Similarity and Dimensional Methods in Biology

They promise to show quantitative similarities between biological organisms and models of biological systems

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Comparison of a small leaf with a large one, or of a child with its parents, leaves the conviction that a "similarity" of some sort is present. It seems reasonable to suppose that an artificial kidney is in some sense physically similar to the natural organ. In order to define biological similarities in a meaningful way it is necessary to review the subject of dimensional analysis, which forms part of the basis for similarity theory.

In the past the subject of dimensional analysis was obscured by certain metaphysical overtones; it is still passed over briefly in many technical courses. However, a number of distinguished physical scientists such as Newton (*1*), Fourier (*2*), Lord Rayleigh (*3*), and P. W. Bridgman (*4*) recognized the importance of similarity and dimensional methods. The basic concept of "similitude" was known to the ancient Greek mathematicians in connection with geometric problems and was noted by Galileo in 1638 (*5*), during a discussion of structural scale-up problems.

During the last few decades dimensional and similarity analysis have been put on a perfectly firm mathematical footing. The method has been applied to all types of engineering problems (*6*), to theoretical hydrodynamics (*7*), to heat flow (*8*), to jet flows (*9*), to chemical engineering (*10*), to magnetohydrodynamics (*11*), to rheology (*12*), to meteorology (*13*), and in numerous other situations. General discussions of the method are also given by Duncan (*14*), Focken (*15*), and others. From the mathematical viewpoint, similarity has been approached from several different viewpoints: geometric transformations, group theory applied to equations, and finally the algebra of the dimensional symbols (*M, L, T,* and so on).

The geometric viewpoint is illustrated by the fact that two triangles are similar when there is a constant ratio relating their sides. In such triangles one may then define a scale ratio:

$$l' = k_L l \qquad (1)$$

where l' is the new length, l is the original length, and k_L is the numerical scaling coefficient. It can then be easily shown that k_L is no other than the L symbol, which appears when one transforms each variable in an equation by some linear coefficient. The physical sense of this substitution is that the given equation must be invariant for arbitrary choice or change of scales of measurement. It would certainly not be desirable if Newton's laws held in English units but not in metric ones. The fact that physically meaningful equations must be dimensionally consistent was recognized in 1823 by Fourier, but is given surprisingly casual attention in most scientific curricula. A derivation of dimensionless numbers based on scale transformations is also provided by Decius (*16*).

Substituting a transformed variable for the original one in an equation is a very general method which leads to the theory of groups connected with solutions of equations. The matter is a highly technical one, and limitations of space preclude its discussion here. Suffice it to say that work by mathematicians such as Birkhoff (*7*) has clearly demonstrated that dimensional analysis is a part of the general theory of invariant parameters of equations. Specifically, dimensional or ordinary similarity analysis deals only with simple linear expansion or contraction of basic axes. Very much more complex geometric transformations are possible. Similarity theory has also been given serious attention in the Soviet Union, particularly through the work of Kirpevich (*8*) and Sedov (*9*). Rather surprisingly, in the U.S.S.R. similarity analysis is often taught without recourse to dimensional symbols at all, with reference only to scaling coefficients such as the k_L noted above.

Still another approach to dimensional analysis has been the careful examination of the way in which dimensional symbols such as *M, L,* and *T* are manipulated. In 1914 E. Buckingham (*17*) stated a basic theorem (the Buckingham pi theorem) to the effect that any equation written in terms of dimensional variables and constants could be converted into one involving only dimensionless numbers. Lord Rayleigh (*3*) developed a systematic method for manipulating the exponents of the various dimensional entities, such as force (ML/T^2), to yield dimensionless numbers. I have stressed elsewhere (*18*) that the dimensional symbols are a simple but consistent mathematical structure, which may be identified technically as an Abelian group. This group is interpreted as the one governing ordinary numbers used *only* for multiplication or division, not for addition or subtraction. It is known (*19*) that the ancient Greeks distinguished natural numbers from numbers used only in ratios and observed that a "ratio number" (λογος) could not be added in the usual way to get a meaningful result.

The older metaphysical connotations of dimensional analysis have been completely removed by modern understanding of similarity transformations. For example, it has become clear that there is nothing sacrosanct about any specific dimensional basis such as *M, L,* and *T*. One may use any elementary dimensions that are found to be genuinely independent of each other, and definable, in a given problem.

Dimensionless Numbers or Similarity Criteria

The term *dimensionless number* is probably an unfortunate one, since careful examination suggests that any ordinary real number is dimensionless. An alternative designation, used with increasing frequency by contemporary

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writers such as Johnstone and Thring (*10*) and the Soviet school, is *criterion of similarity*. The k_L coefficient given earlier is an elementary nondimensional ratio or criterion of similarity, which defines the geometric relations of the two triangles.

