameters whose physical meanings will be discussed later. Moreover, the numerical value of exponent b determines the type of scaling phenomenon, since when $b = 0$ the dependent variable (Y) is constant, whereas when $b = 1.0$ the relationship is linear. On the other hand, when $b < 1.0$ the corresponding curve is a hyperbola, and if $b > 1.0$ the result is a parabola. Contrariwise, when the allometric exponent b has a negative sign, then an inverse relationship exists between the independent variable (M) and the dependent variable (Y). Thus, the exponent b is known as the "scaling factor", because it describes the effects (Y) which are correlated with the changes in body size (M).

Since non-linear relationships are difficult to manipulate, they are usually transformed into logarithmic expressions. When this is done with Eq. 1, a straight line equation is obtained:

$$\log Y = \log a + b \log M \quad (2)$$

where

$$Y' = \text{intercept} + \text{slope } M' \quad (3)$$

since $Y' = \log Y$ and $M' = \log M$.

Thus, Eq. 2 is a simple mathematical expression which is convenient for the statistical treatment of the experimental data, provided that these are represented in a double logarithmic form ($\log Y$ versus $\log M$).

Despite the fact that the allometric equation has been known for more than 150 years (Kleiber, 1932), it was particularly the work of Huxley (1932) who introduced

this simple and powerful tool to the quantitative description of the multiple scaling phenomena which can be observed among living beings. The general acceptance of the allometric equation in the biological sciences is illustrated by the recent publication of four extensive monographs on the subject, where this equation was universally employed (Calder, 1984; McMahon & Bonner, 1983; Peters, 1983; and Schmidt-Nielsen, 1984).

Nevertheless, there are numerous controversial aspects concerning the allometric equation that are still unresolved, as for instance:

- a) that *dimensional analysis* of physics cannot be applied to the results of many biological measurements that are expressed in allometric form (Schmidt-Nielsen, 1984, p. 18);
- b) that *exponent (b)* can be "predicted" on the basis of dimensional analysis and several theories of biological similarity (Lambert & Teisser, 1927; Günther, 1975a, b; Heusner, 1982, 1983, 1984, 1988); a statement which is not accepted by Butler *et al.*, 1987, 1988;
- c) that the *units of the body mass* measurement (mg, g, kg, t) are of importance (Donhoffer, 1986), or that these units are irrelevant (Calder, 1987, Günther & Morgado, 1987);
- d) that the *physical dimensions* of the allometric equation are of real importance, particularly the mass-coefficient *a* (Heusner, 1984, 1985, 1987).

Lambert & Teissier (1927) introduced dimensional analysis and a new theory of biological similarity into biology, based particularly on the mass (M), length (L), and time (T) system of newtonian physics. However, recently a vivid controversy has arisen (for detail see Heusner, 1982-88; Feldman & McMahon, 1983; Butler *et al.*, 1987-88) concerning the applicability of both dimensional analysis and theories of biological similarity to scaling problems in the biological sciences.

B) *The dimensionless body-mass ratio*

For most investigators, the allometric equation only describes the experimental data

at hand in a quantitative manner, and the power equation does not represent a biological law. Nevertheless, in some instances the allometric equations may "reveal principles and connections that otherwise remain obscure" (Schmidt-Nielsen, 1984, p. 32). On the other hand, these equations do not require the dimensional consistency which is obligatory in the physical sciences due to their statistical origin (regression line of the log-log plot). In consequence, a rigorous dimensional analysis should not be mandatory (Riggs, 1963; Calder, 1984).

Moreover, the logarithmic form of Eq. 2 is dimensionless *per se*, otherwise we would have to consider the following alternatives:

- a) the "secondary" units (Schepartz, 1980, p. 4) should be the result of an *addition* and not of a *product*, as it is customary in the physical sciences;
- b) the summation of $\log a$ and $b \log W$ is only possible if both are dimensionless numbers;
- c) since $\log a$ is equivalent to $\log Y$ when the body mass (M) is equal to unity, parameter a should have the same units as the dependent variable Y ; in consequence, the term M^b must be dimensionless, in which case we could not add $\log a$ with $\log M^b$.

