Morphometry of the dog pulmonary venous tree

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GAN, R. Z., Y. TIAN, R. T. YEN, AND G. S. KASSAB. Morphometry of the dog pulmonary venous tree. J. Appl. Physiol. 75(1): 432–440, 1993.—The biophysical approach to the study of blood flow in the pulmonary vasculature requires a detailed description of vascular geometry and branching pattern. The description of the pulmonary venous morphometry in the dog is the focus of this paper. Silicone elastomer casts of a dog lung were made and were used to measure the diameters, lengths, and branching pattern of the pulmonary venous vasculature. The anatomic data are presented statistically with a diameter-defined Strahler ordering scheme, a rule for assigning the order numbers of the vessels on the basis of a diameter criterion. The asymmetric branching pattern of the pulmonary venous vasculature is described with a connectivity matrix. Results show that for the dog’s right pulmonary venous tree 1) a total of 11 orders of vessels lay between the left atrium and the capillary bed; 2) the average ratios of the diameter, length, and number of branches of successive orders of veins were 1.701, 1.556, and 3.762, respectively; and 3) a fractal description of the tree geometry resulted in diameter and length fractal dimensions of 2.49 and 2.99, respectively. The morphometric data were used to compute the cross-sectional area, vascular volume, and Poiseuille resistance in the venous vessels.

vasculature; connectivity matrix; fractal dimension; diameter-defined Strahler system

THE BIOPHYSICAL APPROACH to pulmonary blood circulation is incomplete without quantitative information on the branching pattern of the vascular tree and the geometry (diameters and lengths) of the vessels. In the past Singhal et al. (16) and Horsfield et al. (8, 10) have studied the morphometry of the human arterial and venous trees in the lung. Using resin casts of human vascular trees, they measured the diameters, lengths, and order of all branches of blood vessels in the range of 13 μm to 3 cm for arterial vessels and 13 μm to 1.4 cm for venous vessels.

The only other species besides humans for which detailed morphometric data for the pulmonary circulation have been published is the cat. Yen et al. (24, 26) have studied the morphometry of the cat pulmonary arteries and veins. Therefore, there is an urgent need to develop a morphometric data base for the dog lung.

This paper reports the detailed morphometric data obtained from measurement of silicone elastomer casts of a dog pulmonary venous tree in our laboratory. The morphometric data for the dog arterial tree are reported separately. With these data a fractal description of the pulmonary vascular tree is presented and the Poiseuille resistance, total cross-sectional area, and blood volume in the venous vessels were computed.

METHODS
Preparation of pulmonary venous tree casts. The lung of a mongrel dog weighing 25 kg was prepared by the same method reported earlier by Yen et al. (28). Briefly, after the dog was anesthetized with a pentobarbital sodium solution (30 mg/kg iv), the trachea was cannulated and the lung was ventilated. After a midline incision, the heart and lungs were exposed and the airway pressure was held at a constant pressure of 10 cmH₂O above the pleural (atmospheric) pressure. Through a cannula inserted into the main pulmonary artery, the pulmonary blood vessels were perfused with a low-viscosity (20 cp) silicone elastomer freshly catalyzed with 3% tin octulate (stannous 2-ethyl hexoate) and 5% ethyl silicate. The elastomer was drained from a cannula inserted into the left atria. After perfusion at a pressure of 34 cmH₂O for 20 min, the atrial cannula was closed and the perfusion pressure was lowered and maintained at 3 cmH₂O. In this condition, the fluid pressure in the capillary blood vessels was lower than the airway pressure and hence the capillary vessels were collapsed, separating the arterial and venous trees. After 2–3 h the silicone elastomer was completely hardened, and the lung was frozen for 2 wk to increase the strength of the elastomer. The lung was then
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17  10

(29/67, 132, 66)

FIG. 1. Sketch of pulmonary subtree with diameter and length measurements in 10-μm units. Single number represents diameter of cut-off vessel, and numbers in parentheses represent diameter and length measured in intact vessel, respectively. Largest diameter of vessel segment in tree is 97 units (970 μm), as shown at bottom.

corroded with a 10% KOH solution for several days. On dissolution the capillary vessels disappeared, and casts of the arterial and venous trees were obtained.

