The Fourth Dimension of Life: Fractal Geometry and Allometric Scaling of Organisms

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THE FOURTH DIMENSION OF LIFE:
FRACTAL GEOMETRY AND
ALLOMETRIC SCALING OF ORGANISMS

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Abstract

The existence of fractal-like networks effectively endows life with an additional fourth spatial dimension. This is the origin of quarter-power scaling which is so pervasive in biology. Organisms have evolved hierarchical networks which terminate in invariant units, such as capillaries, leaves, mitochondria, and oxidase molecules, which are independent of organism size. Natural selection has tended to maximize both metabolic capacity by maximizing the scaling of exchange surface areas, and internal efficiency by minimizing the scaling of transport distances and times. These design principles are independent of detailed dynamics and explicit models and should apply to virtually all organisms.
Evolution by natural selection is one of the few universal principles in biology. It has shaped the structural and functional design of organisms in two important ways. First, it has tended to maximize metabolic capacity, because metabolism produces the energy and materials required to sustain and reproduce life; this has been achieved by maximizing the surface area where resources are exchanged with the environment. Secondly, it has tended to maximize internal efficiency which has been achieved by minimizing the distance and time that materials are transported. A further consequence of evolution is the incredible diversity of body sizes, which range over 21 orders of magnitude, from $10^{-15}$g microbes to $10^9$g whales. A fundamental problem therefore is how exchange surfaces and transport distances change, or scale, with body size. In particular, a longstanding question has been why metabolic rate scales as the 3/4-power of body mass, $M^{3/4}$ [1].

Biological scaling can be described by the allometric equation $Y = Y_0 M^b$, where $Y$ is a variable such as metabolic rate or lifespan, $Y_0$ a normalization constant, and $b$ a scaling exponent [1]. While $Y_0$ varies with the trait and type of organism, $b$ characteristically takes on a limited number of values, all of which are simple multiples of 1/4. For example, diameters of tree trunks and aortas scale as $M^{0.25}$, rates of cellular metabolism and heartbeat as $M^{-1/4}$, blood circulation time and lifespan as $M^{1/4}$, and whole organism metabolic rate as $M^{3/4}$. The question has been why these exponents are multiples of 1/4 rather than 1/3 as expected on the basis of conventional Euclidean geometric scaling. 

Recently, we presented a model which suggested that the explanation could be found in the fractal-like architecture of the hierarchical branching vascular networks which distribute resources within organisms [2]. This model is based on three principles: the network branches to fill a 3-dimensional volume; terminal units are invariant; and the energy required for resource distribution in the network is minimized. The model accurately predicts scaling exponents which have been measured for many structural and functional features of mammalian and plant vascular systems. It is not clear, however, how this model can account for the observation that metabolic rates of unicellular algae and protists scale as $M^{3/4}$, because these organisms seemingly have no obvious branched anatomical structure specialized for resource distribution. Here we present a more general model, based on geometrical arguments, which does not require the existence of such explicit structures, and which can account for the pervasive quarter-power scaling in biology. 

We conjecture that organisms have been selected to maximize fitness
by maximizing metabolic capacity, namely the rate at which energy and material resources are taken up from the environment and allocated to some combination of survival and reproduction. This is equivalent to maximizing the scaling of whole-organism metabolic rate, \( B \). It follows that \( B \) is limited by the geometry and scaling behaviour of the total effective surface area, \( a \), across which nutrients and energy are exchanged with the external or internal environment. Examples include the total leaf area of plants, the area of absorptive gut or capillary surface area of animals, and the total area of mitochondrial inner membranes within cells. In general, therefore, \( B \propto a \).

It is important to distinguish \( a \) from the relatively smooth external surface, or "skin," enclosing many organisms. We conjecture that natural selection has acted to maximize \( a \) subject to various constraints while maintaining a compact shape. This is equivalent to minimizing the time and resistance for delivery of resources by minimizing some characteristic length or internal linear distance.