In previous publications (Günther, 1975a, b; Günther and Morgado, 1982, 1987) we have avoided the dimensional problem by establishing dimensionless ratios between the primary units of the prototype (p) and the model (m), in such a way that $M_p/M_m = \mu$, $L_p/L_m = \lambda$, and finally $T_p/T_m = \tau$. As a result, the subsequent analysis was performed entirely with "dimensionless numbers".

C) *The dimensions of the body mass-coefficient (a)*

One of the best known allometric equations is related with areas (A) and volumes (V) of geometric bodies (Günther, 1975a, b), which can be defined by means of Meeh's (1879) equation. In the particular case of a spherical body the relationship between its area (A) and the corresponding mass (M) obeys the following formula:

$$A = 4.84 M^{2/3} \quad (4)$$

where A is the surface area of the sphere, in dm^2 , and M , is its mass, in kg.

The original deduction of Eq. 4 was based on the relationship between the radius (r) and the mass (M) of a sphere, whose density (ρ) was assumed to be 1 kg/dm^3 , hence

$$V = (4/3) \pi r^3 \quad (5)$$

and

$$A = 4\pi r^2 \quad (6)$$

From Eq. 5 we obtain

$$r = (3V/4\pi)^{1/3} \quad (7)$$

and by introducing the radius (r) into Eq. 6, we have

$$A = 3^{2/3} (4\pi)^{1/3} V^{2/3} \quad (8)$$

Finally, when all numerical terms are condensed into one parameter (a), we obtain

$$A = 4.84 V^{2/3} \quad (9)$$

where parameter a is a dimensionless constant, which is numerically different for each geometric body; only in the case of the sphere does it attain a value of 4.84.

It is worth mentioning that Eq. 4 is basic for establishing a "geometric" similarity, which assumes that the body density (ρ) of prototype (p) and a model (m) are the same. In consequence, body density represents a constant ($\rho_p/\rho_m = 1.0$), in such a way that the characteristic radius (r) is equivalent to the cubic root of the volume (V) of the sphere. In the present example we have seen that one fundamental unit (length) is expressed as a power function of another fundamental unit (volume). However, a more rigorous treatment of Eq. 4 would yield.

$$A = 4.84 (\rho^{-2/3}) M^{2/3} \quad (10)$$

where M is body mass and ρ its density ($\rho = M/V$) which assumed to be constant, thus it is part of parameter a . As a result, the dimensions of A in Eq. 8 depend on the dimensions of $V^{2/3}$, because $V^{2/3} = (r^3)^{2/3} = r^2$.

On the other hand, Heusner (1984) has postulated that when the mass-exponent (b) differs from unity ($b \neq 1$), the allometric power formula (M^b) is physically meaningless, and should be considered as an "intensive" property. In that case, the dimensions of area (A) in Eq. 10 are defined by the power formula of body density ($\rho^{-2/3}$). But, it should be recalled that our findings do not agree with Heusner's conclusion (1984) due to the fact that density (ρ) is an "intensive" variable.

D) *Is the body mass exponent (b) adimensional?*

The mass-exponent b (slope of the double logarithmic plot) of any power formula (M^b) is a dimensionless number, because b is equivalent to a logarithm, and, as result, all the terms of the allometric equation should be dimensionless. Yet, it is worth mentioning that the allometric equation can be deduced from some basic assumptions, namely that:

a) the growth of a system (von Bertalanffy, 1968) is directly proportional to the number of elements (Q) present in the system defined by number one:

$$dQ_1/dt = a_1 Q_1 \quad (11)$$

For a second system, we have

$$dQ_2/dt = a_2 Q_2 \quad (12)$$

If we further assume that both systems are in "competition", an allometric equation of the form

$$Q_1 = a_3 Q_2^b \quad (13)$$

can be obtained after integration of equations (11) and (12).