Measurement of the casts. Pulmonary veins with diameters >20 μm branch like a tree. We defined each vessel between two successive points of bifurcation as a segment. The diameters and lengths of the segments were measured from the silicone elastomer casts with a special "dimensional analyzer" or "image shearing device." This analyzer consists of a dissection microscope, a video camera, an image rotator, and an image splitter. By moving the image of a blood vessel segment in a direction perpendicular to the longitudinal axis of the vessel over the distance equal to that from one side of the vessel to the other, a measure of the vessel diameter was obtained. The displacement was displayed digitally and was calibrated to yield the vessel diameter in proper units. In the present study, the distance of 10 μm was calibrated in a unit used in the following sketches of the vascular trees. More details of the dimensional analyzer are given by Intaglia and Tompkins (11).

The venous tree of the dog lung has millions of branches. It is impractical to measure every branch, so pruning and statistical methods were used. To facilitate the measurement of the branches, each whole tree of the upper, middle, and lower lobes was trimmed into several main trees. Small subtrees, with the largest branch having a diameter of 600–800 μm, were cut off and separated from the main tree. Some small trees were systematically selected as samples to be measured in detail. The rest of the small trees were further pruned to remove sub-subtrees with a diameter of ≤200 μm. Each tree was then viewed under the dissection microscope for measurement. The remaining main trees were also pruned and measured. The diameter was measured at the midpoint of each vessel segment from the grabbed image. The length was measured between bifurcation points along the centerline. The branching pattern of each pulmonary venous tree was sketched with its measured diameters and lengths. Figure 1 shows an example of a reconstructed pulmonary venous subtree.

Assignment of order numbers to venous branches. Two of the best-known mathematical models of treelike branching systems in physiology are Weibel's generations model (21) and Strahler's orders model (29). Weibel (21) grouped the human airways in generations by assuming a symmetrical branching pattern. The trachea is designated generation 0, the right and left main bronchi generation 1, and so on down the tree. The generation scheme was also used for the pulmonary arterial and ve-
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Fig. 2. Comparison of different versions in Strahler ordering system. A: Horsfield orders, B: Strahler orders, stage 1. C: Strahler orders, stage 2. D: diameter-defined Strahler orders. Each number represents designated order for corresponding vessel segment. Segments AB, BC, BD, DE, and DF, vessels with different values of diameter.

ous trees (22). The grouping in orders was developed by Strahler for rivulets collecting into a river (19). Horsfield et al. (8, 10), Cumming et al. (1), and Singhal et al. (16) adapted Strahler orders to describe the vessel branches in the bronchial tree and the pulmonary arteries and veins. In contrast to the generations approach, Strahler orders begin at the smallest vessels and count upward. In this method, the smallest vessels are defined as order 1, two order 1 vessels join to form a larger vessel of order 2, and so on toward the main trunk. Strahler’s method has been developed into several versions. The first version (Fig. 2A) is called Horsfield’s method of ordering, which is the reverse of the Weibel system: at each junction, the order increases by 1 from the higher order of the two merging branches. The second version (Fig. 2B) is the conventional Strahler system. When two vessels of different orders meet, the order of the mother vessel remains the same as that of the larger daughter vessel. After all the branches are thus ordered, contiguous branches of the same order are redefined as constituting just one vessel branch (Fig. 2C).

Previous studies on pulmonary arteries and veins of humans and cats by Horsfield and co-workers (8, 10) and Yen et al. (28, 29) have shown that Strahler’s method deals with the asymmetric bifurcations nicely. However, an unsatisfactory feature of the Strahler scheme occurs when two daughter vessels are no smaller than the parent but are assigned two different order numbers or when a long vein has many small branches such that the main trunk appears tapered but is assigned a fixed order number. In either case, the ranges of the diameters of vessels in successive orders overlap extensively. These overlaps make the calculation of the resistance to flow in successive orders of vessels inaccurate. Alternatively, such overlaps may reduce the applications of the data for hemodynamic analysis. To remedy these unsatisfactory effects, a diameter-defined Strahler ordering scheme (DDS) has been introduced by Kassab et al. (12, 13).