In principle, a dimensionless ratio of any physical entities whatever may be formed and called a criterion of similarity. Some 50 to 60 such terms are now in use in the physical sciences. The best known is no doubt the Reynolds number

$$vL\rho/\eta \qquad (2)$$

in which, v is the velocity (L/T), L is the characteristic length, ρ is the density (M/L^3), and η is the viscosity (M/LT). The Reynolds number can be interpreted as the ratio of inertial to viscous forces in a fluid. High values of this ratio indicate that turbulence is likely to occur. Typically the Reynolds number is used to design a model which will be physically similar to the full-scale prototype. By this is meant that if the model is geometrically similar to the prototype, constancy of the Reynolds number will assure a predictable proportionality between inertial and viscous forces.

Nondimensional combinations of variables are very useful for the efficient analysis of experimental results and the design of models. Quite generally a model must be physically similar to the prototype, and such similarity is precisely defined by constancy of certain dimensionless criteria of similarity. Alternatively, the specific criteria of similarity may be combined in equations with constant coefficients, to give a still more complex type of similarity definition. The choice of efficient dimensionless numbers for a given system is not simple and requires much experience. They may be obtained from study of governing differential equations for the system (when these are known), from direct manipulation of the dimensional variables, or from insight into the physical nature of the problem. There is every reason to suppose that numerous dimensionless numbers or similarity criteria will be useful in biology. Elsewhere I have given an extended discussion of such parameters (*18*, *20*) and have also listed a number of unfamiliar "dimensions," such as areal growth rate (L^2/T); change of volume with frequency, as in the lung or heart (L^3T); acceleration of mass growth rate (M/T^2); and others.

Biological Similarity

The concept of biological similarity is certainly not new. It was given serious attention by D'Arcy Thompson, who remarked (*21*, p. 1032): "In a very large part of morphology, our essential task lies in the comparison of related forms rather than in the precise definition of each structure." Papers on biological similitude first appeared some three decades ago (*22*). N. Rashevsky (*23*) used the method of "dimensional proportionality" in analyses of the vascular system, of skeletal size, and so on. Gunther and Guerra (*24*, *25*) discuss biological similarity but start with the assumption that a single scaling law or similarity criterion will govern all the variables found in biological systems. Similarity reasoning is used in the major works on bioenergetics by Brody (*26*) and Kleiber (*27*). The latter author points out that thermal similarity of animals was investigated in 1888 by von Hoesslin; he also offers a number of germane criticisms of oversimplified models in biomathematics.

Use of dimensionless numbers for making models of the mammalian cochlea is considered by von Bekesy (*28*), Tonndorf (*29*) and others. Nondimensional terms and ratios appear in a great many physiochemical and physiological analyses. However, there do not seem to have been any prior discussions of biological similarity which take advantage of the full resources of the modern dimensional technique. By this is meant use of multiple similarity criteria combined in functional equations to define classes of physiological systems. In earlier works (*18*, *20*, *30*, *31*) I have provided a preliminary listing of biological "dimensions" and dimensionless numbers. Illustrations have been given of the way in which sets of nondimensional criteria are chosen for a given problem. The comparative neglect of similarity methods is indicated by the fact that dimensionless numbers are not mentioned in a recent volume on biological analogues and models (*32*) or in a symposium on "bionics" (*33*).

A review of Soviet publications during the last 8 years (*34*), also reveals no general or systematic applications of biological similarity principles, even though similarity methods are being given much attention in technology. D'Arcy Thompson has apparently not been translated into Russian, and very little attention has been devoted to the biological form determination problem.

One of the most important but least appreciated attributes of the similarity method is that it is very concrete and nonhypothetical. Possible nondimensional combinations of variables or dimensional constants are accepted only when experimental data prove that they are invariant properties of the system under study. Relationships between such parameters are also deduced by direct experimental investigations. When dimensionless ratios are derived from differential equations it is quite fair to say that confirmation of the relative invariance of the given ratios suggests that the analysis was correct. Many times similarity criteria are obtained from oversimplified, idealized models, but it is then found that they continue to be applicable to very complex situations, where a full analysis is impossible. Exactly this kind of situation obtains, for example, in the mammalian circulatory tree.

Discussion of Tables

Table 1 lists biological similarity criteria which are shown to be independent of the mass of the animal (only mammalian data are used). The data in Tables 1 and 2 are based on the so-called allometric equation of Huxley (*35*):

$$D_i = kM^n \qquad (3)$$

where D_i is a variable such as pulse rate, blood volume, or liver mass; M is the mass of the animal; and k and n are numerical coefficients. Experience has shown that this power law fits a remarkably wide range of biological data. There are good theoretical justifications for Eq. 3, but space limitations preclude discussion of its derivation.

The values in Tables 1 and 2 are taken directly from Adolph (*36*), Brody (*26*), and Gunther and Guerra (*24*). Combining known allometric values to give derived relationships was proposed by all of these authors, but they failed to generalize the method. It must be stressed that a dimensional constant may also be an invariant property of a system, as in the case of the velocity of light or the charge-to-mass ratio of an electron. However, in biology the dimensional constants are very much more limited in scope and serve to characterize systems of limited range. A few constants seem to be of very general applicability, such as the heat output, which is known to scale as $M^{0.74}$

Table 1. Mammalian similarity criteria.

