

The proximal airway of the bat *Tadarida brasiliensis*: a minimum entropy production design

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Abstract The bronchial tree of most mammalian lungs is a good example of an efficient distribution system whose geometry and dimensions of branched structures are important factors in determining the efficiency of respiration. Small and flying endothermic animals have high-energy requirements, requiring morphological and physiological adaptations to reduce energy loss. Here we show that *Tadarida brasiliensis*, a nocturnal small bat whose energy requirements are exacerbated by this small size and by their frequent exposure to high altitude, has a different morphology in the proximal airway, sustained by a wider trachea and better scaling factors, than other non-flying mammals. This design allows a great decrease of the volume specific resistance of the proximal airway and in consequence a very low entropy production during breathing, approximately 1/18 of that expected for a non-flying mammals of similar body size.

Keywords Bats · Airway · Optimization · Entropy

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Introduction

In mammals there is a group of respiratory dimensions that have a practically linear relationship with body mass over a large range of mass, which suggests a highly conserved similarity in the design of the respiratory tree. For example, lung volume, tidal volume, dead space, alveolar surface and oxygen diffusion capacity are related to body mass with exponents close to unity (Weibel et al. 1981; Peters 1983; Schmidt-Nielsen 1984; Calder 1996). This contrasts with the known increase of energetic requirements of animals. Basal oxygen consumption and maximum oxygen consumption are related to body mass with exponents ranging between 0.65 and 0.87 (Weibel et al. 1981; Calder 1996; White and Seymour 2005) resulting in higher mass-specific energetic requirements in small mammals. Thus, there is a poor adjustment of oxygen diffusion capacity in relation to requirements. In spite of this, however, the respiratory system seems to adjust the respiratory frequency and tidal volume and several other respiratory parameters to value in which the work and consequently the energy cost are minimum (Weibel and Gomez 1962; Wilson 1967; Andrade et al. 1998; Weibel et al. 1998; Massaro and Massaro 2002; Mauroy et al. 2004; Canals et al. 2005a). Respiratory frequency shows an important increase in small animals (Lindstedt 1984), is known to be high in flying mammals (Neuweiler 2000), and should affect the dimensions of the airway. The greater the respiratory frequency, the greater the velocity of ventilation flow through the bronchi, and the smaller the diameter, the greater the flow resistance.

Endothermic animals with high-energy requirements, such as small animals, those which live at high altitudes and hypoxic environments or use high-cost forms of locomotion, require behavioral, morphological or

physiological adaptations which allow an adequate equilibrium between the energy cost imposed by their way of life and the allocation of energy to growth, homeostasis and reproduction, among others. Bats combine a generally small size with a high energetic cost of flight; some are found at altitudes of more than 3,000 m a.s.l., exposed to cold and in conditions of low partial oxygen pressures. In these latter species, a number of refinements in the design of the cardiovascular and respiratory systems have been described, such as larger heart and cardiac output (Jurgens et al. 1981; Canals et al. 2005a); elevated hematocrit, high concentrations of hemoglobin and high oxygen transport capacity (Wolk and Bogdanowics 1987); and optimization of structural lung parameters such as lung volume, density of the respiratory surface and thickness of the alveolar-capillary barrier (Lechner 1985; Maina et al. 1991; Maina 1998, 2000a, b; Canals et al. 2005a).

Respiratory work depends on the resistance of all the components of the respiratory system to respiratory movements and airflow. It increases with airflow velocity and is inversely proportional to the fourth power of the diameter. Respiratory work depends principally on the resistance generated in the proximal airway, which is a key factor in energy saving, especially in small animals whose high respiratory frequency may be accompanied by increments in the work to overcome flow turbulence and viscosity resistance (West 2000). However, in asymmetric airways the distal airway may be important (Majumdar et al. 2005).

It was recently reported that the proximal airway of the bat *Tadarida brasiliensis* has higher optimization values in its geometry than do other small rodents, compared to the expected value for a symmetric bronchial tree with minimum volume and pumping power (Canals et al. 2005a). The loss of energy during respiration was reduced due to adjustments in the diameters, angles of bronchial bifurcation and scaling ratios of the bronchial dimensions. However, comparisons based on models of physical optimization with the assumption of the symmetry of bronchial bifurcations are not realistic, since the airway of the majority of mammals is asymmetric (Horsfield 1990; Canals et al. 2002a), which may change the characteristics of scaling and bronchial diameters necessary to reduce the loss of energy during respiration. It is thus necessary to design studies, which directly measure the resistance of the airway and estimate the dissipation of energy considering the anatomical characteristics of each species, which is one of the objectives of this contribution.

