

**A SIMPLE GEOMETRICAL PATTERN FOR THE BRANCHING
DISTRIBUTION OF THE BRONCHIAL TREE, USEFUL TO ESTIMATE
OPTIMALITY DEPARTURES**

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ABSTRACT

The design of the bronchial tree has been largely proposed as a model of optimal design from a physical-functional perspective. However, the distributive function of the airway may be more related with a geometrical than a physical problem. The bronchial tree must distribute a three dimensional volume of inspired air on a two dimensional alveolar surface, included in an limited volume. In this way, it is valid to ask whether an optimal bronchial tree from a physical perspective, is also optimum from a geometrical point of view.

In this paper we generate a simple geometric model for the branching pattern of the bronchial tree, deducing relationships that permit to estimate the departures from the geometrical optimum of each bifurcation. We also, for comparative purpose, estimate the departures from the physical optimum. From the geometrical assumptions: i) a symmetrical dichotomic fractal design, ii) with minimum volume and iii) maximum dispersion of the terminal points, and several simulations we suggest that the optimality is characterized by a bifurcation angle $\theta \approx 60^\circ$ and a length reduction scale $\gamma = (1/2)^{1/3} = 0.7937$. We propose distances from the physical and geometrical optimality defined as Euclidean distances from the expected optima. We show how the advanced relationships and the distances can be used to estimate departures from the optimality in bronchographs of four species. We found, lower physical and geometrical departures in the distal zone than those of the proximal zones. We also found lower physical than geometrical departures from the optimality.

1. INTRODUCTION

Animal species show a great diversity in their structural design as a consequence of their adaptation to different life conditions. But, is this structural design optimized in any sense? Answer to this question is actually controversial and object of a great debate (Duddley and Gans 1991, Garland 1998, Weibel, et al. 1998, Bacigalupe and Bozinovic 2002). One example of economical design is the fine structure of bones, qualitative and quantitatively adjusted to the mechanical strengths that it supports (Weibel et al. 1998, Dullemeijer 1998). Another example is the variation of the arterial branching, minimizing the blood mass, the energy of transport and the flow resistance (Zamir 1976, 1978, 1986, Zamir and Bigelow 1984, Weibel et al. 1998).

One hypothesis that includes the economical design is the symmorphosis. That, in its essential aspect suggests that whether the matching structure-design (regulated morphogenesis) is combined with the strict economy of mass and energy, then this implies that the design of biological structures must tend to be optimized for the specific function they serve (Weibel et al. 1991a, 1991b). However, this proposition raises considerable criticism (Alexander 1995, 1998, Gordon 1998, Garland 1998). From a functional perspective, there are several optimization criteria which could account for the design, for example, maximal functional capacity, minimum costs of mass and energy, minimum entropy production, maximum space filling, etc. Moreover, these criteria could conduct to different optimal designs, where the privilege in one aspect could determine trade off in the others.

The airway, including the respiratory bronchiole and the alveoli, has two basic functions: i) a distributive function whereby the system reaches out physically every

part of the alveolar surface contained in a limited volume, and ii) a gas exchange function whereby the system brings down the velocity of the air flow to a level sufficiently low to permit gas exchange. The design of the bronchial tree has been largely proposed as a model of optimal design from a physical-functional perspective, and associated to an adequate air flow to the alveoli (Rhorer 1915), minimum work (Murray 1926), minimum entropy production (Weibel and Gomez, 1962; Wilson, 1967) and minimum costs of mass and energy (Weibel et al., 1991a, 1991b, 1998).

However, the distributive function of the airway could be more related with a geometrical than a physical problem. The bronchial tree must distribute a three dimensional volume of inspired air on a two dimensional alveolar surface, included in a limited volume (Mc Namee 1991). In this way is valid to ask whether an optimal bronchial tree from a physical perspective is also optimum from a geometrical point of view. Moreover, if the geometrical and physical optimal design were different, animals living in different environmental conditions could privilege one or other optimal design, depending on the life style requirements.

Several authors have studied the bronchial tree and other pulmonary structures showing their fractal geometry (Rigaut 1984, Mandelbrot 1982, Glenny and Robertson 1990, Horsfield 1990, Nelson et al. 1990, Canals et al. 1998, 2000). West et al. (1986) showed a decrease of the airway diameter modulated by a function that introduces harmonic fluctuations in the scale of diameter decrease, different to the exponential decrease (one scale) expected from minimum entropy criteria. This model predicts adequately the airway diameter over twenty generations in man, dogs, rats and hamsters (West et al. 1986, Nelson et al. 1990). However Horsfield (1990) shows that the result of West et al. (1986) could be by one way a consequence of the asymmetry of the

bronchial tree (see also Canals et al. 2002a) and by other way a consequence of the numerical order (generations) used by West et al.(1986).

Recent results from the physical optimality of the airway of rabbits, studied with Zamir's model (Zamir 1978, Zamir and Bigelow 1984), suggest a gradual approach to the physical optimum from proximal to distal regions (decreasing diameters). These results can be explained by a transition from a central distributive zone, to a physical domain along the generations of the airway (Canals et al. 2002b). The proximal branching process could be dominated by higher flow velocities with turbulent or transitional flow and the necessity to increase the branches to fill a space (geometrical problem). In the distal zone, the dominant principles gradually change from a volume and pumping power problem in the conductive zone, to a drag and surface problem in the respiratory zone, where diffusion is relevant.