b) the allometric equation can also be obtained (Schepartz, 1980) from the growth processes of two entities of the same physical dimension which follow first order kinetics. If X and Y are two variables that can be expressed by the same units, the growth processes are functions of time (t), which can be defined as follows:

$$dY/dt = k_1 Y \quad \text{and} \quad dX/dt = k_2 X \quad (14)$$

If both processes occur at the same time we have:

$$dY/Y = (k_1/k_2) dx/X \quad (15)$$

which, after integration, yields:

$$Y = aX^b \quad (16)$$

Moreover, in Eq. 16, parameter a defines the initial conditions (intercept), while exponent b is equivalent (see Eq. 15) to the ratio k_1/k_2 . Since both constants (k_1 and k_2) have the physical dimensions of the physical dimensions of the reciprocal of time (T^{-1}), i.e., of a frequency, consequently the ratio of both constants (k_1 and k_2) is a dimensionless number. Due to the fact that we have initially assumed that the units of X and Y are identical, the homogeneity of the allometric equation can be achieved only if parameter a is raised to the power function $(1-b)$ of either variable X or of variable Y . Therefore, the physical units of the dependent variable Y are equivalent to the units of the corresponding power formula (aX^b) of the independent variable X . If both growth processes have the same constant (k_1), the power formula (X^b) will have the same units as Y . On the other hand, if k_2 is much greater than k_1 , the dimensions will depend on parameter a . These particular relationships were thoroughly discussed by Heusner (1982-88).

In sum, the adimensionality of the mass-exponent (b) can be deduced from basic growth processes, as well as from the logarithmic nature of this exponent.

E) *The physical dimension of the dependent variable (Y) is correlated with the power formula (W^b).*

The applicability of allometric equations is not restricted to the condition that variables Y and X should have the same physical dimensions (length, time, mass, among others). One of the most quoted allometric equations, which deals with Kleiber's (1975) relationship between the basal metabolic rate (m) and body weight (W), in kg, is:

$$m = 70W^{3/4} \quad (17)$$

In this equation, the physical units of the two terms of the equation are different.

We have previously mentioned that the allometric equation can be deduced analytically from some basic growth processes (see Eqs. 11 and 14). Therefore, we can reformulate Eq. 15 in the following manner:

$$(dY/Y)/(dX/X) = k_1/k_2 = b \quad (18)$$

Eq. 18 illustrates the fact that, even if the growth processes of X and Y are different, and are expressed by means of different physical units (White and Gould, 1965), the mass-exponent (b) is still a dimensionless number.

Another characteristic of the allometric equation is that the exponent (b) may have the same value irrespective of the physical variables involved; as for instance, $b = 0$ may represent g/l, moles/l, or calories/g, whereas $b = 1$ can represent mass, energy, volume, work, etc. Even when exponent b is of fractional nature, the allometric equation can sometimes represent a primary physical variable, as for instance, a length $L = V^{1/3}$, where V is a volume.

It is worth mentioning that Lambert & Teissier (1927) formulated the first theory of "biological similarity" based on the principles of a "geometric similarity" by assuming the validity of two postulates, i.e.:

- 1) that the body composition of different mammals is similar, and in consequence their *densities* should be identical, or that $\rho = M/V = \text{constant}$. This postulate is also based on the fact that all mammals are on the verge of floatation when placed in water;
- 2) that biological periods (T) vary in proportion to the corresponding length (L), i.e., that *velocities* (v) are the same in prototype (p) and model (m), or that $v = L/T = \text{constant}$.

From these postulates we can deduce:

- 1) That the *density* equivalence ($\rho = M/V = \text{constant}$) can be rewritten—in accordance with a geometric similarity—as:

$$\rho = M/L^3 \text{ or } L = M^{1/3} \rho^{-1/3} \quad (19)$$

and

- 2) That the *velocity* equivalence ($v = L/T =$ constant) can be expressed as:

$$T = v^{-1} L \quad (20)$$

If time (T) is now correlated with body mass (M), we obtain:

$$T = v^{-1} M^{1/3} \rho^{-1/3} \quad (21)$$

As a result, basal metabolic rate (m), whose physical dimension is equivalent to "power", will yield

$$[m] = [ML^2 T^{-3}] \text{ or } [m] = [\rho^{1/3} v^3 M^{2/3}] \quad (22)$$

Since ρ and v are the two postulated biological constants, it stands that basal metabolic rate (m) must vary in proportion to $M^{2/3}$.

However, Heusner (1984-1988) has postulated that the physical units of variable Y depend on those of parameter a . In accordance with his assumption one obtains the following expression for the metabolic rate (m):

$$[m] = [ML^2 T^{-3}] = [M^{1-b} L^2 T^{-3}] [M^{2/3}] \quad (23)$$

Since in this particular case the allometric mass-exponent is equal to $2/3$, we can introduce this value into Eq. 23 and obtain:

$$[ML^2 T^{-3}] = [M^{1-2/3} M^{2/3} M^{-1}] [M^{2/3}] \quad (24)$$

The result is that parameter a is dimensionless (M^0), a conclusion which is in contradiction with Heusner's original assumption, namely, that the physical dimensions of Y are given by the dimensions of parameter a .