Broadly speaking, two sets of variables can be used to describe the size and shape of an organism: a conventional Euclidean set describing the external surface, \( A \), enclosing the total volume, \( V \), and a "biological" set describing the internal structure, which includes the effective exchange area, \( a \), and the total volume of biologically active material, \( \nu \) (Table 1). Although it is clearly a very difficult technical problem to calculate \( a \), there are some general scaling properties that it must obey regardless of the detailed dynamics. Before examining these, it is instructive to consider the simpler case of how the area of skin, or external physical surface, of an organism, \( A \), scales.

We first show formally how, and under what conditions, the classic 2/3-power Euclidean scaling law for \( A \) arises [3]. In general, \( A \) is some complicated function of the various length scales, \( L_1, L_2, L_3, \ldots \), which parametrizes size and shape: \( A = A(L_1, L_2, L_3, \ldots ) \). Now, on purely dimensional grounds this can be expressed as: \( A(L_1, L_2, L_3, \ldots ) = L_1^2 \Phi(L_2/L_1, L_3/L_1, \ldots ) \), where \( \Phi \) is a dimensionless function of the dimensionless ratios \( L_2/L_1, L_3/L_1, \ldots \). Suppose that we change the overall size by making a uniform scale transformation on all the lengths, \( L_i \): \( L_i \rightarrow L'_i = \Lambda L_i \), \( i = 1, 2, 3, \ldots \), where \( \Lambda \) is some arbitrary number. This similarity transformation preserves the shape of the object as its size varies. In this case \( \Phi \) clearly does not change so \( A \) responds in the following fashion:

\[
A \rightarrow A' \equiv A(\Lambda L_1, \Lambda L_2, \Lambda L_3, \ldots ) = \Lambda^2 A(L_1, L_2, L_3, \ldots ) \tag{1}
\]
The Euclidean volume of the object, \( V = V(L_1, L_2, L_3, \ldots) \), can be treated similarly: on dimensional grounds, \( V = L_1^2 \Psi(L_2/L_1, L_3/L_1, \ldots) \), where \( \Psi \) is a dimensionless function of the dimensionless ratios \( L_2/L_1, L_3/L_1, \) etc. After the scale transformation, which leaves \( \Psi \) unchanged,

\[
V \rightarrow V' = V(AL_1, AL_2, AL_3, \ldots) = \Lambda^3 V(L_1, L_2, L_3, \ldots)
\]

From Eqs. (1) and (2) it is clear that \( A'/V'^{2/3} = A/V^{2/3} \), that is, \( A \propto V^{2/3} \); similarly \( L \propto V^{1/3} \). Notice that these are consistent with writing \( V = AL \), where \( L \) is some length which is a function of the \( L_i \) and scales as \( L \rightarrow L' = AL \). Assuming a size-invariant uniform density, these then give the conventional Euclidean geometric scaling results \( L \propto L_i \propto M^{1/3} \) and \( A \propto M^{2/3} \). These should apply, for example, to the limbs and skin of vertebrates.

The above argument ignores two basic facts of biology. First, the metabolic process relies on the hierarchical fractal-like nature of resource distribution networks. Examples include the macroscopic branching vascular networks of plants and animals and the complicated ultra-structure within cells. We emphasize that the network can be “virtual”; it need not be a physical system of branching tubes, so long as it exhibits hierarchical pathways of material flow. Second: although organisms vary widely in size, these networks terminate at invariant units of fixed size which can be characterized by a biological length scale, \( l_0 \). At the whole-organism level they include capillaries of mammals and leaves of plants. At the cellular and molecular levels, they include mitochondria and chloroplasts, and the metabolic rate-limiting cytochrome oxidase and rubisco molecules within these organelles. We now modify the above scaling argument by incorporating these two important biological features.

