Complex Fractal Dimension of the Bronchial Tree

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The architecture of the mammalian lung has been shown to be correctly described using a fractal model with a complex dimension, related to a Cantor set with random errors, for four different species. Here we provide an interpretation of that model that has implications for biological evolution. We argue that fractals are more error tolerant than other structures and therefore have an evolutionary advantage.

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Recent work has implemented the ideas of fractal geometry and renormalization-group theory to study the architecture of physiological forms [1–4]. The descriptive success of these investigations suggests that there is an evolutionary advantage to branching systems having a fractal dimension [5]. Here we focus attention on how the size of the airways in the mammalian lung [6] changes as one proceeds down the bronchial tree. The fractal model overcomes limitations of classical analysis [1].

The morphology of the bronchial airway of the mammalian lung has fascinated physiologists for well over a century. Until recently the architecture of the lung has been understood in terms of the quantitative symmetric scaling model of Wiebel [6]. The investigation of Wiebel and Gomez [6] demonstrated the existence of fundamental relations between the size and number of lung structures. They considered the conductive airways to be a dichotomous branching process, so that if z denotes the "generation" and $n(z)$ the number of branches in the zth generation, then $n(z)=2n(z-1)$. This functional equation has the solution $n(z)=2^z$, since there is only a single conduit at the $z=0$ generation (trachea). A similar argument based on the conservation of air volume between successive generations leads to the expression for the average diameter of the bronchial airway $d(z)=e^{-\alpha z}d_0$, where d_0 is the diameter of the trachea, $\alpha=\frac{1}{3}\ln 2$, and we have used the scaling relation $d(z)=2^{-1/3}d(z-1)$ [6].

The above symmetric model of the mammalian lung is consistent with the mathematical view of a self-similar branching process. Consider, for example, the Cantor set depicted in Fig. 2.2.1 in Ref. [5]. In this example we consider a line of unit length in generation $z=0$ (cf. Fig. 2.2.1). In the first generation ($z=1$) we remove the middle third from the line segment. In the second generation ($z=2$) we remove the middle third from each of the two remaining line segments. This procedure is repeated until at generation z the length of any one line segment is given by $L(z)=1/3^z$. Equivalently, the length of a single line segment can be written in the exponential form [7]

$$L(z)=e^{-z\ln 3}, \tag{1}$$

just as was found for the average diameter of the bronchial tube.

There are a number of properties of the mammalian lung which do not satisfy the symmetric branching model. The first is that the predicted exponential decrease in the average diameter of an airway is not supported by the data beyond $z=10$, after which there is a marked deviation as shown in Fig. 3A of Ref. [1]. The second is the asymmetry observed in the branchings of the bronchial tree. West, Bhargava, and Goldberger [1] have attempted to take these properties into account by using the concept of a fractal, i.e., by assuming the lung to be a scale-free branching process described by a renormalization-group relation. In Fig. 1 we see that the fractal model does an excellent job of capturing the features of the average diameter:

$$D(z)=A(z)/z^{\mu}, \tag{2}$$

where $A(z)$ is a harmonic function in the logarithm of the generation index z and $\mu>0$ yields a dominant inverse power-law behavior. This functional behavior, mathematically valid for large z, is observed for four

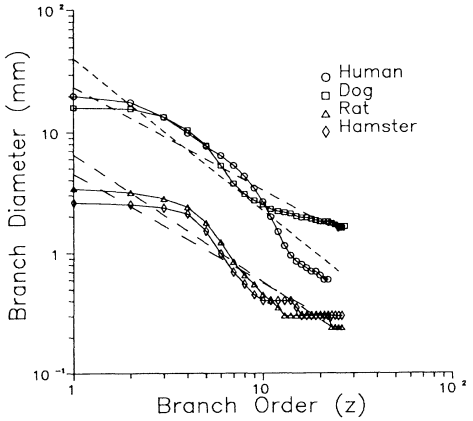

FIG. 1. The data from Raabe *et al.* [8] for the average diameter of the mammalian lung for four distinct species is compared with the predictions of the fractal model of the lung [5]. The symbols are the data points and the solid curve the results of the fractal model (taken from Ref. [5]).

separate species, human, dog, rat, and hamster, for apparently all z and therefore may well be a general property of mammalian lungs.