In this study, we analyze the characteristics of the proximal airway of the bat *T. brasiliensis*, the rodents *Rattus norvegicus*, *Abrothrix olivaceus* and *Abrothrix andinus* and the rabbit *Oryctolagus cuniculus*. We hypothesized that the bat, a small flying animal which may

be found at high altitudes, should present adjustments in the design of its airway that create lower resistance and energy loss than is found in other mammals.

Materials and methods

We studied the airway of 20 individuals of *T. brasiliensis* ($M_b = 10.6 \pm 2.21$ g), 17 individuals of *A. olivaceus* ($M_b = 31.1 \pm 4.5$ g), 8 individuals of *A. andinus* ($M_b = 27.1 \pm 5.7$ g), 20 individuals of *R. norvegicus* ($M_b = 276.15 \pm 115.3$ g) and 2 individuals of *O. cuniculus* ($M_b = 3011.7 \pm 220.2$ g). All individuals were adults, donated by the Environmental Health Service or captured in the spring between the years 2000 and 2005. All animals were weighed on an electronic balance (± 0.05 g) and were sacrificed by exposing them to CO_2 (bats and rodents) or by an intraperitoneal injection of a lethal dose of sodium thiopental (rabbits), according to the norms of the Ethics Committee of the Science Faculty of the University of Chile. A bronchography under radioscopic visualization was performed for each animal, introducing diluted barium sulfate by means of an endotracheal cannula. X-rays were taken at a distance of 1 m, sufficient to avoid magnification of the image; 100 mA for 0.04 s with 24–34 kV (Fig. 1). The resulting images were digitalized and analyzed using the software SCION image.

In each image the diameters and length of the bronchi, indicating the generation (0 the trachea, 1 the main bronchus, and so forth) were measured. Diameters of the bronchi were measured at the base and their lengths were measured between the bronchial bases and the basis of the bifurcation (Fig. 2). A sensitivity analysis of the methodology was performed. Considering the film-focus distance $D = 100$ cm, the magnification obtained in the film is

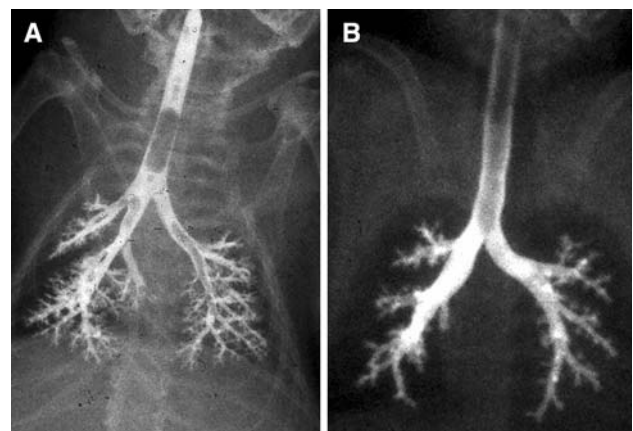


Fig. 1 Bronchogram of the proximal airway of the rodent *Abrothrix olivaceus* (a) and the bat *Tadarida brasiliensis* (b). In the bat, trachea and proximal bronchi are wider than those of the rodent

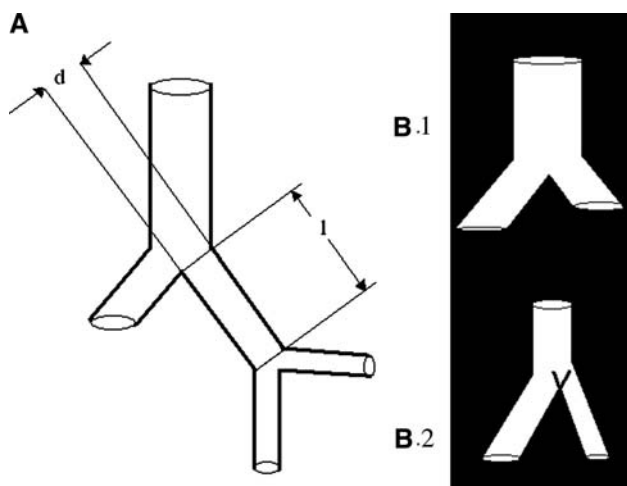


Fig. 2 **a** Diameter (d) and length (l) measurements done in each bronchial bifurcation; **b** representation of unrotated (**b.1**) and rotated (**b.2**) bronchial bifurcations. When a bifurcation is rotated in a significant way, the bases of daughter bronchi are superposed (X sign)

