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## ENERGY METABOLISM AND BODY SIZE. II. DIMENSIONAL ANALYSIS AND ENERGETIC NON-SIMILARITY

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**Abstract.** The allometric equation  $P = aM^b$  ( $P$ : standard metabolism,  $M$ : body mass,  $a$ : mass coefficient,  $b$ : mass exponent) can be theoretically derived from the following relations:  $l/L = t/T = \lambda$ ,  $m/M = \lambda^3$  where  $l$  and  $L$  are homologous lengths,  $t$  and  $T$  homologous times and  $\lambda$  is the coefficient of similitude between two animals. Animals are homomorphic when  $b = 2/3$ ,  $a = \text{constant}$ , and when their density is the same. These conditions appear to be realized in mature mammals of the same species, but mammals of different species are not homomorphic. Homomorphism means that the physiological time-scale is the same in small and large animals, but that the energy spent per unit mass and unit of physiological time remain the same in homomorphic animals [mass-specific physiological power,  $\Phi$ ]. The mass coefficient 'a' is equal to  $\Phi$ , therefore 'a' is physiologically the most significant parameter in the allometric equation. The physiological implications of  $\Phi$  are discussed.

Allometry	Mass coefficient
Basal metabolism	Mass exponent
Homomorphism	Physiological time

A critical review of data from literature has shown that in a group of 7 mammalian species (mice to cattle) the interspecific relationships between body mass and basal metabolism are best described by a set of power functions in the form of eq. (1), one for each species, with a mass exponent of 2/3. However, each power function has a different mass coefficient, which tends to increase with the size of the species (Heusner, 1982). A single interspecific regression line with a mass exponent of 0.75 and the same mass coefficient for all species does not accurately describe the available experimental data.

The aim of this paper is to examine the allometric equation in light of these new statistical results, from the point of view of thermodynamics and of Lambert and Teissier's theory of biological similitude (Lambert and Teissier, 1927). This theory

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provides the basis for a concept of energetic non-similarity which is consistent with the available anatomical and zoological evidence and with the statistical description of the experimental metabolic data (Heusner, 1982). The proposed interpretation of the allometric equation opens new avenues for experimentally analyzing the biological implications of the metabolic allometric equation.

#### Historical background

The standard metabolism and body mass of animals are related by the well established allometric equation:

$$P = aM^b, \quad (1)$$

where the dependent variable 'P' represents the rate of basal (Homeotherms) or standard (Poikilotherms) energy metabolism, the independent variable 'M' the body mass of the animal, 'b' the mass exponent, and 'a' the mass coefficient.

The large amount of experimental data accumulated over the last half century on this relationship in all phyla of the animal kingdom has led to a general agreement about the mathematical form of this relationship, irrespective of considerable structural differences in animals (Brody, 1945; Zeuthen, 1947; Hemmingsen 1960; Kleiber, 1947, 1961; Kayser and Heusner, 1964). However, a general agreement as regards the actual values of the parameters 'a' and 'b' of this equation and their physiological meaning has not yet been reached.

The ubiquity of the allometric relation between energy metabolism and body mass in the animal kingdom seems to indicate that this relationship is governed by a general law, and several attempts have been made to discover it. Sarrus and Rameaux (1838-1839) related the physiological observations on animal heat and body mass to the physical law of heat loss (Fourier's Law), but it soon became obvious that this explanation was not sufficiently general to account for the same relationship in poikilotherms which do not regulate their body temperature. This is particularly true of those living in water, which has high thermal conductivity (Krogh, 1941).

Von Hoesslin (1888) derived a mass exponent of 2/3 from speculations on geometric similitude. Lambert and Teissier (1927) extended the concept of geometric similitude to include the dimension of time and formulated their theory of biological similitude, which also predicts a mass exponent of 2/3. An attempt to reconcile theoretically predicted mass exponents with experimentally obtained values has been made by altering the values derived from theoretical assumptions with mathematically appropriate but arbitrary coefficients of the dimension of time (Gunther and Guerra, 1955; Gunther, 1971, 1975). The alteration first proposed (Gunther and Guerra, 1955) led to a prediction of different mass exponents for the allometric equations relating energy metabolism and mass ( $b = 0.73$ ) and oxygen consumption and mass ( $b = 0.69$ ). As a result of this adjustment, the thermal equivalent of oxygen

is no longer a thermochemical property of nutrients independent of an animal's mass. Indeed, in this case a liter of oxygen consumed by a cat and a lion eating the same meat would not correspond to the same number of calories. This would be contrary to the First Law of Thermodynamics. Later, in 1971, Gunther modified the adjusting factor by introducing the concept of operational time. But, since Gunther's theories are based on geometrical similarity and animals of very different sizes are not geometrically similar, one should not expect the experimentally observed exponent to equal the theoretical one.