Then, to explore the optimality of the airway is at least necessary to consider the geometrical and physical perspective. This is possible generating structural models of the branching ductal systems useful for studying the correlation between structure and function (Horsfield et al. 1971, Kitaoka et al. 1999).

In this paper we generate a simple and exclusively geometric pattern for the branching distribution of the bronchial tree, deducing useful relationships that permit to estimate the departures from the geometrical optimum of each bifurcation. We also, for comparative purpose, estimate the departures from a physical optimum. We use X-ray images of the bronchial tree of two individuals of four species to show how the pattern can be used.

2. THEORETICAL ANALYSIS

We consider a bronchial tree as having an standard geometry if it satisfies simultaneously the following three conditions:

- i) it is a symmetric fractal dichotomic tree,
- ii) it fills a volume as small as possible (minimum enveloping volume), and
- iii) it distributes their terminal points (or branches) filling uniformly the space (minimum aggregation or maximal dispersion).

As in several conduction systems, we expect a dichotomic fractal like design in the bronchial tree. We impose the symmetry condition because although most of the mammal airway show a considerable and variable asymmetry, we need the symmetry as a reference fix point, for comparative purposes. The asymmetry is variable among different bifurcation, individuals and species, so we did not impose a priori anything particular degree of asymmetry to our geometric standard.

The second condition incorporates explicitly the space constraint, and the third condition, the distributive function of the airway.

2.1 ANALYTICAL APPROACH

Dichotomic fractal tree

Considering previous reasoning from Mandelbrot (1982) and West et al. (1997), we consider a parent branch of a “k” generation with a length l_k originating two daughter branches with length l_{k+1} (dichotomy) but scaled by a constant factor γ :

$$l_{k+1} = l_k \cdot \gamma \quad [1]$$

Until the generation k, a dichotomic tree has $N_k = 2^k$ terminal branches (k =0 represents the trachea). If each terminal branch were continued by one alveolar sac, a

sphere of “u” radius, the total alveolar volume until this generation, V_k , can be expressed as:

$$V_k = 4/3 \cdot \pi \cdot u^3 \cdot N_k \quad [2]$$

For larger number of branches, this estimate does not depend significantly on k, then this fractal structure can be characterized by the preservation of the volume from one generation to the next:

$$V_{k+1} = V_k \quad [3].$$

Considering $u = c \cdot l_k$ with c as a constant, and replacing this expression in eq. (3), a constant ratio, “ γ ”, between the length of the daughters and the parental bronchi is obtained:

$$l_{k+1}/l_k = (1/2)^{1/3} = \gamma = 0.7937 \quad [4].$$

Minimum Circumscribed Volume.

Considering a dichotomic fractal tree, we can see that the end points are crowded whether the bifurcation angle is small and dispersed whether the bifurcation angle is large. This is true, independent on the number of branches.

If we consider only one bifurcation (unitary bifurcation), it is easy to see that the area (A) of the triangle circumscribing the three terminal points is:

$$A = (l_k + \gamma \cdot l_k \cos \alpha) \cdot \gamma \cdot l_k \sin \alpha \quad [5]$$

This relationship, for $\gamma = (1/2)^{1/3}$ has a maximum value in $\alpha = 62.67^\circ$.

A fractal tree is composed by a set of scaled unitary bifurcations connected from one generation to another and rotated in a variable angle, generating a volumetric structure. Thus, the area of the triangle circumscribing the tips of the first bifurcation determines, in a plane, the total area of a fractal tree, but the volume is generated at

random by rotation of each bifurcation. Then, we expect that the total enveloping volume of the structure (V_e) follows a similar figure that an unitary bifurcation:

$$V_e = (1 + \gamma \cos \alpha) \gamma \sin \alpha \quad [6],$$

with a maximum value in the same angle.

Maximal dispersion.

The bronchial tree must distributes their terminal points (or branches) filling uniformly the space. This is associated to an adequate dispersion of their terminal points. From the observation that small angles conduct to low distances between two terminal points and crowding of the end points and large angles conduct to high distances and dispersion of the end points, we can propose that the distance is directly related to the dispersion.

On the other hand crowded distributions have higher variance-mean coefficients (V/M) and uniform (regular) distribution of points in the space is characterized by a minimum variance-mean coefficients (V/M) (see Kitaoka et al., 1999 for some similar reasoning). Then the variance-mean coefficient would decrease with the increasing end point distance.

Considering one side of the unitary bifurcation, the distance between two terminal points (dispersion) follows:

$$d = \gamma \sin \alpha, \quad [7]$$

and has a minimum value of 0 and maximum value of 1 (when $\alpha = 90^\circ$ and $\gamma = 1$), then with a appropriate re-scaling, we can expect that the variance mean coefficient varies from a relative maximum (1) to a relative minimum (0) following:

$$V/Me = (1 - \gamma \sin \alpha), \quad [8] \text{ (Fig. 1).}$$

Cost function

As each function has been defined in relative terms to the same maximum (=1), we can now define a cost function as $C(\alpha) = \max\{V_e, V/Me\}$. This function is minimized in the intersection of the curves V_e and V/Me at $\alpha = 27.79^\circ$ or $\theta = 2 \cdot 27.79 = 55.58^\circ$ (Fig. 1).