The question we address now is how to infer the geometry of the lung from the algebraic law of Eq. (2). We argue that, surprisingly, only slight random modifications in the Cantor-set picture are needed to yield a branching process consistent with the exponential law for early branching and the algebraic law for later branching.

One might suspect that nearly symmetric branching could explain the crossover between Eqs. (1) and (2). If the branching segment split into two nearly equal diameters of p and $q=p+\epsilon$ with ϵ small, then the asymmetry would not be noticed until several generations of branchings, and Eq. (1) would appear to be satisfied. This two-scale multifractal Cantor scheme would yield $z+1$ different size (p and q) diameters in the zth generation in contrast to the single size diameter in the one-scale Cantor-set picture. As appealing as this sounds, once average diameters are calculated the exponential law remains for all generations. Explicitly, after one generation the average length is $L(1)=\frac{1}{2}(p+q)$, after two generations $L(2)=\frac{1}{4}p^2+\frac{1}{2}pq+\frac{1}{4}q^2$, and so on. At the zth generation the average length of a line segment is

$$L(z)=(1/2^z)(p+q)^z=e^{-z/z_0}, \tag{3}$$

where $z_0^{-1}=|\ln[(p+q)/2]|$. Thus if $p=q=\frac{1}{3}$, then (3) reduces to the previous result (1) for the symmetric tetradic Cantor set. For $p\neq q$, however, the zth iteration of this process looks quite different in that it is significantly more irregular than the tetradic Cantor set, even though the average length (diameter) follows the same exponential law.

As we mentioned, the exponential scaling fits the bronchial data for the first ten generations, but fails completely afterwards. It is possible to introduce a saturated exponential, which for certain parameter values will "appear" as an inverse power law modulated by a single oscillation over the range of z values. However, such a model has not been developed seriously and applied to the data. We argue that the proper fit to the data is an algebraic law with logarithmic oscillations [1]. Thus the observed average diameter at a given generation for $z\geq 10$ is larger than would be expected from the Wiebel-Gomez law.

To systematically account for the new scale sizes in the bronchial tree let us assume that we can write the exponential scaling law as $d(z)=q_0 d(z-1)$, where q_0 is the appropriate constant. Now we extend this model by assuming that a new scaling parameter q_1 occurs at each branch node with a probability p and the branching ratio remains the same with probability $1-p$. If there are two scales q_0 and q_1 permitted, then in generation z,

$$D(z)=(1-p)^z q_0^z+p\sum_{m=1}^{z-1} q_0^{z-m}q_1^m(1-p)^{z-1}. \tag{4}$$

The first term in (4) accounts for no change in the branching ratio q_0 in z generations. The second term has the first $z-m$ generations with the branching ratio q_0 followed by m generations with the branching ratio q_1. Thus the total contribution to the average diameter is the sum over all these possible intermediate states weighted by the appropriate probabilities. We introduce the parameter $f=q_0/q_1<1$ and assume $p\ll 1$ so that the first change to a larger diameter occurs at large z and we can rewrite (4) as

$$D(z)=d(z)+\gamma d(z/N)+\cdots. \tag{5}$$

The parameters γ and N in (5) are those introduced by West, Bhargava, and Goldberger and are given by $\gamma=pf_1/(1-p)(1-f_1)$ and $N=1+\ln f_1/\ln[q_0(1-p)]$ in terms of the new parameters. It is possible to show by the introduction of additional scales $q_2,q_3,\ldots$ that the higher-order terms in γ and N in (5) impose the relations

$$\frac{\ln f_{n-1}}{\ln(1-p)q_{n-1}}=\frac{\ln f_n}{\ln(1-p)q_n},$$

where $f_n=q_{n-1}/q_n$, $n=0,1,\ldots,z$, so that (5) can be written as the infinite-order series expansion of the renormalized-group relation

$$D(z)=\gamma D(z/N)+d(z)=\sum_{j=0}^{\infty}\gamma^j d(z/N^j), \tag{6}$$

where, in general, γ and N restrict the allowed scales $\{q_i\}$.