For a given type of organism the effective surface area is a function of the invariant length, \( l_0 \), together with various independent length scales, \( l_i \), that parameterize its fractal-like structure. It is important to distinguish biological length scales, \( l_0 \), which characterize the interior networks of the organism, from Euclidean ones, \( L_i \), which characterize its exterior shape. For example, in a mammal one of the \( l_i \) is the length of the aorta, whereas one of the \( L_i \) is its overall body length; similarly, in unicellular organisms one of the \( l_i \) is the distance between mitochondria, whereas one of the \( L_i \) is the cell radius. Working as before, the effective exchange area, \( a \), can be expressed as
where \( \phi \) is a dimensionless function of the dimensionless ratios \( l_2/l_1 \), etc. Now, as the size of the organism changes, \( l_0 \) remains fixed. Consider, then, an arbitrary scale transformation on the network: \( l_i \rightarrow l'_{i} = \lambda l_i \) \( (i = 1, 2, 3, \ldots) \) keeping \( l_0 \) fixed. The analog of Eq. (1) reads

\[
\alpha(l_0, l_1, l_2, \ldots) = \lambda l_0^2 \phi\left(\frac{l_0}{l_1}, \frac{l_0}{l_2}, \frac{l_0}{l_3}, \ldots\right) \tag{3}
\]

Because \( l_0 \) is fixed, the right-hand-side is no longer simply proportional to \( \lambda^2 \) as in Eq. (1). Although we do not know the \( \lambda \)-dependence of \( \phi \), we can parametrize it as a power law reflecting the hierarchical fractal-like organization:

\[
\phi\left(\frac{l_0}{l_1}, \frac{l_0}{l_2}, \frac{l_0}{l_3}, \ldots\right) = \lambda^{\alpha} \phi\left(\frac{l_0}{l_1}, \frac{l_0}{l_2}, \frac{l_0}{l_3}, \ldots\right) \tag{5}
\]

where \( \alpha \) is an "arbitrary" exponent. In this case

\[
\alpha \rightarrow \alpha' = \alpha\left(l_0, l_1, l_2, l_3, \ldots\right) = \lambda^{2+\alpha} \alpha(l_0, l_1, l_2, l_3, \ldots) \tag{6}
\]

Regardless of the power law assumption, the crucial point here is that \( \alpha \) does not scale simply as \( \lambda^2 \) because of the presence of \( l_0 \). The power law does not require the existence of an idealized mathematical self-similar fractal with no "fundamental" length scale such as \( l_0 \). Even though the actual physical structure is not a pure fractal because it has terminal units of fixed size and can be asymmetric, it is still natural to use the fractal language. We can therefore interpret the exponent in Eq. (6), \( (2 + \epsilon_\alpha) \equiv \delta_\alpha \), as the fractal dimension of \( \alpha \) [4]. As such, it satisfies \( 0 \leq \delta_\alpha \leq 1 \). The lower limit, \( \epsilon_\alpha = 0 \), is the conventional Euclidean case discussed above; the upper limit, \( \epsilon_\alpha = 1 \), represents the "maximum fractality" of a volume-filling structure in which the effective area scales like a conventional volume.

The biological volume, \( \nu \), associated with \( \alpha \), can be similarly expressed as \( \nu(l_0, l_1, l_2, l_3, \ldots) = \nu(l_0/l_1, l_0/l_2, l_0/l_3, \ldots) \), where \( \psi \) is a dimensionless function of the dimensionless ratios \( l_2/l_1 \), etc. This represents the total volume of protoplasm and other biologically active material in the organism. It is not necessarily identical to \( V \), since most organisms contain empty spaces enclosed by the skin; however, \( \nu \propto V \). By analogy with \( \phi \), we assume that,
under a scale transformation, $\psi$ transforms as a power with an exponent $\epsilon_v$:

$$\psi(l_0, l_1, l_2, l_3, \ldots) = \lambda^{\epsilon_v} \psi(l_1, l_2, l_3, \ldots)$$

Consequently, $v$ scales as

$$v \rightarrow v' \equiv v(l_0, l_1, l_2, l_3, \ldots) = \lambda^{\epsilon_v} v(l_1, l_2, l_3, \ldots)$$

with $0 \leq \epsilon_v \leq 1$. Combining Eqs. (6) and (7) straightforwardly leads to