McMahon (1973) introduced the concept of elastic similarity and provided an apparent theoretical explanation for the 3/4 mass exponent. His theory is based on the assumption that 'the speed of shortening  $\Delta l/\Delta t$ , is a constant in any particular muscle from species to species', an assumption which Hill (1950) has shown to be incorrect. MacMahon's theory explains structural non-similarity in terrestrial animals but fails to predict metabolic allometry, particularly in unicellular and aquatic animals. Finally, Blum (1977) introduced the concept of four-dimensional bodies to explain the 3/4 mass exponent. Unfortunately Blum did not provide any convincing evidence as to what this fourth dimension in animals could be. It is interesting to note that while the discussion has revolved around the magnitude of the mass exponent little attention has been paid to the mass coefficient and its significance.

Recently an empirical and pragmatic approach has been adopted which consists of simply accepting the 3/4 mass exponent on the basis of its experimental reproducibility and its value as a predictor for energy metabolism in animals. Thirty years of experimental work with this approach have failed to offer any direction for understanding the physiological significance of the allometric equation within or beyond the realm of energy metabolism, a situation which illustrates Claude Bernard's statement: 'Empiricism may serve to accumulate facts, but it will never build science' (Bernard, 1865).

How might the physiological meaning of the allometric relation be discovered? The relationship between mass and energy metabolism is a relation between matter, structure, and power, all variables thermodynamics deals with. Therefore, a conceptual approach such as the one proposed by Lambert and Teissier, based upon the principles of dimensional analysis and consistent with thermodynamics, should give some insight into the general laws governing the relationship between body mass and energy metabolism.

The success of thermodynamics, it can be argued, is due to the use of postulates and abstract theoretical concepts such as the ideal gas, the ideal steam engine, reversibility, and the Carnot cycle, all of which *do not exist in nature*. These concepts, even though they can only be approximated in the real world, provide the conceptual framework against which observed phenomena can be analysed and described in a consistent manner. They provide specific criteria or hypotheses which can then be tested by means of appropriate statistical methods; they also permit prediction of the most appropriate experimental conditions under which experi-

ments can be carried out. By analogy the concept of similarity in animals is an abstraction which can only be approximated in nature but is nevertheless useful for providing well defined criteria of similitude expressed in terms of the magnitude of the mass exponent and both the magnitude and dimensions of the mass coefficient.

It should be emphasized that to consider the allometric relation from the point of view of dimensional analysis and similarity is a complete departure from the traditional standpoint. Sarrus and Rameaux (1838-1839), Rubner (1883), Richet (1885), and to a large extent Kleiber (1961) saw in the thermal aspect of energy metabolism and in temperature regulation an explanation for the power function between body mass and basal metabolism. For these investigators this relationship was an expression of cause and effect based on Fourier's law: the surface area not only determines heat loss but becomes a determinant of energy metabolism. Surprisingly, the emergence of thermodynamics in the second half of the 19th century had little impact on the conceptualization of this relationship. According to the Second Law of Thermodynamics, heat is a consequence of metabolism and not its cause, an idea already expressed by von Hoesslin (1888) when he claimed that the loss of heat is the result of heat production. Heat is a necessary waste in living organisms, and, since temperature differences within the body of animals are not thermodynamically useful, heat is for them an unavailable form of energy. Despite the fact that homoiotherms make successful use of this waste to gain thermal independence over the environment, the thermal aspect of energy metabolism is not the most significant aspect from a thermodynamic point of view. If Fourier's Law is considered the physical law underlying the allometric relation the more fundamental role of energy metabolism is lost or masked: *i.e.* free energy is necessary to build and maintain the structure and physiological functions of an organism. This aspect of energy metabolism is an intrinsic property of an organism. From this perspective the allometric equation relates two intrinsic properties (power and structure) in animals of different size, and the theory of similitude provides a criterion for similarity in animals. It would be a grave error to believe that this theory permits us to derive or predict causal relationships. This is clear because we can predict the dimensions of the mass coefficient but not its magnitude.