Then, from our simple analytical approach, we can expect a geometrical bifurcation pattern characterized by a scaling factor $\gamma = 0.7937$ and bifurcation angle $\theta = 2\alpha = 55.58^\circ$.

2.2 SIMULATION APPROACH

Model

We studied the effect of the bifurcation angle on both, the enveloping bronchial tree volume and the variance/mean coefficient. We made a simulation program in BASIC language. The program consisted in the generation of two branches (dichotomy) from each parental branch. The daughter branches were scaled by a factor $\gamma = 0.7937$ (fractal), following the previous analytical approach:

$$l(i+1) = \gamma \cdot l(i) \quad [9].$$

The branches originated from the junction describe an angle $\theta = 2\alpha$ (symmetry). The bifurcation plane (the plane formed by the two daughter branches) was rotated with a random angle δ characterized by an homogeneous distribution ranging between 0 and 180° , generating a three dimensional structure. Starting from a standardized initial

bronchi (“trachea”) of “ l_0 ” length, the generation law for the angles with the horizontal axis (φ) and for the two terminal points from the junction point was:

$$\varphi(i+1) = \varphi(i) \pm \alpha, (+ \text{ for the superior branch and } - \text{ for the inferior branch}) \quad [10]$$

$$x(i+1) = x(i) + l(i)\cos[\varphi(i+1)] \pm dx \quad [11]$$

$$y(i+1) = y(i) + l(i)\sin[\varphi(i+1)] \pm dy \quad [12]$$

$$z(i+1) = z(i) \pm l(i)\sin\alpha\sin\delta \quad [13],$$

where, dx and dy were the deviations in the x and y coordinates generated for the rotation of the bifurcation plane:

$$dx = l(i)\sin\alpha\cos\delta\sin[\varphi(i)] \quad [14]$$

$$dy = l(i)\sin\alpha\cos\delta\cos[\varphi(i)] \quad [15].$$

The program determinates the maximum values for the coordinates (x,y,z) calculating the volume of the cube enveloping the bronchial tree (simulated enveloping volume: V_s). Also, the program generates a 3-D grid of 8^3 cells, determining the variance/ mean coefficient of the number of terminal points in the cells (V/M_s). Twenty simulations were performed for each one, from 4 to 20 generations, varying α from 1 to 90 °.

Results

The simulations showed images whose resemblance with real bronchial trees depends on the bifurcation angle (Fig. 2). The terminal tips were crowded in a small volume for small angles, but were dispersed and unorganized in a great volume for great angles.

The enveloping volume of the bronchial tree followed a curve that fully adjust to the expected curve from the analytical approach (Fig. 3). We performed a quadratic regression analysis that yields

$$V_s = -0.197 + 0.035277 \alpha - 0.000274 \alpha^2 \quad (r = 0.99066, R^2 = 0.981).$$

As we expected to find, the V/Ms coefficient decrease as α increase (Fig. 3).

Considering $u = \sin \alpha$ we performed a linear regression that yields

$$V/Ms = 1.147 - 0.974 \sin \alpha \quad (F = 644.9, p < 0.01, r = 0.91, R^2 = 0.83),$$

similar to the expected, $V/Me = 1 - 0.79 \sin \alpha$, from the analytical approach.

The two curves intersected at $\alpha = 31.35^\circ$ (Fig. 3). This angle is slightly higher than the expected $\alpha = 27.79^\circ$. Therefore, we think that a good and useful estimation of the bifurcation angle is $\alpha \approx 30^\circ$ (or $\theta = 2\alpha \approx 60^\circ$).

3. MODEL APPLICATION

Material and methods

To study the usefulness and validity of the geometric model prediction we analyzed bronchographs of two individuals in four species: rabbit (*Oryctolagus cuniculus*), rodents (*Rattus norvegicus* and *Abrothrix olivaceus*) and the bat (*Tadarida brasiliensis*). Twelve generations of bronchi were contrasted. We analyzed six or seven junction points in each bronchograph, in which the diameter, length and bifurcation angle ($\theta = 2\alpha$) were easily visible. About three or four distal and proximal bifurcation were selected for the analysis. We considered a point as distal if the relative Horsfield order of the thinnest bifurcation branch was lower than three, and as proximal if its order was higher than four. The diameter, length and bifurcation angles of the parent and daughter branches of each bifurcation were measured in a digitalized image. The

length and diameter ratio (γ and γ_d) were estimated by dividing the average diameter and length of the daughter branches by that of the parent branch. Also, a diameter and length ratio (D_r and L_r) between the daughter branches were computed considering always the lower value in the numerator of the ratio (so D_r and $L_r \leq 1$).

From the geometrical perspective of our model we could expect to find $\theta \approx 60^\circ$ and $\gamma = 0.7937$. However, from a physical perspective, in a symmetric bifurcation with laminar flow a $\theta = 74.934^\circ$ ($= 2 \cdot 37.4673$) and a $\gamma_d = 0.7937$ can be expected on basis of a minimum energy loss and minimum volume and pumping power principles (Kamiya et al., 1974; Zamir, 1978; Zamir and Bigelow, 1984).