negligible allowing comparisons between diameters of bronchi obtained in different planes and for different species: $d_m = d_r(D/(D - \delta))$, where d_m is the diameter in the film, d_r the true diameter, D the focus-film distance and δ the object-film distance. $D = 100$ cm and δ ranged between few millimeters and centimeters which determines that $d_m \approx d_r$. A second factor considered was the rotation of the bifurcation plane around the axis constituted by the mother bronchus. In a rotated bifurcation the length of a bronchus in the film (l_m) is: $l_m = l_r \sqrt{\cos^2 \theta \cos^2 \alpha + \sin^2 \alpha}$, where l_r is the true length of the bronchus, 2α the bifurcation angle and θ the rotation angle. If the bifurcation plane is unrotated, $\theta = 0$ and $l_m = l_r$. For usual bifurcation angles (α about 20 or 30°) and if $\theta < 20^\circ$ the differences between l_m and l_r are lower than 5%. Major rotation angles are easily detected in the images (see Fig. 2).

The bronchi were studied up to generation 5, analyzing two bifurcations for each generation beginning at generation 1. Thus in generation k , measurements were the diameter and the length of the mother bronchus d_k and l_k and the diameters and lengths of the daughter bronchi $d_{1,k+1}$ and $l_{1,k+1}$ (values for the branch with lesser diameter), and $d_{2,k+1}$ (the larger diameter) and $l_{2,k+1}$. Four scaling dimensionless factors were obtained for each generation with these values; two for the diameter,

$$h_{md} = d_{1,k+1}/d_k \text{ and } h_{Md} = d_{2,k+1}/d_k; \tag{1}$$

and two for length, $h_{ml} = l_{1,k+1}/l_k$ and $h_{Ml} = l_{2,k+1}/l_k$. These scale factors serve to indicate the asymmetries that are produced among the diameters and bronchial lengths.

The flow $Q_{i,j}$ is defined for each airway (i, j), where $Q_{0,0}$ is the flow in the trachea. This flow may be estimated considering that the minute volume (V') is related with the

body mass by $V' = 379 M_b^{0.8}$ (Q in ml/min; M_b in kg; Stahl 1967; Schmidt-Nielsen 1984) and that $Q_{0,0} = 2V'$. At each bifurcation, the flow $Q_{i,j}$ of a parent airway is partitioned between its daughters $Q_{1,j+1}$ and $Q_{2,j+1}$ according to

$$Q_{1,j+1} = rQ_{i,j} \text{ and } Q_{2,j+1} = (1 - r)Q_{i,j}, \tag{2}$$

where $r \leq 1/2$, a dimensionless number determines the asymmetry of flow partitioning. Assuming that

$$Q_{i,j} = (d_{i,j})^n \tag{3}$$

from the optimization of diameters of a single tube in order to minimize dissipation while maintaining biological viability and combining Eqs. (1)–(3) yields

$$h_{md} = r^{1/n} \text{ and } h_{Md} = (1 - r)^{1/n} \tag{4}$$

where the optimum value is $n = 3$ for laminar flow and 2.33 for turbulent flow (see Majumdar et al. 2005). Following Mauroy et al. (2004) but introducing asymmetry in the bifurcations, it may be seen that the resistance of a bronchus in generation $k + 1$ (R_{k+1}) is related to the resistance in generation k by $R_{m,k+1} = f_m R_k$ and $R_{M,k+1} = f_M R_k$, in the smaller and larger bronchi, respectively, where $f_m = h_{ml}/(h_{md})^4$ and $f_M = h_{Ml}/(h_{Md})^4$, since the resistance obeys Poiseuille's law; proportional to the length and inversely proportional to the fourth power of the diameter. It follows that in a dichotomous tree after $N + 1$ generations (from 0 to N), the total resistance is given by:

$$R_N = R_0 \cdot \left(1 + \sum_{p=1}^{p=N} \left(\frac{f_{m1} \cdot f_{M1}}{f_{m1} + f_{M1}} \right) \cdot \left(\frac{f_{m2} \cdot f_{M2}}{f_{m2} + f_{M2}} \right) \cdots \left(\frac{f_{mp} \cdot f_{Mp}}{f_{mp} + f_{Mp}} \right) \right).$$