This scaling law produces an average diameter of the form (2) with $\mu=-\ln\gamma/\ln N$ and $A(z)$ periodic in $\ln z$ with period $\ln N$. The solution to the renormalization-group relation given by (2) is only valid mathematically for large z as discussed by West, Bhargava, and Goldberger [1]. Thus we would have expected that (2) is a faithful description of the lung asymptotically and not for small z. A good fit to the data from the four mammalian species mentioned is $A(z)=A_0+A_1\cos(2\pi\ln z/\ln N)$ [cf. (2)]. From the quality of the fit to the data it appears that for z beyond the fifth or sixth generation we are in the asymptotic regime. The question remains: "What branching structure is implied by the scaling equation (4)?"

In order for the series (5) to converge we must have $\gamma<1$. We have found that μ can be both greater than or less than unity depending on the species [9]. From the data depicted in Fig. 1 we obtain $\mu=0.86$ and 0.90 for the dog and hamster, respectively [9], from the slopes of the average diameter curves and $N\approx 9$ as the period of oscillation in $A(z)$ [1]. In a similar way we obtain $\mu=1.26$ and 1.05 for the human and rat [9], respectively, with $N\approx 11$ [1]. These parameters yield $\gamma_{\text{human}}\approx 0.05$, $\gamma_{\text{rat}}\approx 0.08$, $\gamma_{\text{dog}}\approx 0.15$, and $\gamma_{\text{hamster}}\approx 0.12$, which are overestimates based on the complete data sets as are the values for N. A smaller and perhaps more realistic value of N would be obtained by ignoring the first few data

points (low z) in estimating it. We do not do that here.

If we select the scale q_0 to have the optimal value [6] $1/2^{1/3}=0.7937$, we find from the above data that $q_1 \approx 1.0$ for all four species to within 1% and therefore $f \approx 0.80$. This implies that the typical increase in scale size is about 25% when it occurs. The parameter with the greatest variability across species is the probability of such an event occurring:

$$p_{\text{human}} \cong 0.012\,, \quad p_{\text{rat}} \cong 0.02\,,$$

$$p_{\text{dog}} \cong 0.04\,, \quad p_{\text{hamster}} \cong 0.031\,,$$

in which we see a variation of a factor of nearly 4 between humans and dogs. Note that the p's are the probability of having a scale change $q_0 \rightarrow q_1$ at each branch point; that is the reason they exceed the γ's which denote the probability that the average diameter possesses a certain overall scale larger than q_0. Note that these numbers are estimates based on the assumption that the asymptotic form for the average diameter at each generation of the bronchial tree is appropriate. We note that the solution to the scaling equation that provides the best fit of the data can be written as the real part of $1/z^{\beta}$, where β is a complex number given by $\beta=\mu+i2\pi/\ln N$. We refer to the parameter β as the complex fractal dimension for the branching process.

A rationale for why nature chooses the above fractal ordering rather than the classical scaling may be presented in terms of the added tolerance of the former to error (variability) in the bronchial tree over that of the latter. If we assume that the scale z_0 in (3) has a random component such that $1/z_0=1/\bar{z}_0+\zeta$, where ζ is a zero-centered Gaussian random variable of width σ^2 and $\bar{z}_0$ is a constant, then the average error in the classical diameter propagates as $\epsilon_c(z)=\exp[\sigma^2(\ln z)^2/2]$, where σ is the mean-square level of the error fluctuations. If in a similar way we assume that the index μ in the fractal model has a random component such that $\mu=\bar{\mu}+\zeta$, where ζ is again a zero-centered Gaussian variable of width σ^2 and $\bar{\mu}$ is a constant, then the average error in the fractal diameter propagates as $\epsilon_F(z)=\exp[\sigma^2(\ln z)^2/2]$. Thus we can determine the relative sensitivity of the two models to errors. For example, if $\sigma^2=0.02$, we have a relative average error ϵ_c/ϵ_F of 2.6 between the classical and fractal models at $z=10$ and one of 8.82 at $z=15$. Even at the extreme value of $z=20$ the fractal model has an average error of 1.09, whereas the classical model has one of 54.6, indicating how insensitive the fractal model is to fluctuations. These results imply that in a large population of lungs satisfying classical scaling with errors the average diameter could differ from the exponential result by an order of magnitude beyond the fifteenth generation. An organism with this sensitivity to error would not survive over many generations of the species.

We tentatively conclude from this simple argument that the fractal architecture is significantly more error tolerant than the classical one. This implies that there is an evolutionary advantage to the fractal structure [5] suggesting an explanation for its apparent ubiquity in physiology.

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