Considering these, we can build estimators of the physical and geometrical distances to the expected optima for each bifurcation in the following way: i) we define a coordinate Z as

$$Z = D_r \quad [16]$$

for a physical domain and

$$Z = L_r \quad [17]$$

for a geometrical domain (D_r and L_r estimating the symmetry of the bifurcation), and

ii) we defined two coordinates X and Y as

$$X = \sin (\theta/2) \quad \text{and} \quad Y = \gamma_d \quad [18]$$

for a physical domain;

$$X = \sin (\theta/2) \quad \text{and} \quad Y = \gamma \quad [19]$$

for a geometrical domain.

We note that X , Y and $Z \leq 1$.

Then from our geometrical model we can expect an optimum point $(X_o, Y_o, Z_o) = (\sin 30^\circ, 0.7937, 1) = (0.5, 0.7937, 1)$ and from the physical perspective an optimum point $(X_o, Y_o, Z_o) = (\sin 37.467^\circ, 0.7937, 1) = (0.6083, 0.7937, 1)$.

We define $dX = X - X_o$, $dY = Y - Y_o$ and $dZ = Z - Z_o$ and the geometrical (G_d) and physical distances (P_d) as Euclidean distances in each domain: $\sqrt{[(dX)^2 + (dY)^2 + (dZ)^2]}$.

Results

When analyzed as a hole, the length ratio ($\gamma = 0.757 \pm 0.037$) and diameter ratio ($\gamma_d = 0.778 \pm 0.014$) were not different from the expected value ($= 0.7937$) ($p > 0.05$ in a t-Student test), but the bifurcation angle ($\theta = 66.54 \pm 3.05^\circ$) is just between the geometrical optimum ($\theta = 60^\circ$) and the physical optimum ($\theta = 74.934^\circ$) ($t_{47} = 2.03$ and $t_{47} = -2.60$, $p > 0.05$). A more fine analysis (factorial ANOVA) showed that there were not effect of the zone (proximal or distal) on γ_d , a marginal effect of the zone on γ ($F_{1,47} = 3.62$, $p = 0.064$) varying from $\gamma = 0.68 \pm 0.063$ in the proximal zone to $\gamma = 0.826 \pm 0.046$ in the distal zone (Table 1). Only the rabbit showed a different γ_d value ($F_{3,47} = 18.59$, $p < 0.05$ for species effect, and significant difference in a Tukey test). However, the bifurcation angle showed no differences among the species, but clear differences between proximal ($\theta = 57.22 \pm 4.67^\circ$) and distal ($\theta = 74.42 \pm 3.87^\circ$) zones ($F_{1,47} = 7.52$, $p < 0.01$). The first value near the geometrical optimum ($\theta = 60^\circ$) and the last value fully adjusting to the optimum expected from a physical criteria ($\theta = 74.934^\circ$).

The symmetry ratios L_r and D_r (0.809 ± 0.309 and 0.779 ± 0.251) although statistically different from the expected 1 ($p < 0.05$) were similar and not excessive different from the unity ranging both variables approximately from 0.3 to 1.

Considering the distance as the response variable, and the criteria (geometric or physic), species, individuals and generation (proximal or distal) as variation sources in a factorial ANOVA, we found differences among criteria ($F_{1,47} = 4.78$, $p < 0.05$), species ($F_{3,47} = 2.91$, $p < 0.05$) and generation ($F_{1,47} = 29.1$, $p < 0.01$), but not between the individuals of each species ($p < 0.05$). When considered each criteria separately, for the geometrical distances we found differences among species ($F_{3,47} = 3.73$, $p < 0.05$) and between generations ($F_{1,47} = 8.0$, $p < 0.01$). For the physical distance, we found differences between generations ($F_{1,47} = 36.6$, $p < 0.01$) and interaction between generation and species (Table 2, Figures 4 and 5). The more relevant results are those, with only one exception, for all species the physical distance (0.37 ± 0.02 ($\bar{x} \pm 1SE$)) is lower than the geometrical distance (0.439 ± 0.03), and that both, the geometrical and physical distance are lower in the distal zone (0.33 ± 0.02) than that in the proximal zone (0.49 ± 0.03) (Figures 6 and 7).

4. DISCUSSION

The standard pattern generated in this work is restricted exclusively to the geometry of the branching pattern and in this sense is unrealistic, but it is a fixed and idealized standard pattern as counterpart of the other physically optimized models (Kamiya et al. 1974, Kitaota et al. 1999), yielding useful relationships to study the departures from a geometrical optimality. The analytical approach is very simple and predicts adequately the optimum bifurcation angle, when compared with the simulations. Simulations generated plausible images of the bronchial tree in the range of the predicted optimum angle. These also show that if the bifurcation angle is small the enveloping volume of the bronchial tree is small, but the terminal branches are very crowded. In contrast, when the bifurcation angle is high the terminal branches fill the space better, but its enveloping volume also increases. In other words, as predicted by the analytical approach and confirmed by simulations, lower costs in the spatial distribution determine higher costs in volume and higher costs in the spatial distribution determine just the opposite in the volume.