To be general, any theoretical approach must take into account the following two physical requirements:

(1) The allometric equation must conform to Fourier's principle of dimensional homogeneity;

(2) Animals of different size cannot remain structurally similar (Galileo, 1638):

These two requirements impose constraints on the parameters of the allometric equation, the nature of which depends on the chosen criteria of similarity.

After a discussion of preliminary definitions in sect. 3.1, in sect. 3.2 we will:

(1) define the criteria of homomorphism,

(2) examine the allometric equation in light of these criteria.

### Theory of energetic non-similarity

#### PRELIMINARY DEFINITIONS

Animals can be described in terms of physical quantities, which with respect to their dimensions fall into two groups: primary quantities (mass, length, time and temperature) and secondary quantities, which are combinations of primary quantities (surface area, volume, weight, power, density, heat capacity, pressure etc.). The choice and number of primary quantities are arbitrary. Secondary quantities are expressed as products of powers of primary quantities, and according to Bridgman's definition (1963) 'the exponent of the power of any particular primary quantity is by definition the 'dimension' of the secondary quantity in that particular quantity'.

Since relationships between physical quantities must be expressed by dimensionally homogeneous equations, the relation between mass (a primary quantity) and energy metabolism (a secondary quantity), as given in eq. (1), can be rewritten in dimensional form as follows:

$$[M \cdot L^3 \cdot T^{-3}] = [M^1 \cdot L^3 \cdot T^{-3}] [M^b] \quad (2)$$

Relation (2) shows that in the allometric equation the mass coefficient is the sole parameter with dimensions, the mass exponent being a simple number. Since the exponent 'b' figures in the dimensions of the mass coefficient 'a',  $[M^1 \cdot L^3 \cdot T^{-3}]$ , the magnitude of 'b' determines the dimensions of 'a'. Therefore, the magnitude of the mass exponent puts a *dimensional* constraint on the mass coefficient.

Similarity is a mathematical concept. It is based on well defined, simple relations between the ratios of the *primary quantities* in which all the secondary quantities are expressed. These relations, which must be consistent with the Laws of Thermodynamics, determine the ratios between all the secondary quantities. Since the ratios of primary quantities may be related in various ways, different types of similarity are possible (geometric, mechanical, chemical, thermodynamic similarity) and it should be emphasized that one type of similarity does not necessarily entail all others. For example, two steam engines of different size which are thermodynamically similar cannot remain geometrically similar, an observation which led Watt to design his steam engine. The question is then to discover which types of similarity hold in certain animals. This requires that we mathematically define a type of similarity and then test whether the experimental data are consistent with the criteria of this particular type of similarity.

From a thermodynamic point of view a physical quantity describes either an extensive or an intensive property of a thermodynamic system. An extensive property is one whose magnitude depends on the size of a system (mass, surface area, volume, energy, heat capacity, etc); an intensive property is one whose magnitude is size-independent (density, pressure, temperature, etc.).

If two systems are geometrically, mechanically, and chemically similar, the magnitudes of their respective intensive properties are the same. The constancy of intensive properties is a necessary condition for similarity. Animals that are similar must also meet this requirement.

Energy is the product of an extensive property and its conjugated intensive property. Supposing that we can analyse the allometric equation from this thermodynamic point of view,  $M^b$  is an extensive property, and the mass coefficient 'a' must be an intensive property: its dimensions must be such that it is mass-independent. Since the mass exponent 'b' places dimensional restrictions on 'a', the dimensions of 'a' in turn place restrictions on the magnitude of 'b'. If 'b' does not fall within these restrictions, the allometric equation becomes thermodynamically meaningless. If, however, we can show that 'b' falls within these restrictions, then the constancy of 'a' in two animals becomes a necessary condition for their similarity.

Approaching this problem from a biological point of view, what restrictions on 'b' does a set of criteria for biological similarity impose? Are these restrictions compatible with those that a thermodynamic interpretation of the allometric equation places on 'b'?

#### CRITERIA OF HOMOMORPHISM AND THE ALLOMETRIC EQUATION

When are two animals biologically similar? Lambert and Teissier (1927) postulated that two animals of different size are biologically similar when the following relations hold between the primary quantities:

$$l/L = t/T = \lambda, \quad (3)$$

$$m/M = \lambda^3 \quad (4)$$

where  $l$  and  $L$  represent homologous lengths,  $t$  and  $T$  homologous times,  $m$  and  $M$  the masses, and  $\lambda$  is the coefficient of similitude.