The volume of the airway depends directly on the length and the square of the diameter, by which $V_{m,k+1} = f_{vm} V_k$ and $V_{M,k+1} = f_{vM} V_k$, where $f_{vm} = h_{ml}/(h_{md})^2$ and $f_{vM} = h_{Ml}/(h_{Md})^2$, and the total volume is:

$$V_N = V_0 \cdot \left(1 + \sum_{p=1}^{p=N} (f_{vm1} + f_{vM1}) \cdot (f_{vm2} + f_{vM2}) \cdots (f_{vmp} + f_{vMp}) \right).$$

The initial resistance and volume are: $R_0 = \frac{128\eta l_0}{\pi d_0^4}$ and $V_0 = \frac{\pi d_0^2 l_0}{4}$, respectively, where η is the viscosity of air; $\eta = 1.846 \times 10^{-5}$ kg/ms (or N s/m²) at 300 K. These quantities allowed the estimation of energy use (power, P in W) for a given flow ($Q_{0,0}$) using $P = Q_{0,0}^2 R_N$ and the rate of entropy production per unit volume using $S = P/(V_N T)$, where T is the temperature in Kelvin (W/m³ K).

The data matrix was thus formed by the bronchial characteristics (diameter and length), the resistance and the volume of the airway from generations 0 to 5 for each

Table 1 Diameters and length of the airway of five mammals along the first five bronchial generations (G_i)

Species	Dimension (mm)	G_0	G_1	G_2	G_3	G_4	G_5
<i>Rattus norvegicus</i>	Diameter	2.52 ± 0.11	2.07 ± 0.11	1.73 ± 0.11	1.60 ± 0.12	1.44 ± 0.13	1.29 ± 0.13
	Length	37.48 ± 4.02	4.64 ± 0.43	3.68 ± 0.44	2.76 ± 0.46	2.21 ± 0.52	2.11 ± 0.52
<i>Abrothrix olivaceus</i>	Diameter	1.25 ± 0.05	1.04 ± 0.05	0.74 ± 0.05	0.60 ± 0.05	0.48 ± 0.06	0.43 ± 0.07
	Length	11.05 ± 1.24	2.66 ± 0.35	1.72 ± 0.35	1.46 ± 0.37	1.32 ± 0.42	1.21 ± 0.54
<i>Abrothrix andinus</i>	Diameter	1.10 ± 0.07	1.02 ± 0.08	0.79 ± 0.08	0.60 ± 0.11	0.52 ± 0.11	0.48 ± 0.11
	Length	10.09 ± 1.13	1.91 ± 0.26	1.76 ± 0.28	1.14 ± 0.37	1.01 ± 0.37	0.95 ± 0.37
<i>Oryctolagus cuniculus</i>	Diameter	4.58 ± 0.43	4.18 ± 0.43	2.92 ± 0.43	3.31 ± 0.43	2.21 ± 0.43	1.33 ± 0.43
	Length	77.80 ± 3.52	6.28 ± 0.99	4.39 ± 0.99	3.13 ± 0.99	3.69 ± 0.99	2.95 ± 0.99
<i>Tadarida brasiliensis</i>	Diameter	1.06 ± 0.03	0.86 ± 0.03	0.62 ± 0.04	0.55 ± 0.04	0.45 ± 0.05	0.42 ± 0.05
	Length	9.54 ± 1.48	1.54 ± 0.20	1.06 ± 0.24	0.77 ± 0.26	0.89 ± 0.29	0.61 ± 0.34

Data are presented as average ± standard deviation calculated over all subjects within a species

individual of the studied species. We first analyzed the characteristics of the trachea (generation 0), diameter and length, with a one-way covariance analysis, using the body mass as a covariate and also the tracheal volume (observed/expected by $V_0 = 0.82 \text{ Mb}^{1.18}$; Calder 1996). We then analyzed the behavior of the ratio of R_N/V_N to R_0/V_0 : $RR/V = R_N V_0 / R_0 V_N$, which represents the proportional change of the resistance–volume ratio (dimensionless), using a proportion of one as the base value. Additionally, we analyzed the behavior of the scale factors over generations. Repeated measures ANOVA and homogeneity of the slopes test using general linear models (when necessary) were performed. In spite of the unbalanced model, generated by the low number of rabbits analyzed, the results are identical whether this species is included in, or excluded from the analysis.

Using the relationship $V' = 379 \text{ Mb}^{0.8}$, Mb in kg and V' in ml/min, we estimated the flow velocity in each bronchus using $v_i = Q/S_i$, where S_i is the sectional area, Q is the flow ($Q = 2V'$) and v_i is the velocity in generation i , and thus estimated the Reynolds number (Re) for each generation: $Re = v_i d_i \rho / \eta$, where d_i is the diameter, ρ is the density of the air ($1,000 \text{ kg/m}^3$) and η is the viscosity at a temperature intermediate between ambient and body temperatures, about 300 °K. We also estimated the rate of entropy production per unit of volume during respiration in the proximal bronchial tree (5 generations), using: $S_5 = Q^2 R_5 / V_5 T$ ($\text{W/m}^3 \text{ K}$), where R_5 is the resistance, V_5 is the volume and T is the temperature in Kelvin.