The expected bifurcation angle $\theta = 60^\circ$ is different to the average θ of the species of this study, but is very close to the average in the proximal zone ($\theta = 57.22 \pm 4.67^\circ$). Also, bifurcation angles of about 60° are usually found in the proximal zone of the bronchial tree of rabbits, rats and humans (Canals et al., 2002a; 2002b; Weibel, 1963; Thurlbeck and Horsfield, 1980). The expected γ is a common result of the modeling of dichotomic fractal trees constrained to the volume preservation (Mandelbrot, 1982; Wets et al., 1997). It is very interesting that the expected γ from the

analytical approach, is equal to the expected γ_d (diameter ratio) from a physical completely independent analysis. These are two approaches to expect a unique scale of size decrease in the bronchial design. This is in agreement with most morphometric studies that have revealed a positive correlation between diameter and length of a branch (Horsfield and Cumming, 1968; Kitaota and Suki, 1997; Weibel, 1963) and with a constant length to diameter ratio (Kitaota et al., 1999).

The bronchial tree of the species showed asymmetry ranging between 0.3 and 1 for L_r and D_r . These are evident in the dz axis of both, the physical and geometrical domain, and that was an expected result. Several previous reports reveal the asymmetry of the bronchial tree (Horsfield, 1990; Maina and van Gils, 2001; Ramchandani et al., 2001) and other reports showed that asymmetric flow distribution occurs even in a symmetric structure (Andrade et al., 1998). This asymmetry factor fortunately was similar and with similar distribution for both L_r and D_r so, the contribution to the geometrical and physical distance is also similar. This implies that in our distance estimators there were not distortions introduced for the asymmetries. Also the average values (≈ 0.8) although statistically different from 1, are not very different from the unity and it does not invalidate our geometrically symmetrical pattern and neither other physical symmetrical models.

The results in our species showed that the bifurcation angle increases from the proximal to distal zone, approaching in the proximal zone to the geometrical optimum, and in the distal zone to the physical optimum. On the other hand, the scales of length and diameter reduction (γ and γ_d) agree with the expected from the physical and

geometrical criteria. Only the length ratio varies lightly, increasing from proximal to distal zone.

When we study the geometrical and physical distances we can see that both distances decrease from proximal to distal zones, the physical distance mainly by the increase of the bifurcation angle and the geometrical distance by fine adjusts in their length ratio. In that distal zone both, geometrical and physical distances are small, but the physical distance is always lower, the first ranging from 0.282 to 0.452, and the latter from 0.249 to 0.332. This is in agreement with previous results in rats that show a gradual approach to the physical optimum with the decrease of the bronchial diameter from proximal to distal zone (Canals et al., 2002b). The proximal branching process could be dominated by higher flow velocities associated to high breathing rate, implying high Reynolds number, and then as a consequence lower optimum angles, as expected in turbulent flow from the Kamiya et al. (1974) relationship. The exponent “n” in the Murray’s law (1926) for turbulent or transitional air flow (<2.7), and as a consequence the optimum angle can be lower than the expected for laminar flow (74.9°), for example $\theta = 66.7$ for $n = 2.7$ and $\theta = 50.1$ for $n = 2.33$. If there were high bifurcation angles ($\theta \approx 60$) in the proximal zone even in a fully symmetric tree with more than three generations, the flow distribution becomes significantly heterogeneous at increased Reynolds number (Andrade et al., 1998). Furthermore, the proximal branching process is more asymmetric and could be dominated by the necessity to increase the branches to fill a space. In the distal zone, the dominant principles gradually change from a volume and pumping power problem in the conductive zone, to a drag and surface problem in the respiratory zone where convection and diffusion are relevant.

In summary, our proposed simple geometrical pattern for the branching distribution of the bronchial tree, agree with several theoretical expected values and with empirical observations. Also, it proposes a geometrical counterpart to physical optimal models and it yields useful relationships that can be used to estimate the departures from the optimality of observed bronchial trees. Their usefulness is mainly for comparative studies looking for differences in the approaching to different optimalities depending of life style, environmental conditions or evolutive relationships.

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Table 1.- Bifurcation angle (θ), length ratio (γ) and diameter ratio (γ_d) of the bronchial tree of four species.

Species	Zone	q	g	g_d
<i>Oryctolagus Cuniculus</i>	Proximal	61.10	0.842	0.974
	Distal	79.66	0.818	0.911
<i>Rattus Norvegicus</i>	Proximal	48.84	0.757	0.723
	Distal	75.04	0.818	0.745
<i>Abrothrix Olivaceus</i>	Proximal	58.85	0.649	0.640
	Distal	78.71	0.832	0.716
<i>Tadarida Brasiliensis</i>	Proximal	61.00	0.407	0.700
	Distal	60.03	0.841	0.736
Average ($\pm$Sd)		66.54 $\pm$ 3.05	0.758 $\pm$ 0.037	0.778 $\pm$ 0.013

Table 2.- Average Geometrical (G_d) and Physical (P_d) distances from the expected values in proximal and distal zones of the bronchial tree of Rabbits (*Oryctolagus cuniculus*) (Oc), two rodents (*Rattus norvegicus* (Rn) and *Abrothrix olivaceus* (Ao)) and the bat *Tadarida brasiliensis* (Tb).