Besides metabolic rate (m), many other functions can be submitted to a dimensional analysis and incorporated into some theory of biological similarity. For this purpose, Newton's reduction coefficient (χ) can be expressed in accordance with the MLT-system of physics:

$$\chi = M^\alpha L^\beta T^\gamma \quad (25)$$

Nevertheless, the question of which are the convenient primary units which should be used when dimensional analysis is applied

to the biological sciences is the first to arise. Platt & Silvert (1981, p. 857) have suggested that the following general equation can be utilized when three independent entities (A, B, C) are present:

$$Q = f(A^a B^b C^c) \quad (26)$$

As mentioned above, in the physical sciences the equivalences could be A = mass, B = length, and C = time, or any other relevant units. Therefore, Eq. 25 can be written as

$$Q = f(M^\alpha L^\beta T^\gamma) \quad (27)$$

and the postulated two basic assumptions of the theory of biological similarity could be expressed as follows

$$M = L^m \quad (28)$$

and

$$M = T^n \quad (29)$$

Consequently, from these two assumptions, and through the use of Newton's reduction coefficient (χ), we obtain

$$\chi = M^\alpha L^\beta T^\gamma \text{ or } M^\alpha M^{\beta/m} M^{\gamma/n} \quad (30)$$

and finally

$$\chi = M^{\alpha + \beta/m + \gamma/n} \quad (31)$$

In consequence, the theoretically deduced exponents (Eq. 31) can be now compared with the empirical findings (exponents b) because, and in accordance to Yates (1979, p. R1), we shall have

$$b = p_1 \alpha + q_1 \beta + r_1 \gamma \quad (32)$$

where the coefficients p_1 , q_1 , and r_1 represent the corresponding numerical factors for each of the three similarity principles (mechanical, biological, and transport), and where α , β , γ are the corresponding physical dimensions (Günther 1975a, b). As a result, any empirical allometric exponent (b) will be equivalent to the theoretical reduced exponent for a given function

$$b = \alpha + \beta/m + \gamma/n \quad (33)$$

With regards to the metabolic rate (m), which we have briefly discussed above, it should be noted that the small difference between allometric exponents for basal metabolism $b = 2/3$ (Eq. 22) and $b = 3/4$ (Eq. 17) has been the cause of a recent controversy (Heusner, 1987, 1988; Feldman & McMahon, 1983; Butler *et al.*, 1987, 1988).

F) *Dimensionless numbers from ratios of allometric equations*

In order to obtain size-invariant dimensionless groups, as first suggested by W.R. Sthal (1962), it is possible to avoid the physical dimensions involved in biological morphology through the establishment of ratios between two allometric equations pertaining

to the same biological variable. The resulting formula, whose exponent is zero or almost zero, was designed by Stahl as the "residual mass exponent" (RME), and in it, the corresponding mass coefficient (a) is a numerical index of the relationship between the two allometric equations under consideration.

The dimensionless groups presented in Table 1 were obtained from empirical allometric equations of equivalent functions in mammals, birds and reptiles. From these ratios one obtains the corresponding "dimensionless numbers" in which the RME is very close to zero in each case. These dimensionless numbers are of particular interest when intraspecific or interspecific comparison are of biological relevance, since the structural or functional charac-

TABLE 1

Dimensionless numbers from allometric ratios of different functions.
mainly pertaining to animals of different species.