$$a \propto \psi^{(2+\epsilon_v)/(3+\epsilon_v)}.$$

Now $v$ can always be expressed as $v = al$, where $l$ is some length characteristic of the internal structure of the organism. We can therefore relate the scaling behaviour of $v$ to that of $a$ and $l$, with $l$ expected to be proportional to one of the $l_i$. It is instructive, however, to consider the more general case and write $l = l(l_0, l_1, l_2, \ldots) = \sigma l_0^{1/\epsilon_v} l_1^{1/(1+\epsilon_v)} l_2^{1/(2+\epsilon_v)} \ldots$, as was done with $a$ and $v$; $\sigma$ is a dimensionless function, analogous to $\phi$ and $\psi$. This scales as $l \rightarrow l' = \lambda^{1+\epsilon_l} l$, where $d_\ell = 1+\epsilon_l$ is the fractal dimension of $l$, with $0 \leq \epsilon_l \leq 1$. Consequently, $v \rightarrow v' = \lambda^{2+\epsilon_v+\epsilon_l} v$ which, when compared to Eq. (7), gives

$$\epsilon_v = \epsilon_a + \epsilon_l \quad [4].$$

Assuming a uniform constant density, so that $v \propto M$, then gives

$$a \propto v^{\frac{2+\epsilon_v}{3+\epsilon_v}} \propto M^{\frac{2+\epsilon_v}{3+\epsilon_v}}.$$

Our conjecture that organisms have evolved so as to maximize the scaling of $a$ implies that the exponent, $b \equiv (2+\epsilon_v)/(3+\epsilon_v+\epsilon_l)$, must be maximized. It is straightforward to verify that this occurs when $\epsilon_v = 1$ and $\epsilon_l = 0$, thereby giving $b = 3/4$. Metabolic rate must therefore scale as $B \propto M^{3/4}$, regardless of the details of the branching architecture [6] and dynamics governing the metabolic process and distribution of resources.

There are several important consequences which follow from this. First, since $a \propto M^{3/4}$, the number of invariant units in the network also scales as $M^{3/4}$. Second, the result $\epsilon_l = 0$, which gives $d_\ell = 1$, implies that internal distances associated with the network are not themselves fractal. This is consistent with the constraint that times for supply of resources, and therefore path lengths, should be minimized. Third, and perhaps the most significant consequence of the derivation, is that $\epsilon_a = 1$, which implies that the fractal dimension of $a$ is $d_a = 3$, rather than the canonical Euclidean value of 2. Thus, the effective surface area is "maximally fractal" and the network architecture volume-filling. It is in this sense that organisms have exploited a fourth spatial dimension [5] by evolving hierarchical fractal-like structures to maximize resource acquisition and allocation. More specifically: the area of
the effective exchange surface scales as if it were a volume: \( a \to a' = \lambda^3 a \), (rather than \( \lambda^2 a \)) whereas characteristic internal lengths associated with the fractal-like structure scale as \( l \to l' = \lambda l \). Consequently, the biological volume scales as \( v \to v' = \lambda^3 v \), so, in addition to \( a \propto M^{D/4} \), we also have \( l \propto M^{1/D} \). These relationships should apply to all organisms which have been selected to maximize metabolic power under the constraint of minimizing internal transport distances and thereby having a maximally compact 3-dimensional body shape; (Table 2). For organisms such as roundworms and flatworms, which may be functionally 1- or 2-dimensional, these geometric relationships can be appropriately modified. In \( D \)-dimensions, for example, our argument straightforwardly generalizes to give \( a \propto B \propto M^{D/(D+1)} \) and \( l \propto M^{1/(D+1)} \) for the biological variables, and \( A \propto M^{(D-2)/D} \) and \( L \propto M^{1/D} \) for the Euclidean ones. These relationships are not expected to apply to a few organisms, such as filamentous algae and fungi, which have been selected to maximize linear dimensions so as to sparsely occupy a maximal volume.

The present derivation is more general than our original model in which it was assumed that resource distribution networks are volume-filling and energy dissipated minimized. Dynamics played a central role leading to a complete detailed description of the networks which were shown to be fractal-like with 1/4-power allometric scaling[2, 7]. These physically explicit models should therefore be viewed as manifest examples which show how the more universal geometric argument given here is realized in specific network systems. Consequently it is no accident, for example, that vastly different biological networks exhibit area-preserving branching, a key result arising from very different dynamical considerations in each of these systems [2, 7]. Unlike the genetic code, which has evolved only once in the history of life, fractal-like distribution networks and a subsequent additional effective fourth dimension have developed many times. Examples include the extensive surface area of leaves, gills, lungs, guts, kidneys, chloroplasts and mitochondria, the whole-organism branching architectures of trees, sponges, hydroids, and crinoids, and the tree-like networks of diverse respiratory and circulatory systems. It is not surprising therefore that even unicellular organisms exhibit 1/4-power scaling and, in particular, the 3/4-power scaling law for metabolic rate. Although all of life is embedded in a 3-dimensional space, its internal physiology, anatomy, and architecture operate as if it were 4-dimensional.