	G_d				P_d			
	Oc	Rn	Ao	Tb	Oc	Rn	Ao	Tb
Proximal	0.324	0.586	0.573	0.638	0.479	0.593	0.467	0.329
Distal	0.282	0.452	0.377	0.374	0.295	0.266	0.249	0.332
Average	0.300	0.514	0.466	0.506	0.374	0.417	0.348	0.330

Figure legends

Figure 1.- Variations of the expected circumscribed volume (V_e) and the expected variance mean coefficient (V/Me) with the medium bifurcation angle ($\alpha = \theta/2$) from the analytical approach. The cost function $C(\alpha) = \max \{V_e, V/Me\}$ is minimized in the intersection of both curves at $\alpha = 27.79^\circ$

Figure 2.- Variations of the branching pattern with the medium angle ($\alpha = \theta/2$) from the simulations (Eqs. 9 to 15).

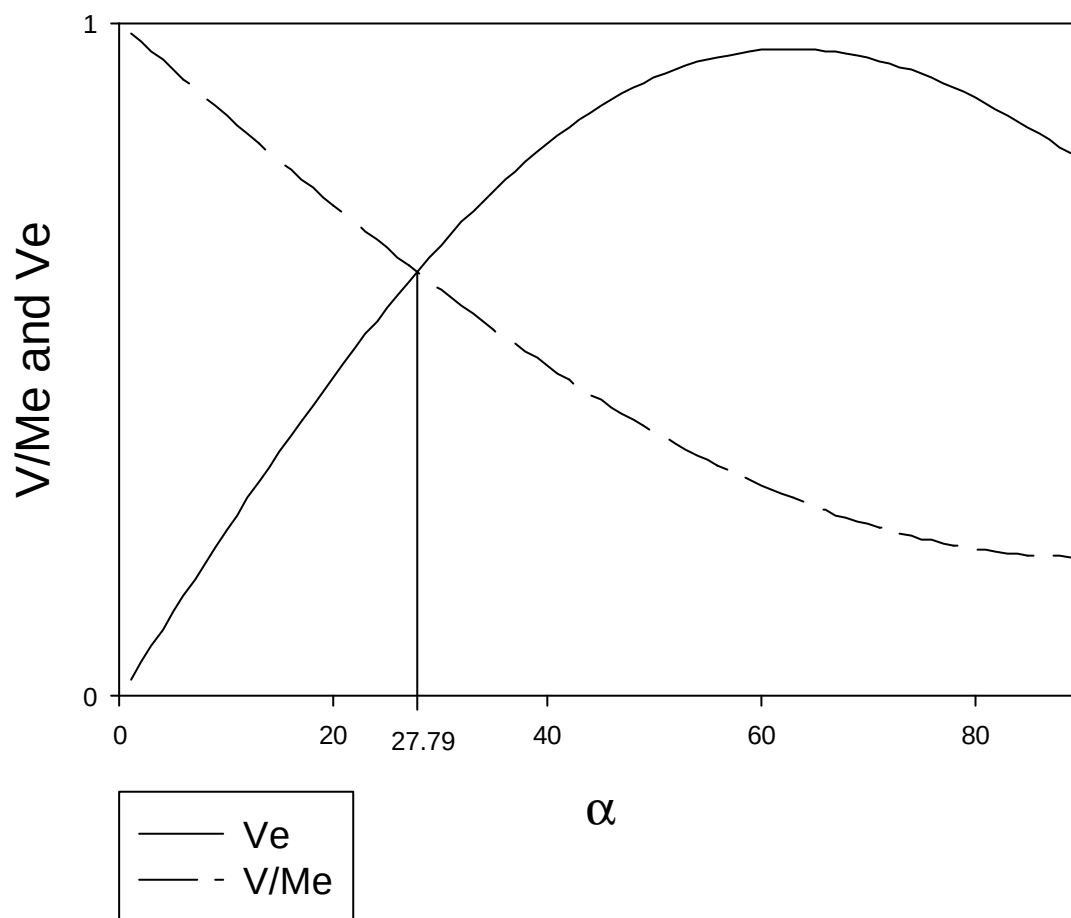
Figure 3.- Variations of the computed enveloping volume (V_s) and variance mean coefficient (V/Ms) with the medium angle ($\alpha = \theta/2$) from twenty simulations for twelve generations of bronchi. The fill circles are the observed variance mean coefficients with their standard deviations. The empty circles and the lines are the predicted values from the regression. The two curves intersects at $\alpha = 31.35^\circ$.