Item	Ratios and allometric equations'	References
A)	HEART RATE (min^{-1}) in resting conditions: $\frac{\text{Mammals}}{\text{Birds}} = \frac{241 M^{-0.25}}{156 M^{-0.23}} = 1.54 M^{0.02}$ $\frac{\text{Mammals}}{\text{Marsupials}} = \frac{241 M^{-0.25}}{106 M^{-0.27}} = 2.27 M^{-0.02}$	Calder (1984) p. 108
B)	RESPIRATORY CYCLE (sec): $\frac{\text{Mammals}}{\text{Birds}} = \frac{1.12 M^{0.26}}{2.63 M^{0.28}} = 0.43 M^{-0.02}$	Calder (1984) p. 142 - 143
C)	HEART RATE AND RESPIRATORY RATE (s^{-1}) in mammals: $\frac{\text{Heart rate}}{\text{Respiratory rate}} = \frac{3.61 M^{-0.27}}{0.885 M^{-0.028}} = 4.08 M^{0.01}$	Peters (1983) p.255 & 257
D)	METABOLIC RATE ($\text{Kcql} \cdot \text{day}^{-1}$) $\frac{\text{Passerines (activity)}}{\text{Passerines (rest)}} = \frac{140.9 M^{0.704}}{114.8 M^{0.726}} = 1.23 M^{-0.022}$ $\frac{\text{Nonpasserines}}{\text{Passerines}} = \frac{3.31 M^{0.723}}{4.98 M^{0.724}} = 0.66 M^{-0.001}$	Schmidt-Nielsen (1984) p. 69 & 88

Item	Ratios and allometric equations'	References
	Resting energy in mammals (watt) and M (kg)	
	$\frac{\text{Eutherian}}{\text{Marsupial}} = \frac{3.35 M^{0.75}}{2.97 M^{0.737}} = 1.13 M^{0.013}$	
	$\frac{\text{Eutherian}}{\text{Monotreme}} = \frac{3.35 M^{0.75}}{2.99 M^{0.75}} = 1.12 M^{0.00}$	
	Oxygen consumption (ml O ₂ /min) in Eutherians:	
	$\frac{\text{Exercise}}{\text{Rest}} = \frac{116.4 M^{0.79}}{11.6 M^{0.76}} = 10 M^{0.03}$	Calder (1984) p. 114
E)	MAXIMUM LIFESPAN (days):	Peters (1983) p. 283
	$\frac{\text{Mammals}}{\text{Wild Birds}} = \frac{4240 M^{0.20}}{6400 M^{0.20}} = 0.66 M^{0.00}$	
F)	KIDNEY: Inulin clearance (ml s ⁻¹)	Peters (1983) p. 261
	$\frac{\text{Mammals}}{\text{Birds}} = \frac{0.089 M^{0.72}}{0.035 M^{0.78}} = 2.54 M^{-0.06}$	
	$\frac{\text{Mammals}}{\text{Reptiles}} = \frac{0.089 M^{0.72}}{0.0083 M^{0.75}} = 10.72 M^{-0.03}$	
G)	SKELETON MASS (kg) and M (in kg):	Peters (1983) p. 264
	$\frac{\text{Mammals}}{\text{Birds}} = \frac{0.061 M^{1.06}}{0.065 M^{1.071}} = 0.94 M^{-0.011}$	

teristics can now be defined quantitatively by a single number, which is dimensionless from a physical point of view, and which is able to define the ratio between both variables, irrespective of body size ($M^0 = 1.0$).

In order to illustrate the general relevance of these comparisons, let us examine for instance the ratio between heart rates and respiratory rates in mammals at rest (Table 1, item C), which yielded a figure of 4.0, i.e., four cardiac cycles per one respiratory cycle, irrespective of body size. Another example is the ratio of oxygen consumption (ml O₂ · min⁻¹) in wild mammals (Table 1, item D) between maximal exercise and at rest, and which turns out to be equal to 10, i.e., the maximum oxygen uptake is ten times greater during this type of exercise than under resting conditions, again irrespective of body size.

Finally, a further type of allometric ratio can be conceived, namely, the quotient of two allometric equations whose functions have different physical dimensions. These have been summarized in Table 2. Again, the RME is zero or close to zero, and which means that we are dealing with dimensionless numbers whose numerical values are given only by the allometric coefficient (a). Among the dimensionless ratios obtained from these empirical allometric equations, the first one (Table 2, item A) deals with the relationship between heart rate (s⁻¹) and the mass-specific metabolic rate (watt · kg⁻¹), which yields a direct correspondence between both functions, i.e., the frequency of the heart varies proportionally with the metabolic rate per unit mass. The second example (Table 2, item B) correspond to the ratio between cardiac output (ml · s⁻¹) and the surface area of the body (m²), a

TABLE 2

Allometric ratios of structures and functions of mammals, whose physical dimensions are different.

