THEORY OF BIOLOGICAL SIMILARITIES, NONDIMENSIONAL PARAMETERS AND INVARIANT NUMBERS

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In previous papers (1955–1957) a theory of biological similarity was established, assuming that the limits are the mechanical and the electrodynamical similarity criteria. The range of this theory lies between the coefficient of the time exponent (γ) for mechanical (0.5γ) and electrodynamical (1.0γ) similarities, being the mode 0.93γ . Moreover, for certain functions this restricted theoretical range should be extended to the hydrodynamical similarity criterion (2γ) , so that the dimensionless numbers commonly used in Physics (Reynolds, Froude, Weber, etc.) can be included within the total range $(0.5-2\gamma)$ of biological similarities. From dimensional analysis of physiological functions it was possible to obtain, by means of dimensional and solution matrices, a group of "nondimensional numbers" by applying Buckingham's Pi-theorem. Nevertheless, only if a single similarity criterion was applied, the residual weight exponent was exactly zero; in all other instances the weight exponent was not zero, due to the existence of a range for biological similarities and to the statistical meaning of exponent (b) of the allometric equations. From the similarity criteria "invariant numbers" can be obtained, by means of which it is possible to establish correlations between numerous morphological and physiological characteristics of a particular system (circulation, respiration, metabolism, etc.).

The idea of geometrical similarity was first analyzed by Greek mathematicians in connection with ratios and proportions of similar triangles. The same reasoning was afterwards extended to the ratios of physical quantities by Galileo (1638), who studied structural and functional changes involved in biological scale-up phenomena. Newton in 1735 applied similarity criteria mainly to mechanical problems. Modern mathematicians and physicists, as Bridgeman (1922), Langhaar (1951), Birkhoff (1960) and Sedov (1959) among others, have been concerned for many years with dimensional analysis and similarity principles.

Several attempts were made in the past to introduce dimensional analysis and similarity principles into the Biological Sciences, particularly by von Hoesslin (1888, 1927), Lambert and Teissier (1927), von Bertalanffy (1951), D'Arcy Thompson (1952), Günther and Guerra (1955, 1957), Rashevsky (1960), Kleiber (1961), and more recently this particular matter has been thoroughly discussed by Stahl (1961, 1962a, 1962b, 1963).

Years ago we tried to find a single similarity rule for all biological phenomena (Günther and Guerra, 1955), where dimensions are power functions of M, L, and T. Nevertheless, in Stahl's (1963) own words (page 296) our previous attempts "to find a *single* physical similarity criterion for scaling of *all* biological variables" should fail, because "the systems are much too complex to be governed by so simple a requirement as invariance of one similarity criterion".

In the present paper we have tried to reexamine certain assumptions of the previous theory of biological similarities, particularly the problem related to the coefficient 0.93 for the exponent γ of the time ratio τ . Furthermore, due to the fact that certain dimensionless numbers (Reynolds, Froude, Weber, etc.) which are commonly used in Physics were not considered in the original formulation of the theory, steps were taken so that they could be included. Finally, through the applications of Buckingham's Pi-theorem, similarity criteria were found and when they were combined it was possible to obtain "invariants", whose residual weight exponent is almost zero, i.e. that all these constants are practically independent of body mass.

A. New approach to the theory of biological similarities. The original equation of the theory of biological similarity was:

$$A = a \cdot W^{\frac{1}{2}(3\alpha + \beta + 0.93\gamma)}; \qquad (1)$$

being

A =physiological function;

a =parameter of the same dimensions as A;

W = numerical value of body weight in arbitrary units (Kg, g, mg, etc.);

 α = exponent of the mass ratio $M/m = \mu$;

 β = exponent of the length ratio $L/1 = \lambda$; and

 $\gamma =$ exponent of the time ratio $T/t = \tau$.

The coefficient 0.93 for γ was obtained as the most probable value from the exponents of the allometric equations, corresponding to heart frequency and to the heat generation rate, both as functions of body weight.

For these reasons it seems necessary that the basic assumptions leading to the general theory of biological similarity should be discussed briefly.

1. Dimensional analysis and theories of similarity. The derived physical magnitudes (Q) can be expressed as power functions of M, L, and T, as for instance: $Q = M^{\alpha}L^{\beta}T^{\gamma}$. Considering (Q) the prototype and (q) the model $q = m^{\alpha}l^{\beta}t^{\gamma}$. The ratio between prototype and model is therefore:

 $\chi = Q/q = \mu^{\alpha} \cdot \lambda^{\beta} \cdot \tau^{\gamma};$

or

$$Q = q \cdot \chi = q \cdot \mu^{\alpha} \cdot \lambda^{\beta} \cdot \tau^{\gamma}.$$
⁽²⁾

a) Mechanical similarity. The model theory of mechanical systems assumes that acceleration (g) and density (d) should be considered constant, so that $g(\stackrel{d}{=} L \cdot T^{-2}) = C$, implying $\lambda \cdot \tau^{-2} = 1.0$.