Relation (3) expresses the condition of geometrical similarity (same form). Relation (4) states that similar animals have the same density (intensive property). These relations express the basic conditions for homomorphism: animals exist in space as well as in time, and, if the ratios of their homologous spatial and temporal extensions are equal, they have the same form in space and in time and are therefore homomorphic (Cara, 1958) or biologically similar (Lambert and Teissier, 1927).

In two systems we can not only compare primary quantities but all quantities with the same dimensions. The ratio of any two magnitudes ( $q$  and  $Q$ ) of a particular quantity ( $qu$ ) is expressed by:

$$\chi_{qu} = q/Q, \quad (5)$$

and is itself dimensionless but can be expressed in terms of the primary quantities as follows:

$$\chi_{qu} = \mu^a \lambda^b \tau^\gamma \theta^\delta, \quad (6)$$

where  $\mu$  is the ratio of masses,  $\lambda$  the ratio of homologous lengths,  $\tau$  the ratio of homologous times, and  $\theta$  the ratio of homologous temperatures,  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\delta$  being the dimensions of the given quantity ( $qu$ ) in its primary quantities.

In two homomorphic systems  $\chi_{qu}$  can be expressed in terms of mass, length, and time alone: the ratio of the two temperatures is 1 since temperature is an intensive property.

In addition, since relations (3) and (4) hold between the primary quantities, we can express  $\chi_{qu}$  in terms of the ratio of one primary quantity. We choose mass since it is the most readily measured quantity in animals:

$$\chi_{qu} = \mu^{1/3(3a + \beta + \gamma)} \quad (7)$$

Relation (7) expresses the theoretical relationship which holds between the ratio of the magnitudes of quantity  $qu$  and the ratio of masses in homomorphic animals.  $\chi_{qu}$  is equal to Maxwell's reduction coefficient.

For energy metabolism  $P$ , [ $M \cdot L^2 \cdot T^{-3}$ ] in homomorphic animals:

$$\chi_p = \mu^{1/3(3 + 2 - 3)} = \mu^{2/3} \quad (8)$$

Relation (8) shows that the allometric equation with a mass exponent of  $2/3$  is a mathematical consequence of homomorphism. Since the mass coefficient does not figure in relation (8), the ratio of its magnitudes must be equal to 1; hence, its magnitude must be the same in homomorphic animals irrespective of their size.

Since the mass coefficient is mass-independent the allometric equation in homomorphic animals is consistent with thermodynamics. Therefore, from both a biological and a thermodynamic point of view, there are two necessary conditions for homomorphism:

- (1) the mass exponent 'b' of the allometric equation must be equal to  $2/3$ ;
- (2) the magnitude of the mass coefficient 'a' must be mass-independent.

Can we show that these conditions are also sufficient? Let us assume that  $b = 2/3$  and 'a' is constant in a group of animals. Can we conclude that these animals are homomorphic? Since

$$\chi_q = \mu^{(1-b)} \lambda^2 \tau^1, \quad (9)$$

from our two assumptions we have:

$$\chi_q = \mu^{1/3} \cdot \lambda^2 \cdot \tau^{-1} = 1 \quad (10)$$

Since eq. (10) can be solved in various ways, it does not establish that the conditions expressed by eq. (3) and eq. (4) are met. If, however, we assume that eq. (4) also holds, in other words, that the density of the animals must also be constant, we can show that the conditions expressed by eq. (3) are satisfied. Therefore, animals are homomorphic when 'b' =  $2/3$ , 'a' is constant, and they have the same density (intensive property). Note that body temperature is assumed to be the same in

homomorphic animals. If the temperature were different, the allometric equation would not be applicable to a discussion of homomorphism.

#### THE CONCEPT OF HOMOMORPHISM IN LIGHT OF THE EXPERIMENTAL DATA

Analysis of covariance of body mass and basal metabolism in 7 mammalian species has revealed that, when 'b' is different from 2/3, 'a' is not mass-independent but increases threefold when body mass varies from 0.020 to 500 kg. The commonly accepted interspecific mass exponent of 0.75 has only one significance: it reveals that 'a' is not the same for all species as was assumed in the derivation. If 'a' is held statistically constant within each of the seven mammalian species, the intraspecific mass exponent is equal to  $0.67 \pm 0.03$  (Heusner, 1982). The theoretical 'b' for homomorphism falls within the confidence interval of the observed intraspecific 'b'. This confirms experimentally the theoretical relationship between 'b' and 'a'.