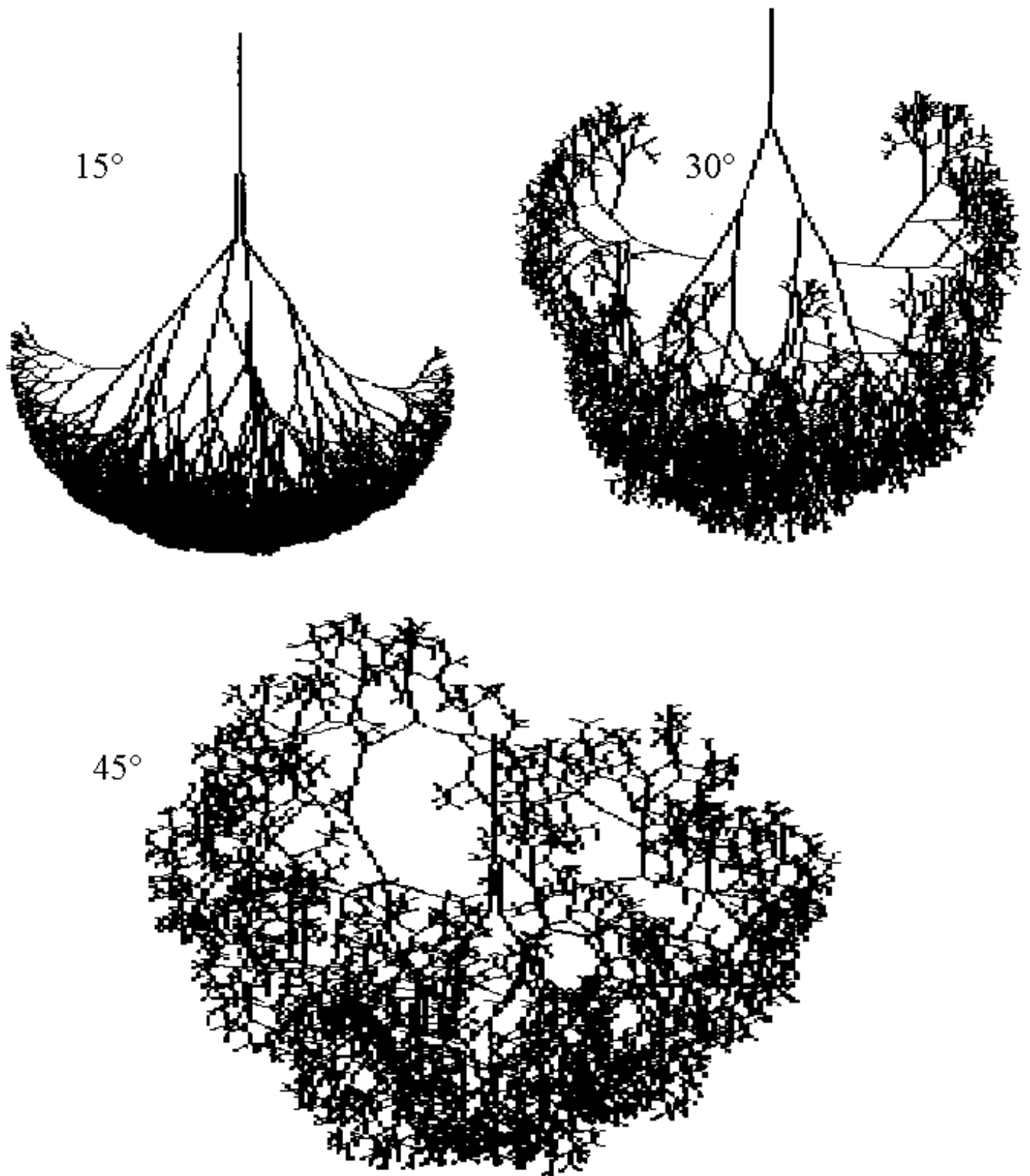
Figure 4.- Geometric distance from the expected optimum of the air way in four species: the rabbit (*Oryctolagus cuniculus*) (Oc), two rodents (*Rattus norvegicus* (Rn) and *Abrothrix olivaceus* (Ao)) and the bat *Tadarida brasiliensis* (Tb).

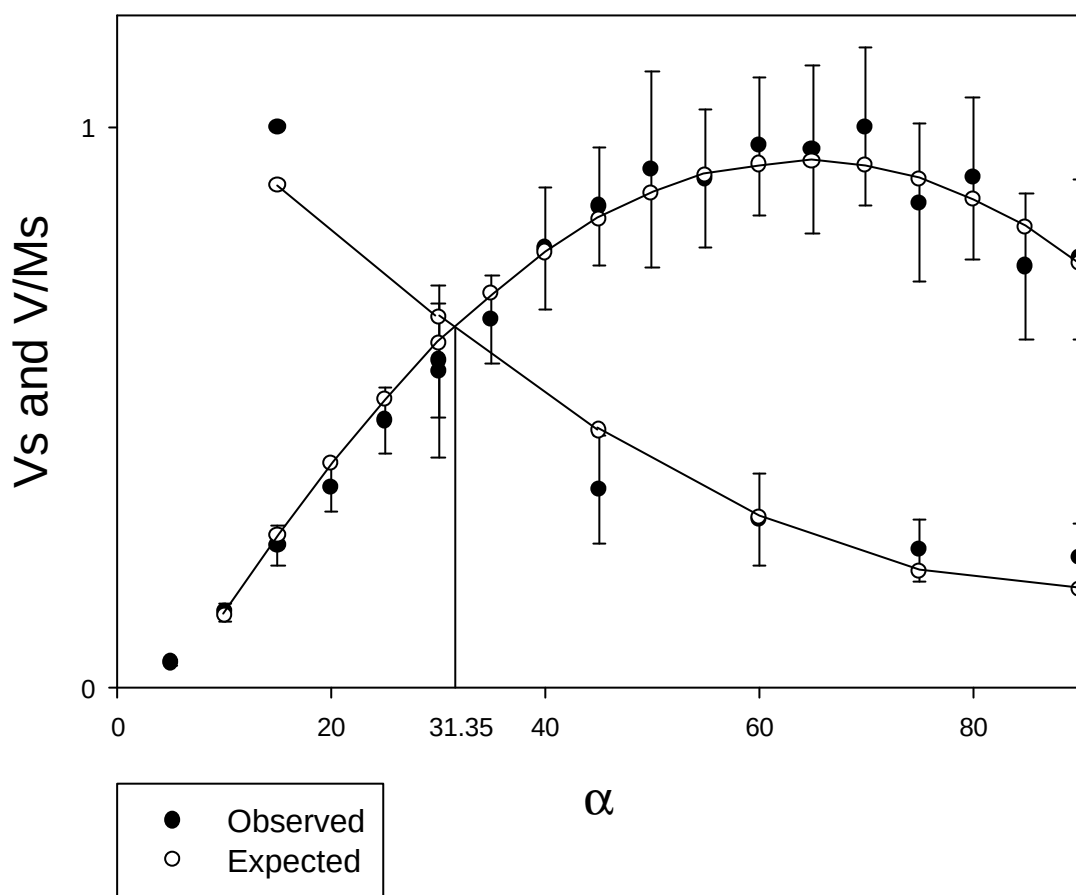
Figure 5.- Physical distance from the expected optimum of the air way in four species: the rabbit (*Oryctolagus cuniculus*) (Oc), two rodents (*Rattus norvegicus* (Rn) and *Abrothrix olivaceus* (Ao)) and the bat *Tadarida brasiliensis* (Tb).