Item	Composition*	Dimensionality*	Allometric ratio form*	Numerical value‡	Residual mass exponent
1.	$\frac{\text{Air flow} \times \text{breath time}}{\text{Lung vol. } (M/\rho)\|}$	$G_V T/V$	$\frac{4.7 \times 10^{-5} M^{0.28} \times 120 M^{0.74}}{1.24 \times 10^{-2} M^{0.99}}$	0.45	0.03
2.	$\frac{\text{Air flow}}{\text{Oxygen flow}}$	G_V/G'_V	$\frac{120 M^{0.74}}{3.8 M^{0.73}}$	32	0.01
3.	$\frac{\text{Tidal vol.} \times \text{pulse time}}{\text{Heart vol.} \times \text{breath time}}$	$(V/T)/(V/T)'$	$\frac{0.62 \times 10^{-2} M^{1.01} \times 1.19 \times 10^{-5} M^{0.27}}{0.66 \times 10^{-2} M^{0.98} \times 4.7 \times 10^{-5} M^{0.28}}$	0.24	0.02
4.	$\frac{\text{Oxygen flow} \times \text{pulse time}}{\text{Blood vol.}}$	$G_V T/V$	$\frac{3.8 M^{0.73} \times 1.2 \times 10^{-5} M^{0.27}}{5.5 \times 10^{-2} M^{0.99}}$	0.00083	0.01
5.	$\frac{\text{Oxygen flow}}{\text{Renal inulin clearance}\S}$	G_V/G'_V	$\frac{3.8 M^{0.73}}{1.74 M^{0.77}}$	2.2	0.04
6.	$\frac{\text{Water input flow}}{\text{Urine output flow}}$	G_V/G'_V	$\frac{0.010 M^{0.88}}{0.0064 M^{0.82}}$	1.5	0.06
7.	$\frac{\text{Renal Diodrast clearance}\S}{\text{Water input flow}}$	G_V/G'_V	$\frac{2.14 M^{0.89}}{0.010 M^{0.88}}$	214	0.01
8.	$\frac{\text{Equivalent organismal vol.}\|}{\text{Tidal lung vol.}}$	V/V'	$\frac{1.00 M^{1.0}}{0.0062 M^{1.01}}$	161	0.01
9.	$\frac{\text{Equivalent lung vol.}\|}{\text{Tidal lung vol.}}$	V/V'	$\frac{0.0124 M^{0.99}}{0.0062 M^{1.01}}$	2.0	0.02
10.	$\frac{\text{Tidal lung vol.}}{\text{Heart vol.}\|}$	V/V'	$\frac{0.0062 M^{1.01}}{0.0066 M^{0.98}}$	0.94	0.03
11.	$\frac{\text{Total hemoglobin mass}}{\text{Mass of lungs}}$	M/M'	$\frac{0.013 M^{0.99}}{0.0124 M^{0.99}}$	1.05	0.00
12.	$\frac{\text{Mass of blood}}{\text{Mass of heart}}$	M/M'	$\frac{0.055 M^{0.99}}{0.0066 M^{0.98}}$	8.3	0.01
13.	$\frac{\text{Mass of blood}}{\text{Mass of lungs}}$	M/M'	$\frac{5.5 \times 10^{-2} M^{0.99}}{1.24 \times 10^{-2} M^{0.99}}$	4.4	0.00
14.	$\frac{\text{Mass of gut}}{\text{Mass of liver}}$	M/M'	$\frac{0.112 \times M^{0.94}}{0.82 \times M^{0.87}}$	1.37	0.07
15.	$\frac{\text{Mass of kidneys}}{\text{Mass of liver}}$	M/M'	$\frac{0.0212 M^{0.85}}{0.082 M^{0.87}}$	0.26	0.02
16.	$\frac{\text{Mass of gut}}{\text{Mass of thyroid}}$	M/M'	$\frac{0.112 M^{0.94}}{2.2 \times 10^{-4} M^{0.92}}$	510	0.02
17.	$\frac{\text{Mass of kidneys}}{\text{Mass of adrenals}}$	M/M'	$\frac{0.0212 M^{0.85}}{0.0011 M^{0.80}}$	19	0.05
18.	$\frac{\text{Mass of hemoglobin}}{\text{Mass of blood}}$	M/M'	$\frac{0.013 M^{0.99}}{0.055 M^{0.99}}$	0.24	0.00
19.	$\frac{\text{Vol. body water}}{\text{Vol. blood}}$	V/V'	$\frac{40}{5.4}$	7.4¶	
20.	$\frac{\text{Nitrogen excretion rate}}{\text{Sulfur excretion rate}}$	G_M/G_M'	$\frac{7.4 \times 10^{-5} M^{0.74}}{1.7 \times 10^{-6} M^{0.74}}$	43	0.00
21.	$\frac{\text{Breath time}}{\text{Pulse time}}$	T/T'	$\frac{4.7 \times 10^{-5} M^{0.28}}{1.2 \times 10^{-5} M^{0.27}}$	3.9	0.01
22.	$\frac{\text{Gut beat time}}{\text{Pulse time}}$	T/T'	$\frac{9.3 \times 10^{-5} M^{0.31}}{1.2 \times 10^{-5} M^{0.27}}$	7.7	0.04
23.	$\frac{\text{Time for 50\% growth}}{\text{Time for 98\% growth}}$	T/T'	$\frac{4.29 \times M^{0.25}}{14.7 \times M^{0.26}}$	0.3	0.01
24.	$\frac{\text{Lifetime}}{\text{Breath time}}$	T/T'	$\frac{8.85 \times 10^{3} M^{0.29}}{4.7 \times 10^{-5} M^{0.28}}$	2×10^{8}	0.01
25.	$\frac{\text{Oxygen flow} \times \text{breath time}}{(M/\rho)}$	$G_V T/V$	$\frac{3.8 M^{0.73} \times 4.7 \times 10^{-5} M^{0.28}}{1.0 M^{1.00}}$	1.8×10^{-4}	0.01