Our analysis shows that from an energetic point of view mammals of different species are not homomorphic. As for mature mammals of the same species, if we can assume that they have the same density, then we can conclude that they are homomorphic. All anatomical and zoological evidence is against homomorphism in animals of different species or in growing animals, which change their form.

#### THEORETICAL LIMITATIONS OF HOMOMORPHISM

The reduction coefficient has been derived using very specific assumptions regarding the spatial, physical, and temporal structures of animals and, therefore, is only applicable to quantities which express structural and functional properties of an organism. Mathematically we could predict the form of the relationship between any quantity and body mass in homomorphic animals, but such predictions are meaningless for quantities which are not organismic properties of animals. For example we predict that energy metabolism varies as the power 2/3 of body mass. The question then arises which energy metabolism? Energy metabolism is a power irrespective of the factors which determine its magnitude (exercise, ambient temperature, etc), so according to the reduction coefficient any energy metabolism, whatever the cause, should vary as the power 2/3 of body mass. Only basal metabolism in homeotherms or standard metabolism in poikilotherms is an 'organismic property\*', metabolism due to exercise is not. We know from thermodynamics that work is in general not a property of a system. How then could animals be similar with respect to a quantity which is not their property? Two animals of different size, even if geometrically similar, cannot remain energetically similar so

\* Organismic property: properties displayed by or in an animal under basal or standard conditions, reflecting structural and/or functional features of the organism considered as a whole.

far as locomotion is concerned, because the heavier animal must spend more energy relative to its resting metabolism than the lighter one for the same locomotor behavior. This does not imply that empirical and statistically significant relationships derived for activity metabolism in animals of different sizes are invalid. It simply means that from these relationships we cannot conclude that animals are similar.

The following biological variables can be classified as organismic properties:

- (1) Morphometric variables;
- (2) Physical properties such as density, temperature, thermal conductivity, mass, heat capacity, heat content, etc., which are properties of all components of an organism, so that at least in theory there exists an average value pertaining to the whole organism. This excludes blood viscosity, which is solely an intensive property of blood but not of an organism as a whole;
- (3) All physiological variables involved in energy metabolism directly related to the maintenance of the integrity of normal structure and function. Physiological variables such as energy metabolism,  $O_2$  consumption,  $CO_2$  production, ventilation, tidal volume, respiratory frequency, arterial pressure, heart rate, stroke volume, cardiac output, blood flow, velocity of blood flow, etc. can only be considered to have structural significance when the animal's energetic interaction with the environment is in a well defined state. In homeotherms this state corresponds to a minimum energy exchange with the environment (thermal neutral zone, resting and post-absorptive conditions). Poikilotherms must be compared at constant body temperature in resting and post-absorptive conditions. Since resting conditions are a prerequisite for the validity of the reduction coefficient, it cannot be applied to physiological variables specifically related to exercise such as properties of contracting muscle (velocity of shortening, maximum load, etc).

Relationships due to similarity are not relations of cause and effect since we cannot identify the causal factor. For example, if we change the radius of a sphere, its surface area and volume will change, and conversely, if we change the surface area or the volume, the radius of the sphere must change. These are necessary geometric relations, which are the consequences of the geometrical similarity of spheres. Likewise, there are necessary relationships between certain quantities within two homomorphic animals of different sizes. Similarity requires that the form of these necessary relationships is predictable, because they are mathematical consequences of some basic underlying relationships between primary quantities.

This requirement excludes a simple regression between body mass and a given quantity as proof for similarity in animals *when the sufficient criteria for similarity are not satisfied*. Only if the experimental data are consistent with the basic assumptions concerning the primary quantities, will animals be similar in the defined type of similarity.

## THE BIOLOGICAL MEANING OF THE ALLOMETRIC EQUATION

The space-time relationship expressed by relation (3) is the cornerstone of the theory of homomorphism. This relation shows that the time-scales for small and large animals are not the same and are different from the physical time-scale. The allometric equation (eq. (1)) relates energy per unit of physical time (physical power) to the body mass of an animal. With eq. (1) we can compute the energy spent per unit mass and per unit of *physiological time-scale* or the mass-specific physiological power ( $\Phi$ ). Since the unit of the physiological time-scale is proportional to body mass to the power  $1/3$  (eq. (3) and eq. (4)),  $\Phi$  is given by the following expression (11):

$$\Phi = P \cdot M^{1/3} / M = a \cdot M^{2/3} \cdot M^{1/3} / M = a, \quad (11)$$

which shows that the mass coefficient of the allometric equation (1) is equal to  $\Phi$  the mass-specific physiological power. In homomorphic animals the energy per unit mass and unit of *physiological time-scale* necessary to maintain the structural and functional integrity is constant.