Results

The morphology of the trachea of *Tadarida brasiliensis* was different from that of the other mammals studied here ($F_{4,64} = 2.65$, $P = 0.04$ for diameter and $F_{4,64} = 153.2$, $P \ll 0.001$ for length in the ANCOVAs). Furthermore, the

tracheal volume was exceptionally large ($F_{4,65} = 3.47$, $P = 0.012$; Table 1; Fig. 3). There were differences in the tracheal resistance among species ($F_{4,65} = 19.05$, $P \ll 0.001$): (7.91 ± 3.85) $\times 10^5 \text{ N s/m}^5$ in *R. norvegicus* (a), (38.51 ± 18.04) $\times 10^5 \text{ N s/m}^5$ in *A. olivaceus* (b), (68.20 ± 50.80) $\times 10^5 \text{ N s/m}^5$ (c) in *A. andinus*, (1.32 ± 0.04) $\times 10^5 \text{ N s/m}^5$ in *O. cuniculus* (a) and (62.22 ± 27.08) $\times 10^5 \text{ N s/m}^5$ in *T. brasiliensis* (c) (different letters indicates differences in resistances in the LSD test).

The volume-specific relative resistance of the proximal airway (RR/V) showed important differences among species (Wilks' $\lambda = 0.079$; $F_{20,110} = 0.633$, $P \ll 0.01$ in the repeated measures ANOVA), supported by the strong relative decrease in the resistance in *T. brasiliensis*. While in this

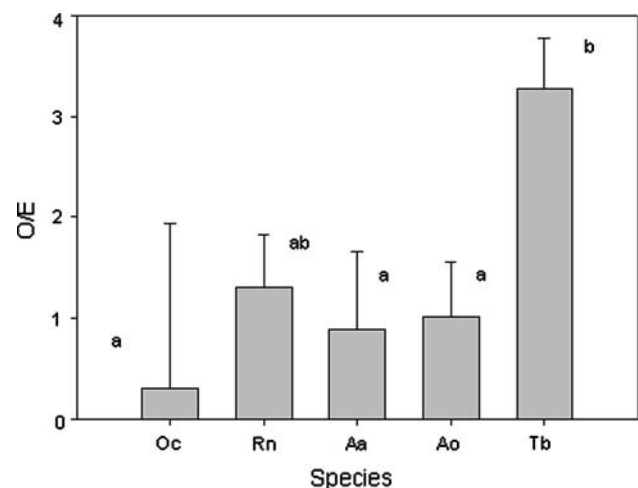


Fig. 3 Observed/expected ratios for the tracheal volume (O/E) in five mammals: Oc = *Oryctolagus cuniculus*, Rn = *Rattus norvegicus*, Aa = *Abrothrix andinus*, Ao = *Abrothrix olivaceus* and Tb = *Tadarida brasiliensis*. Expected tracheal volume was computed from: $V_0 = 0.82 \text{ Mb}^{1.18}$ (Calder 1996). $F_{4,65} = 3.47$, $P = 0.012$. Different letters indicate significant differences in LSD multiple comparisons

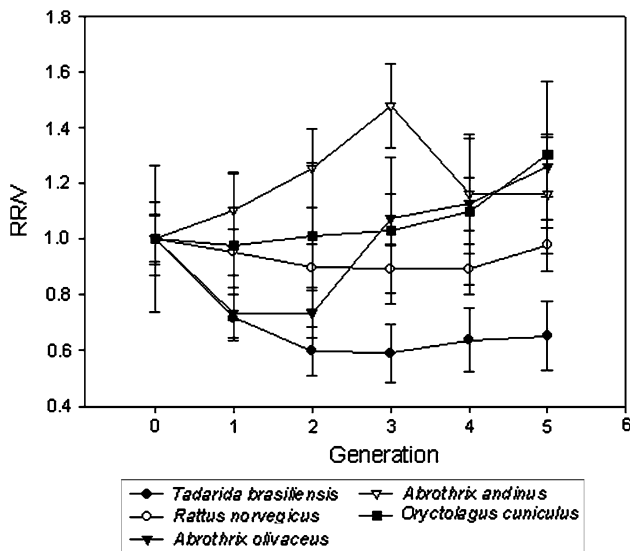


Fig. 4 Variation of the resistance–volume ratio (R_N/V_N to R_0/V_0 ; $RR/V = R_N V_0 / R_0 V_N$, where R_i and V_i are the resistance and the volume of a branch of the “ i ” generation) along the proximal airway of five mammals