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* M = mass of organism; ρ = density; $G_V = L^3/T$, air or blood; $V = L^3$; $G_M = M/T$. The gram-cubic centimeter-hour system of Adolph is used except in items 23 and 24, where mass of animal is in kilograms and time is in months or hours.

‡ Numerical values for animals under basal laboratory conditions. Deviation from these values by a factor of 2 to 3 is possible for other situations.

§ Renal clearance given as a flow with units of L^3/T.

‖ Unity density assumed to relate organismal mass and volume.

¶ Human data; allometric data are needed but not readily available on numerous values of this type.

in nearly all organisms (*37*). Additional allometric studies may reveal that in some cases the values listed in Tables 1 and 2 require modification, or that specific similarity criteria are applicable only to limited groups of rather closely related organisms and not, for example, to all mammals.

Certain items in Tables 1 and 2 call for comment. In Table 1, item No. 1 might have contained the tidal (single breath) lung volume rather than the whole lung volume. Substitution of item No. 9 in No. 1 gives this result and yields a numerical value close to unity; this was to have been expected and shows that the method gives reasonable results. Item No. 3 is best understood as the ratio of air to blood flow at the lung interface. Heart volume, rather than stroke volume, is used in this term because of lack of adequate allometric data on stroke volume. The actual ratio of total air flow to blood flow appears to be 0.8–2.5 and depends somewhat on the physiological state of the animal. Item No. 5 is understandable if one assumes that every oxygen molecule taken into the body will result in an obligatory excretion of protons by the kidneys. Alternatively, renal flow is simply a constant fraction of cardiac output, which relates to air flow.

Considerable variation, by a factor of at least 100 percent, is to be expected in the listed values. For example, the value shown for item No. 6 certainly is not correct for humans in many conditions, for desert animals, and so on; most of the allometric data are obtained with animals in basal condition or under anesthesia. It should also be noted that a residual mass exponent above 0.03 may introduce a substantial error in values for the larger animals. Thus, item No. 14 can only be considered suggestive. The characteristic times given in Nos. 23, 24, and 25 do not apply at all well to primates, which live some 2 to 3 times longer than would be expected on the basis of mass. Item No. 25 implies in a very general sense that mammals tend to breathe a constant number of breaths in their normal lifetime. This certainly should not be taken to mean that athletes or singers will have a shortened life expectancy—numerous complicating factors enter in.

In Table 2 some of the relations are known, such as those of Nos. 1 and 4, but others are new. They may be more or less incidental, but they are nonetheless independent of the mass of the animal. The velocities given in items 6 through 9 are especially interesting. Gunther and Guerra also noted the constancy of air flow velocity. The values are derived on the assumption that organismal lengths scale approximately as the cube root of mass—which Brody has demonstrated to be reasonable. However, velocities obtained in this way are hypothetical averages. For humans, 23 centimeters per second is a very reasonable velocity for the lower aorta, but detailed independent allometric data on velocities are needed. Ratios of velocities constitute further dimension-

Table 2. Dimensional constants deduced from allometric values.