Figure 6.- Departures from the geometrical optimality in the rabbit *Oryctolagus cuniculus*, two rodents *Rattus norvegicus* and *Abrothrix olivaceus* and the bat *Tadarida brasiliensis*.

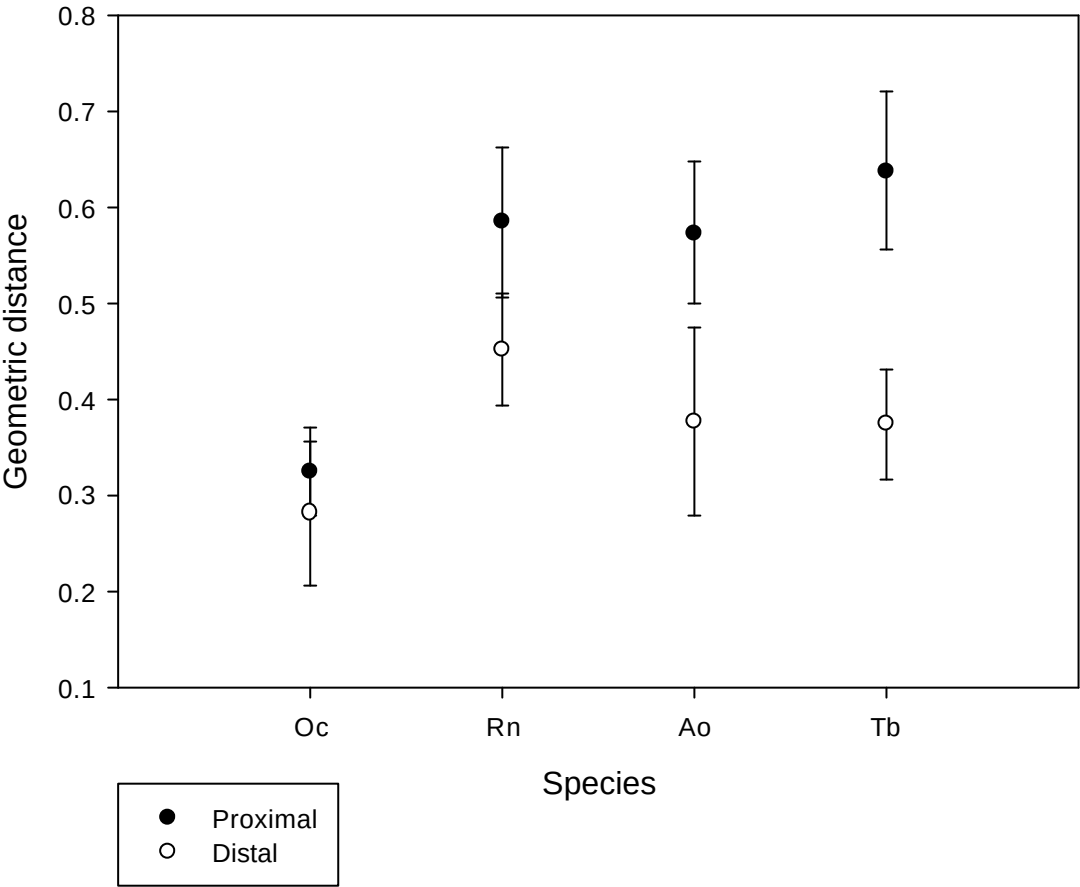
Figure 7.- Departures from the physical optimality in the rabbit *Oryctolagus cuniculus*, two rodents *Rattus norvegicus* and *Abrothrix olivaceus* and the bat *Tadarida brasiliensis*.







Geometric Domain



Physical domain