Now, when density (d) is maintained constant:

$$d (\stackrel{a}{=} ML^{-3}) = C$$
, then $\mu = \lambda^3$ or $\lambda = \mu^{\frac{1}{3}}$.

Furthermore, the ratio between the weights of the prototype (W) and the model (w) gives;

Finally,

$$\omega = W/w = Mg/mg = \mu$$

$$\lambda = \mu^{\frac{1}{3}} = \omega^{\frac{1}{3}}.$$

Introducing these equivalences into equation (2) we obtain:

$$Q = q \cdot \lambda^{(3\alpha + \beta + \frac{j}{2})} = q \cdot \omega^{\frac{1}{3}(3\alpha + \beta + \frac{j}{2})}.$$
(3)

b) Electrodynamic Similarity. The model theory of electrodynamic phenomena considers—besides the constancy of densities—that the following factors are maintained constant $(\mu_0 \cdot \epsilon_0)^{-\frac{1}{2}} = C$, being μ_0 = magnetic permeability and ϵ_0 = dielectric coefficient. But, since this constant is $C \stackrel{d}{=} L \cdot T^{-1} =$ velocity of light in the vacuum, therefore $\lambda \tau^{-1} = 1$ or $\lambda = \tau$.

The electrodynamic similarity formula is obtained by introducing into equation (2) the corresponding relations between μ , λ , τ

$$Q = q \cdot \lambda^{(3\alpha + \beta + \gamma)} = q \cdot \omega^{\frac{1}{2}(3\alpha + \beta + \gamma)}.$$
 (4)

c) *Biological similarities*. As stated above, the general equation of the theory of biological similarities can be defined as:

$$y = a \cdot \omega^{\frac{1}{3}(3\alpha + \beta + \gamma')}; \tag{5}$$

where γ' could assume any value in the interval $[\gamma/2, \gamma]$ that is $\frac{\gamma}{2} \leq \gamma' \leq \gamma$.

The coefficient 0.93 for γ was established only for statistical reasons and as the most likely coefficient for a single biological similarity criterion. Since a detailed study of the possible coefficients of γ was not made at that time, we have now calculated the coefficients directly from the exponent (b) of the empirical allometric equations.

Determination of the coefficient of γ for "compliance." As an example, let us calculate the coefficient for "thoracic compliance", whose allometric equation is:

$$C_T = 1.62 \times 10^{-2} |W|^{0.82}$$
.

According to the dimensional analysis, "compliance" can be defined as $M^{-1}L^4T^2$, with the exponents $\alpha = -1$, $\beta = 4$ and $\gamma = 2$.

From the general equation of biological similarities we have:

$$\omega^{\frac{1}{3}(3\alpha+\beta+\gamma')} = \omega^{0.82};$$

$$\frac{1}{3}(-3+4+\gamma') = 0.82;$$

$$1+\gamma' = 2.46.$$

The value for γ' is 1.46. Since compliance has an exponent $\gamma = 2$, it follows that coefficient of $\gamma' = 0.73$.

The frequency distribution of the numerical values of the coefficient for the time exponent γ are shown in Figure 1. They were determined for 54 allometric equations of physiological functions, with time (T) as one of their dimensions. It can be observed that in the majority of cases the coefficients are located in the range between 0.9 and 1.0 and that the frequency decreases rapidly for the other values of the coefficients. Nevertheless, in few cases (Fig. 1a) the coefficients for γ are beyond the limits established for the mechanical similarity (0.5γ) , probably due to inaccuracies of the exponent (b) of the allometric equations. On the other hand (Fig. 1b, c) in several instances the calculated value of the coefficient of the time exponent is located outside the limits defined for the electrodynamical similarity $(\gamma = 1.0)$. For this reason additional physical similarity criteria should be applied, as for instance certain dimensionless numbers (Reynolds, Froude, Weber, Peclet, Laplace and Womersley), which are commonly used in Physics.

Determination of the coefficient γ for Reynolds model. The Reynolds number is usually defined as:

$$R_e = U \cdot D/\nu;$$

being: U = velocity; D = diameter; $\nu =$ kinematic viscosity, that in this particular case is assumed to be constant.