Item	Composition*	Dimensionality*	Allometric ratio form*	Numerical value	Residual mass exponent
1.	$\frac{\text{Urine output flow}}{\text{Mass of kidneys}}$	G_V/M	$\frac{0.0064\ M^{0.82}}{0.0212\ M^{0.85}}$	$0.3\ \text{cm}^3/\text{g-hr}$ $(0.3\ \text{hr}^{-1})$§	0.03
2.	$\frac{\text{Hippurate clearance}}{\text{Mass of adrenal gland}}$	G_V/M	$\frac{5.4\ M^{0.80}}{0.0011\ M^{0.80}}$	$4.9\ l/\text{g-hr}$	0.00
3.	$\frac{\text{Urine output flow}}{\text{Mass body cytochromes}}$	G_V/M	$\frac{6.4 \times 10^{-3}\ M^{0.82}}{1.0 \times 10^{-4}\ M^{0.84}}$	$64\ \text{cm}^3/\text{g-hr}$	0.02
4.	$\frac{\text{Oxygen flow}}{\text{Nitrogen excretion}}$	G_V/G_M	$\frac{3.8\ M^{0.74}}{7.4 \times 10^{-5}\ M^{0.74}}$	$5.1\ l/\text{g}$ $(6.4\ l/l)$‖	0.00
5.	$\frac{\text{Nitrogen excretion}}{\text{Mass of pituitary}}$	G_M/M	$\frac{7.4 \times 10^{-5}\ M^{0.74}}{13 \times 10^{-5}\ M^{0.76}}$	$0.57\ \text{hr}^{-1}$	0.02
6.	$\frac{\text{Urea clearance}\P}{\text{Equivalent area } (M/\rho)^{0.67}\P}$	G_V/A	$\frac{1.59\ M^{0.72}}{1.0\ M^{0.67}}$	1.59 cm/sec**	0.05
7.	$\frac{\text{Oxygen flow}}{\text{Equivalent area } (M/\rho)^{0.67}\P}$	G_V/A	$\frac{3.8\ M^{0.73}}{1.0\ M^{0.67}}$	3.8 cm/sec**	0.06
8.	$\frac{\text{Equivalent radius } (M/\rho)^{0.33}\P}{\text{Pulse time}}$	L/T	$\frac{1.0\ M^{0.33}}{1.2 \times 10^{-5}\ M^{0.27}}$	23 cm/sec§§	0.06
9.	$\frac{\text{Equiv. radius lung } (M_{LU}/\rho')^{0.53}}{\text{Breath time}}$	L/T	$\frac{(3 \times 0.0124\ M^{0.99})^{0.33}}{0.25 \times 4.7 \times 10^{-5}\ M^{0.28}}$	7.9 cm/sec‖‖	0.05
10.	$\frac{\text{Blood flow}}{\text{Aortic area (rat)}}$	G_V/A	$\frac{0.033\ M^{0.74}}{1.4 \times 10^{-3}\ M^{0.72}}$	24 cm/sec	0.02
11.	$\frac{\text{Heat production}}{\text{Oxygen flow}}$	G_H/G_V	$\frac{70.5 \times M^{0.73}}{14.4 \times M^{0.73}}$	$4.9\ \text{kg-cal}/l$	0.00
12.	$\frac{\text{Basal power} \times \text{lifetime}}{\text{Mass}}$	$G_H T/M$	$\frac{70.5\ M^{0.73} \times 365 \times 7.52\ M^{0.29}}{1.0\ M^{1.0}}$	$1.9 \times 10^5\ \text{kg-cal/kg}$	0.02

* M = mass of organism; $\rho = M/L^3$; ρ' = estimated lung density; $G_V = L^3/T$; $G_M = M/T$; $A = L^2$; $G_H = \text{heat}/T$. Units are in the gram-cubic centimeter-hour system of Adolph, except in items 11 and 12, where kilograms, days or years, and kilogram-calories are used.

§ Reduced to volumetric ratio by taking an equivalent volume of tissue with unit density.

‖ Uses equivalent volume of nitrogen.

¶ Density assumed to be unity.

** Equivalent transport velocities.

§§ Estimated blood flow rate, at specific region of vascular tree not identified.

‖‖ Equivalent air flow rate in lung, with an estimated lung density ρ' of 0.33, flow in ¼ cycle.

less parameters of great interest for correlating the overall design of the respiratory and circulatory systems.

Item 12 in Table 2 gives a basic constant for energy from oxygen in mammals given a typical diet; the numerical value is consistent with well-known nutritional data. Item 13 is especially interesting because it implies that every kilogram of mammalian tissue takes part in the generation of a certain fixed quantity of energy in the lifetime of the animal. The same observation is made by Brody. For primates, which live longer than one would expect on the basis of mass, the energy production per kilogram rises proportionately. Energy per mass is commonly interpreted as a "potential" in physics. It is tempting to suppose that protoplasm has a certain energetic potential, which is used in part for overcoming gravity as long as the animal is alive, but care is always needed in making such generalizations from physical situations.

Nonmammalian Values

A considerable number of allometric data have been collected on invertebrates, microorganisms, plants, and so on. Space limitations preclude a full presentation, but I will give two examples. Some older data of Bjerknes (cited in *25*) on characteristics of birds include allometric values for wing-tip velocity v, wing length L, and beating frequency f. These values may be combined to give:

$$\frac{v}{Lf}=\frac{5.1\ M^{0.01}}{0.03\ M^{0.39}\times 48\ M^{-0.38}}=3.5\ M^{0.00}\quad(4)$$

It is notable, first of all, that wing-tip velocity (presumably obtained by photographic measurement) is an approximately invariant property for ordinary birds. The value of the final ratio indicates a geometric similarity in the wing structure, with a constant relationship of wing length and stroke length. The (v/fL) combination is quite well known in engineering under the names homochronism or Strouhal number and has been of use in the analysis of vibration patterns and other dynamics problems. This term is also called the "advance ratio" in marine hydrodynamics (*14*). Very recent analysis of known allometric data for birds suggests that at least three other similarity criteria used for characterization of marine propellers and of aircraft are useful invariants for the study of bird dynamics.