In the DDS system, vessel diameter is the main focus and a criterion introduced to determine the vessel order as follows. The conventional Strahler’s method (Fig. 2, B and C) was first used to assign order numbers of vessels, and the data on diameters of the vessels were collected. Let the means ± SD of an arbitrary order n be $D_n$ and $\delta D_n$ respectively. The range of diameters around $D_n$ is then computed from the values of means ± SD in vessels of orders $n-1$, $n$, and $n+1$ with the formula

$$D_{n,\text{min}} = [(D_n - \delta D_n) + (D_n - \delta D_n)]/2 \quad (1)$$

and

$$D_{n,\text{max}} = [(D_n + \delta D_n) + (D_{n+1} - \delta D_{n+1})]/2 \quad (2)$$

where $D_{n,\text{min}}$ and $D_{n,\text{max}}$ are the minimum and maximum values of the range of diameters around $D_n$, respectively. With the use of a diameter range as the criterion, the order number of blood vessels is revised to follow the rule that when two vessels of a given order $n$ meet, the order number of the offspring is increased by one, i.e., $n+1$, if and only if its diameter is larger than those of the vessels of order $n$ by an amount specified in the criterion. Fig. 2D shows the changes incurred by the diameter-defined criterion on the tree of Fig. 2C when the diameter of vessel segment AB is greater than the criterion of order 3 vessels. After revision, new values of $D_n$ and $\delta D_n$ are computed for $n = 1, 2, \ldots$, and the process is repeated until convergence is obtained. Our experience shows that the convergence is very rapid and that $\delta D_n$ is reduced with small changes in $D_n$ after one or two iterations. Finally, the diameter ranges of vessels in successive orders have no overlap.

In the present study, we have used the DDS method to order the dog’s pulmonary venous tree. The measured smallest postcapillary blood vessels were defined as vessels of order 1. Larger veins were classified into higher orders according to the above rule. Thus, the pulmonary veins had orders 1, 2, 3, . . . , arranged from the capillary bed to the left atrium. Figure 3 shows the venous subtree of Fig. 1 with the branches ordered according to the DDS method. The definition of vessels of order 1 follows the description of pulmonary venous vessels for cats and humans by Yen et al. (27, 28). From the typical photomicrographs of cat and human lungs, Yen et al. have shown the relationship between the capillary bed and several orders of venules. They consider the very short segment or the exit section of the capillaries as the junction of nonfilled capillary sheets that belong to the capillaries. The smallest noncapillary vessels were then identified as vessels of order 1 with an average diameter of 22 μm. However, their measured results of order 1 vessels were obtained from histological slides instead of casts, as used in the present study. Thus, our measured diameters of order 1 vessels were greater than those measured by Yen et al.

Counting of branches. Because a venous tree of the dog has millions of branches, it is impossible to count and measure every branch. Some statistical methods have to be used to estimate the number of vessels in each order and to correct for the number of broken branches. A statistical iteration method for data reduction based on a single global branching ratio is presented in the appendix of the paper of Yen et al. (29). Another method, based on
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any individual local branching ratios, is reported by Nassab et al. (12, 13). Here we employed the latter method to count the number of branches in the pulmonary venous tree.

In general, vessels of order \( n \) may spring off from vessels of orders \( n + 1, n + 2, \ldots \). Information of this sort is presented in the form of a matrix, the component which is the ratio of the total number of vessels of order \( n \) sprung off from vessels of order \( m \) to the total number of vessels in order \( m \). Kassab et al. (12, 13) called \( n \) the connectivity matrix and denoted its component as \( C(n,m) \). It is clear that when the number of vessels of order \( m \) (\( N_m \)) is known, the numbers of orders \( m-1, \ldots, 2, \) and \( 1 \) that directly arise from the vessels of order \( m \) can be calculated as \( C(m,m)N_m, C(m-1, m)N_m, \ldots, C(2, m)N_m, \) and \( C(1, m)N_m \), respectively. Therefore, after the connectivity matrix is obtained, the number of each order in the missing subtrees of the off or broken-off branches may be computed from

\[
N'_n = \sum_{m=n}^{n_{\text{max}}} C(n,m)(N_m + N_{\text{cut}})
\]

where \( N_{\text{cut}} \) is the number of cut-off branches in order \( m \); and \( N_m \) are the number of vessels of orders \( n \) and \( m \), respectively; and \( m \) is equal to or greater than \( n \), with an upper limit on the orders in the examined tree, \( n_{\text{max}} \). The calculation is done first for \( n = n_{\text{max}} \) and then successively proceeds to \( n = n_{\text{max}} - 2, n_{\text{max}} - 2, \ldots \). This process includes all the missing subtrees. The total number of intact vessels in order \( n \) (\( N_{n,in} \)) is counted from the cast. Thus, the corrected total number of branches in order \( n \) is the sum of \( N_{n,in} \) and \( N'_n \).