species the slope of the curve RR/V versus generation was strongly negative ($\beta = -0.6$; $F_{1,89} = 50.3$, $P \ll 0.001$), in the other species it was close to 0 or positive: $\beta = 0.05$ ($F_{1,33} = 0.08$, $P = 0.78$) in *A. andinus*; $\beta = 0.21$ ($F_{1,93} = 4.21$, $P = 0.04$) in *A. olivaceus*; $\beta = -0.18$ ($F_{1,110} = 3.82$, $P = 0.053$) in *R. norvegicus* and $\beta = 0.73$ ($F_{1,10} = 11.1$, $P = 0.008$) in *O. cuniculus*. If *T. brasiliensis* is removed from the analysis, the slopes of the other species are not significantly different ($F_{3,246} = 2.07$, $P = 0.104$; Fig. 4). The difference in the behavior of the RR/V versus generation curves was produced principally in the first generation, because the diameter scale factors (h_{md} and h_{Md}) of *T. brasiliensis* were different ($F_{4,124} = 8.44$, $P \ll 0.001$), being closer in this species to the optimum value expected for minimum energy dissipation in symmetric trees ($h = (1/2)^{1/3}$) (Table 2). However, in the average over all generations bronchial trees were asymmetric in all species.

Table 2 Average scaling factors of the bronchial tree and the average difference (δ) from the expected optimum scaling factor ($(1/2)^{1/3}$) in five mammals

	$h_{d1} (\delta)$	$h_{dt} (\delta)$	h_{l1}	h_{lt}
<i>Rattus norvegicus</i>	0.801 ± 0.047 (0.126 ± 0.013)b	0.683 ± 0.055 (0.212 ± 0.071)ab	0.139 ± 0.069	0.740 ± 0.180
<i>Abrothrix olivaceus</i>	0.788 ± 0.051 (0.175 ± 0.018)ab	0.719 ± 0.106 (0.202 ± 0.041)a	0.269 ± 0.138	0.780 ± 0.096
<i>Abrothrix andinus</i>	0.828 ± 0.074 (0.208 ± 0.021)ab	0.749 ± 0.028 (0.175 ± 0.006)ab	0.257 ± 0.097	0.816 ± 0.060
<i>Oryctolagus cuniculus</i>	0.925 ± 0.149 (0.185 ± 0.044)a	0.665 ± 0.054 (0.213 ± 0.033)ab	0.082 ± 0.006	0.862 ± 0.244
<i>Tadarida brasiliensis</i>	0.783 ± 0.047 (0.084 ± 0.013)c	0.697 ± 0.039 (0.160 ± 0.055)b	0.176 ± 0.052	0.812 ± 0.120

The symbols h_{d1} and h_{dt} represent the diameter scale factors for the first generation and the average diameter over all generations, respectively. Analogously h_{l1} and h_{lt} are the length scale factors. For species effect on δ in the first generation, $F_{4,124} = 8.44$, $P \ll 0.001$. For species effects on δ over all generations, Wilks’ $\lambda = 0.5$; $F_{20,233} = 2.72$, $P \ll 0.001$. Different letters indicate significant differences in LSD multiple comparisons

Table 3 Average diameter scaling factors (h_{md} and h_{Md}), n exponents and partition of the flow (r) of the bronchial tree in five mammals (n and r computed from Eq. (4) based on average values, following Majumdar et al. 2005)

	h_{Md}	h_{md}	N	r
<i>Oryctolagus cuniculus</i>	0.902 ± 0.104	0.532 ± 0.165	2.405	0.219
<i>Rattus rattus</i>	0.904 ± 0.076	0.508 ± 0.134	2.32	0.208
<i>Abrothrix andinus</i>	0.911 ± 0.063	0.619 ± 0.040	2.95	0.243
<i>Abrothrix olivaceus</i>	0.840 ± 0.093	0.625 ± 0.133	2.34	0.334
<i>Tadarida brasiliensis</i>	0.854 ± 0.032	0.574 ± 0.117	2.20	0.295

As a consequence there was an accentuated partition of flow in each bronchial bifurcation. The partition flow coefficients ranged between 0.208 and 0.334, which was associated with n -exponents ranging between 2.2 and 2.95 (Table 3). Also, the total volume of the airway per unit of mass over the five generations was larger in *T. brasiliensis* than in the rest of the mammals studied ($F_{4,40} = 14.37$, $P \ll 0.01$; Table 4).