A rather novel example is available from the plant kingdom. Turrell (*38*) has reported on citrus trees observed over a 26-year period. He gives allometric data (using the height of the tree rather than the mass) on crown surface and volume, total leaf volume, trunk radius, leaf length, and so on. Most of the exponents are not obviously those of area or mass (L^2 or L^3), but certain combinations of variables do yield invariants, as in Tables 1 and 2. For example, if S is the crown area per volume ratio (L^2/L^3) and L_h is the height of the tree, it is found that S times L_h is dimensionless and nearly independent of tree height. This particular combination $L\times(A/V)$ has also been encountered in chemical engineering (see *10*), where it is used to describe flow patterns in granular solids and other complex situations. In the present case the grouping relates to the crown pattern of the tree and shows that area per volume is inversely proportional to distance from the ground (or start of radial branching), a result which appears reasonable. Allometric studies in which length rather than mass is used as the primary variable make it possible to analyze very complex geometric similarities.

Similarity of Growth Patterns

Growth is one of the most characteristic features of organisms, and it is desirable to define similarity criteria for growth. Such criteria have been used by D'Arcy Thompson and Julian Huxley (*35*), though they were not recognized as dimensionless numbers. The most typical ratio is:

$$[(\mathrm{d}N_1/N_1)/\mathrm{d}T]/[(\mathrm{d}N_2/N_2)/\mathrm{d}T]\quad(5)$$

in which N_1 and N_2 are usually lengths, but may be other variables. Huxley called this ratio the "relative growth potential" and followed changes of its value in different parts of the lobster and other animals. D'Arcy Thompson's analysis of logarithmic growth spirals reveals that any such spiral may be described by Eq. 5 if tangential growth is called N_1 and radial growth is called N_2.

Another useful growth criterion is

$$[(\mathrm{d}N_1/N_1)/\mathrm{d}T]/K_1\quad(6)$$

where K_1 is a time constant, such as a metabolic time. By use of data from H. D. Landahl (*39*) it has been shown (*30*) that very simple expressions for tissue regeneration may be obtained with this term. For example, a time-specific growth rate is found to be directly proportional to the amount of the structure that is missing, relative to final size.

When growth is expressed in terms of nondimensional criteria it becomes possible to include it directly in equations with geometric shape factors and physical similarity criteria. For example, a relative growth ratio may be related to a diffusion-versus-transport criterion, a concentration-to-synthesis term, relative flow velocities, energy ratios, growth in other directions, and many other possible parameters. It has also become evident that the volumetric proliferation rate at a point may be a useful parameter for tissue growth. Studies on tensor formulations of volumetric growth along different axes are now being made.

In the analysis of growth and related matters it has become clear that two principles play a key role in biological analysis: conservation of volume and synchronism of times. While many properties are conserved in an adult organism, volume is of special importance because of the circulatory system and general semifluid state of protoplasm. The idea is certainly not a new one, since it occurs in venerable physiological concepts such as the Fick principle of circulation, but it does deserve more stress. Synchronism of times in the organism is also quite obvious, since corresponding processes are expected to occur in corresponding times. It appears that the time scale is uniformly that of $M^{0.25}$ to $M^{0.30}$ in mammals and probably in many other organisms. Study of "residence" versus "flow" and "diffusion" or "reaction" times has proved helpful in chemical engineering, and the same principles apply to biological systems.

Models of Biological Systems

It is well known that the Reynolds number is useful in making models of hydrodynamic systems. One may therefore ask whether biological similarity criteria can facilitate the design of biological models. There appears to be little question that they will help to some extent, but on the other hand biological systems are hard to model except in a limited way. For example, the simple plastic tube of the artificial kidney can hardly be compared with the complete microscopic nephron. Nonetheless, it is informative to review dimensionless numbers which may characterize natural and artificial kidneys. Only a brief discussion will be given in this article; a more complete list of criteria is available elsewhere (*31*).

A similarity criterion which is already in wide use is the renal clearance (see *40*). This may be easily understood as the ratio of material brought into the kidney to that removed, in a single pass of blood:

$$G_V C_N / G_N \qquad (7)$$

where G_V is the volumetric flow, C_N is the concentration, and G_N is the excretion rate (N/T). Sometimes a ratio of two such variables may be used also. The basic flow pattern in a tube is effectively described by the criterion:

$$G_V / A v_J \qquad (8)$$

where G_V equals L^3/T, A equals L^2, and v_J equals L/T. The linear flow rate may then be compared to an apparent reaction velocity or membrane transport coefficient having the dimensions of a velocity:

$$V_J / V_r \qquad (9)$$

This type of ratio is well known from chemical engineering, as discussed in the next section, and fits in with other velocity ratios discussed previously. Alternatively, one may use a ratio of the flux through the sides of the tube to the flux in the forward direction. Such fluxes relate to flow transport and lateral diffusion, which may lead to the ratio:

$$D / v_r L_r \qquad (10)$$

where D is the diffusivity (L^2/T), v_r is the transport coefficient, and L_r is the radius. This similarity criterion is well known in heat engineering as the Nusselt number and compares diffusion and membrane transport mechanisms. A recent analysis of renal function by Bergmann and Dikstein (*41*) uses ratio 10 centrally in its results, as do many other studies, such as those reviewed by Defares (*42*).