Figure 1. Statistical distribution of the coefficients corresponding to the exponent (γ) of the time ratio (τ) for 54 allometric equations which are functions of time. The values outside the common limits $(0.5 \text{ and } 1.0\gamma)$ correspond to: a) diodrast clearance; water intake; creatinine—N—output and lung weight; b) lung compliance; c) pulmonary flow resistance

Since the product $U \cdot D$, both for the prototype (p) and for the model (m) should be constant (C):

$$\begin{aligned} U_{p} \cdot D_{p} &= C \\ U_{m} \cdot D_{m} &= C \end{aligned} ;$$

leading to $U_p/U_m = D_p/D_m$.

Moreover, $L/l = D_p/D_m = \lambda$ and $D_m/D_p = \lambda^{-1}$ it follows that: $U_p = U_m \cdot \lambda^{-1}$.

Introducing again the reduction coefficient of biological similarities (χ) we have:

$$\chi = \lambda^{3\alpha + \beta + \gamma'};$$

and for a velocity $U \stackrel{d}{=} L \cdot T^{-1}$ the following are the exponents of M, L and T: $\alpha = 0, \beta = 1, \gamma = -1$; which can also be written:

$$\chi = \lambda^{(3\times 0)+(1\times 1)+\gamma'} = \lambda^{-1}.$$

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TABLE 1 Dimensional Analysis and Allometric Exponents of Three Independent Similarity Criteria

	Exponent of			SIMILARITY					
Comment	$\begin{bmatrix} \mathbf{L}\mathbf{x} \\ \mathbf{\lambda} \\ \mathbf{\alpha} \end{bmatrix}$	β	$\frac{1}{r}$	$\frac{\text{Mechanical}}{\frac{1}{3}(3\alpha+\beta+\frac{\gamma}{2})}$	Electro- dynamical $\frac{1}{3}(3\alpha+\beta+\gamma)$	Hydro- dynamical $\frac{1}{3}(3\alpha+\beta+2\gamma)$			
Acceleration	0	1	-2	0.00	- 0.33	-1.00			
Action	1	2	-1	1.50	1.33	1.00			
Area	0	2	0	0.66	0.66	0.66			
Compliance	-1	4	2	0.66	1.00	1.66			
Density	1	-3	0	0.00	0.00	0.00			
Diffusivity	0	2	1	0.50	0.33	0.00			
Energy	1	2	-2	1.33	1.00	0.33			
Flow resistance	1	-4	-1	- 0.50	- 0.66	- 1.00			
Force	1	1	-2	1.00	0.66	0.00			
Frequency	0	0	-1	-0.16	- 0.33	- 0.66			
Length	0	1	0	0.33	0.33	0.33			
Moment of inertia	1	2	0	1.66	1.66	1.66			
Momentum	1	1	-1	1.66	1.00	0.66			
Period	0	0	1	0.16	0.33	0.66			
Power	1	2	- 3	1.16	0.66	- 0.33			
Pressure	1	-1	-2	0.33	0.00	- 0.66			
Surface tension	1	0	-2	0.66	0.33	- 0.33			
Torque or moment of force	1	2	-2	1.33	1.00	0.33			
Velocity	0	1	-1	0.16	0.00	- 0.33			
Viscosity	1	-1	-1	0.50	0.33	0.00			
Volume	0	3	0	1.00	1.00	1.00			
Volume flow	0	3	-1	0.83	0.66	0.33			
Volume elasticity coefficient	1	-4	-2	- 0.66	- 1.00	- 1.66			

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Since $\gamma = -1$ for all velocities:

$$\gamma' = 2\gamma.$$

Finally, the reduction coefficient (χ) becomes:

$$\chi = \lambda^{3\alpha + \beta + 2\gamma};$$

and since $\lambda = \omega^{\frac{1}{2}}$ we have:

$$\chi = \omega^{\frac{1}{3}(3\alpha+\beta+2\gamma)}.$$

TABLE 2

Dimensionless Number and Reduction Coefficients of Biological Similarities

Nondimensional numbers	Composition	Expressed according to Biological Similarity criteria	As constant are considered
FROUDE Relation between inertia and gravity forces	$F = \frac{U}{\sqrt{L \cdot G}}$ $U = \text{velocity}$ $G = \text{gravity acceleration}$ $L = \text{length}$	$ω^{\frac{1}{2}(3\alpha + \beta + \frac{1}{2}\gamma)}$	G
LAPLACE Relation between pressure tension and radius	$\mathscr{L} = \frac{P \cdot L}{\sigma}$ $P = \text{pressure}$ $\sigma = \text{tension}$	$\omega^{\frac{1}{3}(3\alpha+\beta+\frac{3}{2}\gamma)}$	σ
PECLET Ratio between trans- port of thermal energy by fluid and molecular motion	$P_{e} = \frac{\rho \cdot C_{p} \cdot U \cdot L}{K}$ $\rho = \text{density}$ $C_{p} = \text{specific heat at constant}$ pressure $K = \text{heat conductivity}$	$\omega^{\frac{1}{8}(3\alpha+\beta+2\gamma)}$	ρ C _p K
REYNOLDS Relation between inertia and viscous forces in a fluid	$R_e = \frac{U \cdot L}{\nu}$ $\nu = \text{kinematic viscosity}$	ω ¹ (3α + β + 2 γ)	ν
WEBER Relation between inertia forces and surface tension forces	$W_e = \frac{\rho \cdot U^2 \cdot L}{\sigma}$	$\omega^{\frac{1}{2}(\alpha+\beta+\frac{3}{2}\gamma)}$	ρσ
WOMERSLEY Related to pulse wave transmission	$W_o = \frac{L^2 \cdot f}{\nu}$ f = frequency	$\omega^{\frac{1}{2}(3\alpha+\beta+2\gamma)}$	ν

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In Table 2 the coefficients of γ are defined for various dimensionless numbers. For instance, Peclet's, Reynolds' and Womersley's numbers have a coefficient of γ equal to 2.0, while for the rest of the nondimensional numbers the coefficients are distributed between 0.5 and 2.0 γ .

In conclusion, the *range* of the theory of biological similarity corresponds to an infinite number of coefficients of γ , with the limiting values of 0.5 and 1.0 γ , being 0.93 γ the mode.

Exceptionally the coefficient of γ may assume values between 1.0 and 2.0.

B. Biological similarities and allometric equations. From the general equation of the theory of biological similarities it is possible to predict the range of the exponent (b) of Huxley's allometric equation $y = a \cdot |W|^b$, were y = physiologic function, a = parameter, |W| = numerical value of body weight and b = characteristic exponent of an allometric growth.

The relationship between the theory of biological similarity and Huxley's allometric equation can be established through the ratio $W/w = \omega$ of the prototype (W) and the model (w). But, if the weight of the model is established as w = 1.0, it results that $\omega = |W|$ and the general equation will become:

$$y = a |W|^{\frac{1}{3}(3\alpha + \beta + \gamma')};$$

were |W| should be considered as the *numerical value* for any particular weight



Figure 2. Theoretical range according to the biological similarity theory (shaded area) and experimental values of the exponent (b) of empirical allometric equations (dots). In few cases (area, length, volume) there is only one value for the exponent (b) and the experimental data are located around this single figure

scale (kg, g, mg, etc.) and not in the sense of weight as a force $(M \cdot L \cdot T^{-2})$. Apparently, the theoretically calculated exponent of |W| is equivalent to the empirical value of (b) in Huxley's allometric formula $y = a \cdot W^b$.

As it is shown in Table 1, the numerical equivalent of the three similarity criteria or the corresponding values of the exponent (b) are given for each physical magnitude commonly used in biology. As stated before, the range of biological similarities can be established between mechanical and hydrodynamical similarity criteria, being the mean value close to the electrodynamical similarity criterion ($\gamma = 1.0$), which happens to be the same similarity rule ($\lambda = \tau$) established by Lambert and Teissier (1927) in their "Théorie de la similitude biologique".

Now, it is noteworthy to compare the theoretical range of biological similarities with the values of (b) calculated from experimental data (Fig. 2). There is concordance between the theoretical assumptions and the empirical exponents of (b) calculated for numerous physiological functions.

C. Similarity criteria and invariants. The adequate combination of the exponents (b) of the allometric equations gives dimensionless numbers or simi-