Quarter-power scaling laws are perhaps as uniquely biological and as universal as the biochemical pathways of metabolism, the structure and function
of the genetic code, and the process of natural selection. The vast majority of organisms exhibit scaling exponents very close to $3/4$ for metabolic rate and to $1/4$ for internal times and distances. These are the maximal and minimal values, respectively, for the effective surface area and linear dimensions for a volume-filling fractal-like network. On the one hand, this is testimony to the power of natural selection, which has exploited variations on this fractal theme to produce the incredible variety of biological form and function, including the 21 orders of magnitude variation in body size. On the other hand, it is testimony to the severe geometric and physical constraints on metabolic processes, which have dictated that all of these organisms obey a common set of scaling laws. Quarter-power scaling is so universal in biology because fractal geometry has literally given life an added dimension.

References


[5] In particular, this shows that the derivation for mammalian and plant systems presented in ref. [2] does not depend on details of the network such as symmetric branching. This was confirmed numerically by D. L. Turcotte, J. D. Pelletier, and W. I. Newman, *J. Theor. Biol.*, 193, 577 (1998).
[6] Some time ago, Blum noted that, in four Euclidean dimensions, the surface area of a sphere would scale as the 3/4-power of its four-dimensional volume, and that this might in some way be related to the 3/4 exponents in Kleiber’s law. Hainsworth subsequently proposed that this extra dimension be identified with time. Neither of these authors, however, gave any argument to support their conjectures. J. J. Blum, *J. Theor. Biol.*, 64, 599 (1977); F. R. Hainsworth, *Animal Physiology; Adaptions in Function*, (Addison-Wesley, Reading, MA), p. 170.


[8] JHB was supported by NSF Grant DEB-9318906, BJE by NSF Grant GER-9553623 and a Fulbright Fellowship, and GBW by the Department of Energy. We also acknowledge the generous support of the Thaw Charitable Trust.
Table 1: Examples of the biological network variables \( t \), \( a \), and \( v \) in plant, mammalian and unicellular systems.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>PLANT</th>
<th>MAMMAL</th>
<th>UNICELLULAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>( t )</td>
<td>Mean path length from root to leaf, or between leaves</td>
<td>Mean circulation distance from heart to capillary, or between capillaries</td>
<td>Mean distance from cell surface to mitochondrial and between mitochondria</td>
</tr>
<tr>
<td>( a )</td>
<td>Total area of leaves; area of absorptive root surface</td>
<td>Total area of capillaries; gut surface area</td>
<td>Actual cell surface area; total surface area of mitochondrial inner membranes</td>
</tr>
<tr>
<td>( v )</td>
<td>Total wood volume; total cell volume</td>
<td>Total blood volume; total tissue, or cell, volume</td>
<td>Volume of cytoplasm</td>
</tr>
</tbody>
</table>

Table 2: The scaling of length, area and volume associated with biological networks compared to the conventional Euclidean case.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>CONVENTIONAL EUCLIDEAN</th>
<th>FRACTAL LOGICAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>LENGTH</td>
<td>( L \propto A^{1/3} \propto V^{1/3} \propto M^{1/3} )</td>
<td>( t \propto a^{1/3} \propto v^{1/3} \propto M^{1/3} )</td>
</tr>
<tr>
<td>AREA</td>
<td>( A \propto L^{2} \propto V^{2/3} \propto M^{2/3} )</td>
<td>( a \propto L^{2} \propto V^{2/3} \propto M^{2/3} )</td>
</tr>
<tr>
<td>VOLUME</td>
<td>( V \propto L^{3} \propto M )</td>
<td>( v \propto L^{3} \propto M )</td>
</tr>
</tbody>
</table>