Derivation of dimensionless numbers and similarity criteria is not a substitute for analysis by differential equations, but it often helps to show what properties are most important and invariant in related structures.

As a final example, the following combination is useful in analyzing the blood outflow from the aorta into the peripheral vascular tree:

$$(R_F C_V)/T \qquad (11)$$

where R_F is the ratio of pressure to flow rate (M/L^4T), C_V is the ratio of distensibility or volume to pressure (L^4T^2/M), and T is the pulse time. This term appeared in prior studies of the cardiovascular system (*42*) but does not seem to have been recognized as a similarity criterion. It indicates that the time required for ejection from the distended aorta will correspond to the time required for flow into the vascular tree. A numerical value of 1 to 2 was obtained for this criterion from human cardiac catheterization data of Roston (*43; see also 18, 20*). Measurement of R_F and C_V in humans during life presents many problems, but the foregoing results are heartening. This term may be used with other dimensionless numbers for the circulatory system. For example, the ratio of diastolic pressure to pulse or total pressure is known to relate to an exponential function of the criterion in ratio 11. An analysis of data by Crosfill and Widdicombe (*44*) reveals that this term is also a useful invariant for comparison of respiratory systems. A residual mass exponent of not over 0.08 and possibly of zero value has been obtained from the published comparative values.

Chemical and Thermodynamic Similarity

Scaling up of chemical reaction systems has been the subject of a number of studies in chemical engineering. Reviews are available by Johnstone and Thring (*10*) and by Klinkenberger and Mooy (*45*); there are also pertinent Soviet volumes by Reznyakov (*46*) and D'yakonov (*47*). Thermodynamic similarity is specifically reviewed by Perel'shtein (*48*). Several dozen chemical similarity criteria have been listed. Among the oldest, one of the so-called Damkohler numbers, is

$$S_N A / C_N D \qquad (12)$$

where S_N equals N/L^3T, C_N equals N/L^3, D equals L^2/T (diffusivity), and A equals L^2. This term is useful for comparing a synthesis rate with a diffusion rate in a given area. It can probably be applied directly to diffusion in cells, capillaries, and lung alveoli. The Warburg criterion for diffusion into tissue slices is identical in form with ratio 12.

General scaling laws have been formulated for various types of chemical plants and processes. It is usually impossible to state general scaling conditions unless many variables are held constant; commonly these include temperature, pressure, certain concentrations and viscosity. Systems with identical physical parameters are said to be homologous. It is known (*10*) that the basic scaling conditions for homologous heterogeneous reaction systems (reactions occurring on areas rather than uniformly in a volume) are:

$$v_r / v_J = \text{inv. and } J_H = \text{inv.} \qquad (13)$$

where v_r is an apparent reaction velocity, v_J is a linear flow rate, and J_H is heat loss per unit area and unit time. Commonly, the first condition simply reduces to invariance of flow velocity.

It is interesting to note that these conditions appear to be precisely those which apply for the scaling up of mammals. The approximate constancy of metabolic rate per area has been recognized since as early as 1839 (see *27*), but a better fit is obtained with a mass exponent of 0.73 to 0.75, rather than 0.67. In mammals the heat loss can be combined with an oxygen flux and the dimensional constant given in item No. 12 of Table 2 to yield a nondimensional criterion. Applicability of the velocity ratio is suggested by entries 6 to 10 in Table 2, but invariance of blood flow at corresponding points should be confirmed experimentally. Invariance of blood flow velocity was proposed earlier on the basis of scaling relationships for cardiac output and aortic area. Invariance of velocity ratios is also a condition for similarity of free flames, as noted in Johnstone and Thring (*10*) and in Reznyakov (*46*).

Space limitations do not allow an adequate discussion of thermodynamic similarity, but it may at least be noted that dimensional considerations have helped clarify (*20*) the differences and parallels between "information" and entropy, the operational definition of biological "forces," and particularly the concepts of biological "energy" and "potential." It appears that one may speak of "biologically available energy" for energy that is made available without disruption of the biochemical-organismal system. This can be compared with chemical free energy or isothermally available energy. Chemical free energy in food may be further classified as "digestible" energy, "metabolizable" energy, and so on. It appears very useful to define such entities by stating the process through which they are obtained. Biological potential, on the other hand, is well described as energy per biological unit such as a cell, an organism, or a gene. Energy ratios, such as the Arrhenius ratio ($\Delta E/R\theta$) are typical of thermodynamic similarity. Examples of comparable biological criteria include the energetic efficiency values for biomass generation or physical work, and the ratio of basal to maximal energy output of a mammal, as discussed in Kleiber (*27*).

Conclusions

The scale-up capability of biological organisms is quite remarkable by comparison with any known engineering accomplishments. For example, the heart of a mouse weighs about 0.1 gram, while that of a whale may weigh 150 kilograms, and yet the two resemble each other strongly and clearly perform the same physical functions. Such very extensive dilatation of the system is possible only when a number of factors are rigidly controlled, as is known to be the case in the mammalian system (factors such as pressures, concentrations, *p*H, types of reactions, viscosity, membrane coefficients, density, and diffusivity).