Symbols of functions		V	G_v	G_M	A	p	R _F	Ea	v	W	G_{H}	T		
Dimension- al Matrix	M	0	0	1	0	1	1	1	0	1	1	0		
	L	3	3	0	2	-1	-4	-4	1	1	2	0	Similarity	
		0	-1	-1	0	-2	-1	-2	-1	-2	-3	1		
Solution Matrix	π_1	1	0	0	0	0	0	0	0	3	-3	-3	$V \cdot (W/G_H \cdot T)^3$	
	π_2	0	1	0	0	0	0	0	0	3	-3	-2	$G_v\cdot W^3/G_H^3\cdot T^2$	
	π_3	0	0	1	0	0	0	0	0	-2	1	0	$G_M \cdot G_H / W^2$	
	π_4	0	0	0	1	0	0	0	0	2	-2	-2	$A(W/G_H \cdot T)^2$	
	π_5	0	0	0	0	1	0	0	0	- 3	2	2	$p(G_H \cdot T)^2/W^3$	
	π_6	0	0	0	0	0	1	0	0	-6	5	4	$R_F(G_H^5\cdot T^4)/W^6$	
	π_7	0	0	0	0	0	0	1	0	-6	5	-5	$E_a(G_H\cdot T)^5/W^6$	
	π_8	0	0	0	- 0	0	0	0	1	1	-1	0	$v \cdot W/G_H$	

TABLE 3

Dimensional and Solution Matrices for 11 Functions and 8 Independent Similarity Criteria

trodynamic Similarity	invariants for an electro- arity criterion	Denominator	0.6(6) + 0.3(3)	-0.6(6) + 0.6(6)	$0.6(6) + 0.6(6) + 3 \times 0.3(3)$	0.6(6) + -0.6(6)	1.00	0.6(6)	0.6(6)	0.6(6)
dual Exponent for an Ele	Calculated exponents of the dynamic simils	Dalculated exponents of the dynamic similar Numerator $(0,0)$ $(1,0)$ $($	2[0.0 + 0.3(3)]	$3 \times (0.0) + 0.0 + 2 \times 0.3(3)$						
TABLE 4 s of Various Invariants and the Determination of the Resi	Composition		Volume Volume flow × Period	(Pressure) ² Flow resistance × Heat generation rate	(Mass Flow) ² × Volume Heat generation × Weight × (Period) ³	Pressure Volume flow × Flow resistance	(Velocity) ³ × (Period) ³ Volume	(Velocity) ³ × (Period) ² Volume flow	$\frac{(Velocity)^2 \times (Period)^2}{Area}$	(Velocity) ³ × Pressure × (Period) ² Heat generation rate
	Dimension- ality		$rac{V}{G_v\cdot T}$	$\frac{p^2}{R_F\cdot G_H}$	$\frac{(G_M)^2 \cdot V}{G_H \cdot W \cdot T^3}$	$rac{p}{G_v\cdot R_F}$	$\frac{A}{e^{a} \cdot T^{a}}$	$\frac{v^3 \cdot T^2}{G_v}$	$\frac{v^2 \cdot T^2}{A}$	$rac{v^3 \cdot p \cdot T^2}{G_H}$
	Origin		$\frac{\pi_1}{\pi_2}$	$(\pi_6)^2$ π_8	$(\pi_3)^2 \cdot \pi_1$	π ₂ •π ₆	$\frac{(\pi_8)^3}{\pi_1}$	$\frac{(\pi_8)^3}{\pi_2}$	$\frac{(\pi_8)^2}{\pi_4}$	$(\pi_6)^3 \cdot \pi_5$
Analysis	Invariants		I_1	I_2	I_3	I4	I_5	I ₆	I_7	I_8

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larity criteria, which were first systematically studied by Stahl (1962, 1963) by applying Buckingham's Pi-theorem to biological functions.

In order to obtain a complete group of similarity criteria that at the same time are independent from each other it is convenient to arrange the exponents of certain biological functions in a "dimensional matrix" (Table 3). For each function ordered in the first row the corresponding exponent of M, L, and T are arranged in the columns. From the dimensional matrix a "solution matrix" can be derived in which the rows correspond to the Pi-numbers or specific similarity criteria. In this particular case, the application of a single similarity criteria which are invariant, i.e. in all instances the exponent of |W| is exactly zero.

Furthermore, when the Pi-numbers are combined (Table 4) it is possible to obtain a number of new invariants (I_i) , again with a residual weight exponent equal to zero.

Equivalent results may be obtained combining adequately certain empirical allometric equations; but in this case the residual weight exponent is not equal to zero and a "scale effect" is apparent. Only if a single similarity criterion is applied (mechanical, electrodynamical or hydrodynamical) a zero residual weight exponent should be expected.

The invariants (I_i) obtained from the empirical allometric equations of different physiological systems (circulation, respiration, metabolism, etc.) have residual weight exponent close to zero, due to the theoretically established range of biological similarities and also to the statistical variation of the exponent (b).

Further studies are necessary to include other dimensions, as for instance temperatures (t) and heat (H) besides M, L, and T, in order to increase the accuracy of the final equations and its biological applications.

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