As expected, the estimated Reynolds numbers decreased exponentially with the bronchial generation (Table 5) in all species and only in the trachea of *O. cuniculus* a value near the critical limit of turbulent flow was found. The volume specific entropy production rate (S_5) was not correlated with the body mass (Spearman $R = 0.153$, $P > 0.05$; Table 6) and was lower in the bat *T. brasiliensis* in absolute and proportionally terms.

Discussion

In the bat, *T. brasiliensis*, the relative volume of the trachea was larger than that of other mammals. The tracheal volume (V_0) was 337% of the expected value according to Calder (1996): $V_0 = 0.82 \text{ Mb}^{1.18}$, while in the rest of the mammals studied the values ranged from 31 to 131% of the expected value (Fig. 3). Even so, the absolute diameter was still small, thus there was a large initial resistance; but it is notable that a species which weighs around 11 g has an

Table 4 Volume of the first five generations of the airway (V_5) in five mammals

	V_5 (m ³) × 10 ⁻⁸	V_5 /Mb (m ³ /kg) × 10 ⁻⁶	LV (cm ³)	V_5 /LV
<i>Rattus norvegicus</i>	32.059 ± 1.726	1.415 ± 0.143 (a)	7.580	0.042
<i>Abrothrix olivaceus</i>	3.338 ± 1.974	1.069 ± 0.163 (a)	0.940	0.036
<i>Abrothrix andinus</i>	2.915 ± 3.558	1.170 ± 0.294 (a)	1.080	0.027
<i>Oryctolagus cuniculus</i>	169.260 ± 5.032	0.561 ± 0.416 (a)	148.012	0.011
<i>Tadarida brasiliensis</i>	3.212 ± 2.372	2.801 ± 0.196 (b)	0.654	0.049

V_5 /Mb is the mass specific airway volume, LV is the lung volume (Canals et al. 2005a,b), and V_5 /LV is the ratio between air way and lung volume. For the species effects on the mass specific volume $F_{4,40} = 14.37$, $P \ll 0.001$. Different letters indicate significant differences in LSD multiple comparisons. Lung volume values from Canals et al. (2005b)

initial resistance similar to a rodent 2½ times larger (*A. andinus*; 27 g). The resistance to air flow in the trachea was somewhat greater in small species than in larger ones (in our case *R. norvegicus* and *O. cuniculus*). Since the resistance R in a tube depends directly upon its length and inversely upon the fourth power of the diameter, while the linear dimensions depend upon the cube root of body mass, it should follow $R = k Mb^{-1}$ (k an arbitrary constant), a curve which is extremely sensitive to small values, for which the resistance rises sharply. In the present case, the k estimated for *T. brasiliensis* was 0.066×10^5 N s kg/m⁵, while in the rest of the species it ranged from 1.197 to 3.97×10^5 N s kg/m⁵, more than an order of magnitude greater, which clearly shows the effect of that particular trachea in the bat.

The relative resistance (RR/ V) in the bat decreased strongly and in a different way from the rest of the studied mammals, which is associated with the first diameter scale factor close to the expected value for symmetric trees ($h_{md} = 0.72$; $h_{Md} = 0.83$; $r = 0.38$, $n = 2.9$). However, considering average values over the five bronchial generations, diameter scale factors, partition of the flow and n -exponents were similar in all the species here and close to those reported for rats, rabbits, dog and human (Majumdar et al. 2005), showing a clear asymmetric bronchial tree. In this type of airway the resistance is associated with particular combinations of flow partition (r) and n -exponents. Majumdar et al. (2005) showed that in some cases (i.e. $r > 0.25$ and $n < 2.5$) the resistance of an asymmetric bronchial tree may be lower than that of a symmetrical one. In our study, the conditions $r > 0.25$ and $n < 2.5$ were satisfied only by *T. brasiliensis* (Table 3).