What is the relevance of homomorphism for comparative physiology which deals mainly with animals that are not homomorphic? Energetic non-similarity can only be demonstrated when criteria of similarity have been defined.

Homomorphism offers a means to express functional and structural relationships, even between animals that are not homomorphic, with equations that are dimensionally homogeneous with respect to their parameters (as for example: eq. (1)). These mathematical descriptions are no longer empirical curves fitted to experimental data but are based on clearly defined theoretical assumptions, which are either realized in nature or not, and the parameters of these equations have a biological meaning.

Homomorphism is not possible over a large range of body mass, because the form and structure change as the animal weight increases. Is the fact that there are over 6000 different kinds of rodents but only two kinds of elephants (Hill, 1956) an indication that the necessity to support more mass entails a loss of the degree of freedom of form and structure? However, irrespective of size, mature animals of the same species tend to remain homomorphic. This indicates that the form of the time-space relationship is preserved in spite of all the structural changes due to the increasing weight. The increase with size in  $\Phi$  expresses the energetic cost of these necessary morphological and physiological adjustments.

The results obtained from interspecific and intraspecific studies lead us to speculate about the meaning of the allometric relation for an individual organism. However, reliable metabolic data in single animals during their lifespan are yet too scarce to allow us more than speculative considerations.

We can distinguish three phases during an individual's lifespan:

- (1) a phase of growth characterized by changes of structure accompanied by a significant increase in mass;

- (2) a phase where structure is relatively constant, but mass may not necessarily be so;

- (3) a phase of senescence during which there are changes in structure and mass. During phase 1 the mass exponent estimated by regression analysis is greater than  $2/3$  (Brody, 1945). Since according to homomorphism the mass coefficient cannot be constant when 'b' is different from  $2/3$ , we interpret the greater mass exponent as indicative of an actual increase in  $\Phi$  reflecting the structural and organizational changes taking place in the growing organism.

During phase 2 the ratio of basal metabolism to body mass to the power  $2/3$  tends to be constant, indicating that the mass exponent is about  $2/3$ . In this phase an individual tends to remain homomorphic despite changes in mass.

During phase 3 the mass exponent appears statistically to be smaller than  $2/3$ . This statistical result suggests that  $\Phi$  is actually decreasing during senescence.

If this interpretation of the allometric equation applied to a single organism is correct, then a mass exponent greater than  $2/3$  is indicative of an increase in  $\Phi$ , a mass exponent smaller than  $2/3$  of a decrease in  $\Phi$ . An increase in  $\Phi$  would indicate that the increase in mass is accompanied by a change in structure, the organism no longer remaining homomorphic with itself, whereas a decrease in  $\Phi$  during senescence could indicate a deterioration in the tissues and organs and their functions.

In all three cases the magnitude of the mass exponent is a criterion for changes in  $\Phi$  reflecting the structural gains or loss of an organism.

## Concluding remarks

Living beings are aggregates of matter and energy distributed in space and time in very diversified configurations. This diversity of the living world appears to be based on a fundamental relation between space and time, the form of which remains invariant. Organisms live in their own time depending on their size. This leads us to speculate that the difference in the individual time-scales of small and large animals, and the difference between these scales and the physical time-scale of their environment, made it necessary for these animals to acquire a circadian clock in order to maintain meaningful time relationships between themselves and their physical environment. It is interesting to note that the biological clocks are size-independent and to a large extent independent of the metabolic rate, in sharp contrast with physiological time which is both size- and rate-dependent. Even though this might seem paradoxical, biological clocks do not work in the biological time-scale but in the time-scale of the physical environment. From the point of view of physiological or biological time homeothermy appears as another mechanism by which the time relationship between homeotherms and their physical environment is stabilized.

The ubiquity of the allometric relationship between energy metabolism and body

mass may thus reflect the fundamental tendency of organisms to maintain a definite relation between space and time, the mathematical form of which appears to be invariant. The metabolic allometric relation and homomorphism would then be consequences of this space-time relationship.

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