A very interesting prospect for the future is that similarity criteria will make possible a quantitative comparative physiology and also genetic tracing of certain organ systems. In pioneering work beginning in 1922, E. W. Sinnott (*49*) showed that the geometric form ratio for the gourd fruit was controlled genetically. It appears reasonable to suppose that the numerical value of any biological similarity criteria is determined genetically and may be followed in phylogenesis. Presumably genes carry hereditary information in dimensionless form and it is converted into dimensional variables, such as blood pressure, by mechanisms which are not completely understood at this time.

Metaphysical connotations should not be attached to similarity criteria. They are obtained by a well-defined and deductive method, not by mystical revelation. Examination of books such as those of Duncan, of Langhaar, and of Sedov immediately reveals that dimensional methods are as complex as any of those widely used in engineering, but they have been little taught in universities.

An outstanding feature of dimensionless similarity criteria is that they are *convenient* and embody *natural* physical properties of the system under study. They rely on internal rather than imposed standards of measurement. It has been said, for example, that when measured by his own forearm every man is of the same size as every other.

Dimensional methods naturally tend to find a place in biomedical engineering. There will probably be a useful exchange of experience on similarity methods between engineering practice and biomedical work. The ability of mammals to scale up (from mouse to whale) by a factor of over 2 million in mass and 100 in length is remarkable and thought-provoking for the engineering analyst. It also seems conceivable that similarity and scale-up methods will be useful in biomass production studies in agriculture, in certain aspects of clinical physiology, in construction of biological models, in analysis of developmental patterns and in a number of other areas.

The work reviewed in this article (*50*) is in some respects an attempt to apply modern similarity and dimensional methods to the viewpoints expressed by D'Arcy Thompson in his monumental work *Growth and Form.* D'Arcy Thompson always held that in analyzing biological systems one should use clearly defined physical mechanisms, without recourse to unproven "vitalistic" energies or agencies. The outlook of this article is well summarized in his words: "The study of form may be descriptive merely, or it may become analytical. We begin by describing the shape of an object in simple words of common speech. We end by defining it in the precise language of mathematics, and the one method tends to follow the other in strict scientific continuity."

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News and Comment

Space Program: Congress Passes It Unanimously, But NASA Wonders About Durability of Support

The Senate, without asking any serious questions, gave its unanimous endorsement last week to the Administration's space program.

The action followed a similar display of unanimity in the House, where even H. R. Gross, the Iowa Republican who thinks budgets are for cutting, grudgingly went along with a $2 billion increase in NASA's budget, bringing it to $3.7 billion. Gross did add that "it would be my hope that if and when we do get to the moon we will find a goldmine up there because we will certainly need it." But neither he nor any of his colleagues on the floor showed an inclination to debate NASA's activities. In the Senate, William Proxmire, Democrat of Wisconsin, tried to stir up some debate about the space program, but the response was minimal. Two amendments offered by Proxmire—calling for a study of the space program's manpower situation and for more competition in space contracts—were promptly overwhelmed. The Senate then went on to give NASA virtually everything it requested. As in the House, a few items were shaved, but the effect will not extend to any activities that NASA deems even moderately important. If it changes its mind, it has assurances that both houses will review the cuts with sympathy.

Having scored a pair of shutouts on Capitol Hill—as it has in every post-Sputnik year—the space program would seem to have no political clouds in its future. But among persons associated with the program, in and out of Congress, more and more thought is being given to the question of the substance and durability of public and, ultimately, congressional support for the national space effort.

When portrayed in terms of competition with the Soviets, the space effort is assured of public and congressional support, especially since the mortification caused by Sputnik is embedded in the American mind. But the Administration is eager to convince the public that space developments are valuable in themselves and deserve to be supported at a high level of expenditure, regardless of what the Soviets are up to. Just what the future holds in the East-West space competition is something of which no one can be certain; the Administration, however, wishes to make certain that in the unlikely event of a decline in the cold war motivation, the public will be sufficiently enamored of space activities to give support to the continuance of a large-scale program.

Toward this end, the Administration has gone to great lengths to depict the space program as a great national undertaking that is leading to readily discernible benefits such as weather forecasting and satellite communications; indirect benefits, including technologies adaptable to nonspace activities; and, finally, a grand adventure in which all citizens can vicariously participate.

The difficulties involved in winning support for the program outside of a cold-war context are enormous, however, because, while the bill grows bigger each year, the benefits that are easily visible to the general public are few in number. The success of Telstar last week helps convince every television viewer that he has something to gain from space research, but such easily recognizable dividends from space are actually few in number.

One result is that the Administration and its space lieutenants in Congress have undertaken a campaign to convince the public that the "fallout" (or, as it is more discreetly referred to, the "spin-off") from space research is of such great value in nonspace fields as to justify whatever expenditures may be involved. Pronouncements to this effect are becoming fairly commonplace and sometimes are of a euphoric character that suggests a bit too much protesting. (One entry in this educa-