The proximal airway volume per unit of mass in *T. brasiliensis* was at least double the values found in the other mammals. The volume after 5 generations is 5% of the total lung volume in the bat, while in the rest of the mammals here it ranges between 1.1% and 4.2%. Considering that the airway has approximately 20 generations, the volume of the entire airway is probably greater than 15% of the total volume. This value is similar to that reported for the airway volume in *Tadarida mops* (15%) a

24 g bat (Maina and King 1984) and that of *Micromys minutus* (13%), a 5–7 g rodent (Valerius 1996). Also, the diameter of the left main bronchus in this species is 1.24% of the body length (nose–rump), compared to 0.6% for *Cricetomys gambianus*, a rodent of 1,200–1,800 g. In the case of *T. brasiliensis*, the main bronchus measures 0.855 mm and the total length is 60.4 mm (Canals et al. 2002b), giving a value of 1.42% for the relative diameter of that bronchus, which is proportionally greater than that of a mammal about half its size.

The resistance to flow depends not only upon geometric factors, but also on the relation between the inertial and viscosity forces, which operate on the fluid. In a laminar regime the resistance is proportional to the flow velocity, but in a turbulent regime it is proportional to the square of the velocity. The Reynolds numbers for *T. brasiliensis* showed a decrease from 22.94 to 0.72 from the trachea to generation 5. In both species of *Abrothrix*, Re decreased from about 54 to 1.6, while larger animals had much greater values for the trachea; *R. norvegicus* varied from 312 to 9.8 and *O. cuniculus* from 2,105.8 to 65.8. Thus, only *O. cuniculus* approached the Reynolds critical number of $2,000 \pm 40\%$ (Novopashin and Muriel 2002) (Table 5).

The *T. brasiliensis* had the lowest rate of entropy production, 0.18 W/K m³ (Table 6). Comparing this value with the total rates of production of basal entropy (BMR/ T), the energy dissipation in the first 5 generations in *T. brasiliensis* is 0.96% of the basal dissipation, while in the other mammals these values ranged from 1.04 to 3.78%. Thus, *Tadarida brasiliensis* has a proximal airway

Table 5 Estimated Reynolds numbers (Re_i) along the proximal airway of five mammals

	Re_0	Re_1	Re_2	Re_3	Re_4	Re_5
<i>Abrothrix andinus</i>	48.6	24.3	12.1	6.1	2.0	1.5
<i>Oryctolagus cuniculus</i>	2,105.0	1,052.5	525.2	263.1	131.6	65.8
<i>Abrothrix olivaceus</i>	54.3	27.1	13.6	6.8	3.4	1.7
<i>Rattus norvegicus</i>	311.3	155.6	77.8	38.9	19.5	9.7
<i>Tadarida brasiliensis</i>	22.9	11.5	5.7	2.9	1.4	0.7

Table 6 Volume specific relative resistance of the first five generations of the airway in five mammals (RR/V_5) and estimations of the volume specific entropy production rate (S_5) from the movement of air in this zone during breathing

	RR/V_5	BMR (W/g)	BS (W/m^3 K)	S_5 (W/m^3 K)	S/BS (%)
<i>Rattus norvegicus</i>	0.98 ± 0.09	0.0067	21.88	0.228	1.040
<i>Abrothrix olivaceus</i>	1.26 ± 0.11	0.0097	31.52	0.792	2.512
<i>Abrothrix andinus</i>	1.16 ± 0.22	0.0104	33.68	0.792	2.348
<i>Oryctolagus cuniculus</i>	1.30 ± 0.26	0.0034	11.00	0.416	3.780
<i>Tadarida brasiliensis</i>	0.65 ± 0.12	0.0058	18.73	0.180	0.960

BMR is the basal metabolic rate (Canals et al. 2005a; Rezende et al. 2004). BS is the basal volume specific entropy production rate supposing an operative temperature of 310 K and a density near unity (g/cc) (i.e., BMR/K) and S/BS is the ratio between S_5 and BS, expressed as percentage

design adequate for a minimum entropy production (MEP-design), different from the rest of the studied mammals. Our results agreed with previous estimations of energetic costs of breathing. The total energy that euthermic mammals devote to breathing range comprises 0.6–5% in several mammals including man (Otis 1950, 1954; Grosfill and Widdicombe 1961; Pinnardi 1996; Szewczak 1997), a level regarded to be a minor metabolic significance. However, if *T. brasiliensis* had a geometry similar to those of the rest of the species we studied, it would need a trachea with a diameter of 0.43 mm and a length of 7.984 mm (estimated from potential regression between these dimensions and body mass), and would have an entropy production of $3.336 W/K m^3$, which is 18.5 times greater than the estimated rate. Thus the entropy production of this species is 1/18.5 of that expected for a mammal of the same body mass. That entropy production would represent an energetic cost of 17.8 % of the basal dissipation, similar for example to breathing costs of 25% reported in some men with chronic obstructive pulmonary disease (Pinnardi 1996), which would affect significantly the survival probability of a bat.

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