Item	Allometric Ratios	Allometric Equations	References
A	Heart rate (s^{-1}) Mass-specific metabolic rate ($watt \cdot kg^{-1}$)	$\frac{3.61 M^{-0.27}}{3.42 M^{-0.27}} = 1.05 M^{0.00}$	Peters (1983) p. 238 & 257
B	Cardiac output ($ml \cdot s^{-1}$) Surface area (m^2)	$\frac{5.48 M^{0.74}}{0.10 M^{0.67}} = 54.8 M^{0.07}$	Ibid. p. 238
C	Aortic wall tension (Nm^{-1}) Aortic length (m)	$\frac{27.3 M^{0.35}}{0.16 M^{0.32}} = 170.6 M^{0.03}$	Ibid p. 259 & 260
D	Cardiac work (J) Heart volume (ml)	$\frac{8.91 \times 10^{-3} M^{1.06}}{5.72 M^{0.98}} = 1.56 \times 10^{-3} M^{0.08}$	Ibid p. 257 & 260
E	Blood sugar ($g \cdot liter^{-1}$) Cell diameter (μm)	$\frac{1.19 M^{-0.07}}{16.1 M^{0.03}} = 0.07 M^{0.10}$	Ibid p. 259

relationship of wide acceptance in clinical medicine, used to normalize the minute-volume of the heart with regards to different body sizes, i.e., the cardiac output is $54.8 ml \cdot s^{-1}$ per square meter of body surface area.

In consequence, the dimensionless allometric ratios, which are particularly relevant for interspecific comparisons, can be obtained from allometric equations pertaining to the same function, or from allometric equations of functions which have different physical dimensions, a fact that confirms the wide biological applicability of these power equations.

DISCUSSION

After more than 50 years of extensive utilization of Huxley's (1932) allometric equation, the different authors disagree as to its physical dimensionality. Certain investigators have analyzed the dimensional homogeneity of the entire equation, while

others have concentrated their attention on one or both of its components, as for instance on parameter a or on exponent (b).

With regards to *parameter (a)* we have found that, in general, it is dimensionless (see Eqs. 4-9, 17, and also Eqs. 19-24). Alternatively, the physical dimensions of parameter a can be assumed to be present when its dimensions are identical to those of the dependent variable (Y):

a) this happens when we utilize the dimensionless ratio of body masses ($M_p/M_m = \mu$), a condition which we have used preferentially in previous studies (Günther, 1975a, b; Günther & Morgado, 1982, 1987);

b) this also occurs when one considers that M^b represents some "intensive" property (Heusner, 1982-88). This happens when exponent b is 0, and therefore $M^0 = 1.0$; in this case parameter a concentrates all physical dimensions of the right term to the allometric equation, which now is equivalent to the physical dimensions of the dependent variable (Y);

c) finally, Heusner (1984-88) has suggested that parameter a should be considered as the *dimensional part* of the equation, which then is homogeneous with regard to variable Y . On the other hand, the power function of body mass (M^b) is *dimensionless* because it represents an "intensive" property, except when $b=1.0$, in this case we are dealing strictly with a physical mass. Nevertheless, Butler *et al.*, (1987, 1988) have recently pointed out, that neither dimensional analysis nor the theories of biological similarities can predict the body mass exponent (b) for basal metabolic rate (m), a conclusion which has led to a sharp controversy with Heusner (1988). However, this discrepancy is beyond the scope of our present analysis.

The allometric *exponent* (b) is an index of "relative" growth (Huxley, 1932) and is commonly of a fractional nature ($-1 < b < 1$); seldom is the numerical value of b greater than unity. On the other hand, exponent (b) is the result of a comparison between the growth rates of two variables (see Eq. 7-9 and Eq. 18) which always yield pure numbers.

In sum, parameter a is always dimensionless if the three variables of the MLT-system are treated separately, as in Eq. 24. On the other hand, the mass-exponent b is either zero or unity, and the transfer of exponent (b) into the mass-coefficient a (Eq. 24) only changes the physical meaning of the term M^b , due to the introduction of the term M^{1-b} into parameter a . Therefore, the physical units of the dependent variable (Y) are defined exclusively by the dimensions of the term M^b of the allometric equation.

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