Fractal description. Recently, the fractal concepts have extended our insight into many diverse and natural phenomena. Fractal mathematics provides new methods to analyze nonlinear dynamics and morphology (14). The criteria of fractal objects include a large degree of heterogeneity, self-similarity structure over many size scales, and no well-defined (characteristic) scale of measure. Those criteria are met by a number of biophysical structures, such as the tracheobronchial tree, the vascular network, and neural networks (5, 23). The concept of dimension is useful in characterizing the structural complexity of fractal objects. Several definitions of dimension that may be used to describe fractal sets are introduced by many investigators. Here, to make a fractal description of the dog pulmonary venous tree, we used a method similar to that of Nelson (15) to determine the fractal dimensions of vessel branch diameter and length. In these cases, the fractal dimension (\( D_f \)) may be estimated by

FIG. 3. Sketch of same pulmonary venous subtree as that in Fig. 1, with assigned diameter-defined Strahler orders annotated by integers. * Vessel segments remaining in same order.
TABLE 1. Experimental measurements of diameter and length of vessels in each order of dog venous tree

<table>
<thead>
<tr>
<th>Order</th>
<th>Diameter, µm</th>
<th>Length, mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Means ± SD</td>
<td>No. of vessels measured</td>
</tr>
<tr>
<td>11</td>
<td>8,450±250</td>
<td>2</td>
</tr>
<tr>
<td>10</td>
<td>4,480±235</td>
<td>6</td>
</tr>
<tr>
<td>9</td>
<td>2,775±354</td>
<td>20</td>
</tr>
<tr>
<td>8</td>
<td>1,826±137</td>
<td>28</td>
</tr>
<tr>
<td>7</td>
<td>1,167±113</td>
<td>55</td>
</tr>
<tr>
<td>6</td>
<td>737±101</td>
<td>108</td>
</tr>
<tr>
<td>5</td>
<td>441±70</td>
<td>320</td>
</tr>
<tr>
<td>4</td>
<td>251±39</td>
<td>491</td>
</tr>
<tr>
<td>3</td>
<td>142±24</td>
<td>979</td>
</tr>
<tr>
<td>2</td>
<td>78±14</td>
<td>1,122</td>
</tr>
<tr>
<td>1</td>
<td>29±12</td>
<td>2,407</td>
</tr>
</tbody>
</table>

Values were obtained at pleural pressure = 0 cmH2O (atmospheric), airway pressure = 10 cmH2O, and pulmonary venous pressure = 3 cmH2O.

\[
1 - D_f = \frac{\log(\text{total size of object for order } n)}{\log(\text{average size of object for order } n)} \quad (4)
\]

The fractal dimension is then obtained from plotting, on logarithmic scales for both axes, the total size versus the average size of the object.

RESULTS

Our data of the pulmonary venous tree in the dog’s right lung show that there is a total of 11 orders of pulmonary veins lying between the capillaries and the left atrium. Table 1 shows our experimental results of the means ± SD of the diameters and lengths of vessel branches as well as the number of vessels measured. From these data, the relationship between the mean diameter of vessels in each order and the order number is shown in Fig. 4, and the relationship between the mean values of vessel length and the order number is depicted in Fig. 5.

In Fig. 4, if y represents the logarithm of the diameter and x represents the order number, then the least-squares fit regression line is \( y = 1.4128 + 0.2307x \). The slope gives an average diameter ratio of 1.701. Similarly, in Fig. 5, if y represents the logarithm of the vessel length and x represents the order number, then the regression line is \( y = -0.5206 + 0.1920x \), yielding an average length ratio of 1.556.

The connectivity of blood vessels of one order to another is expressed in the connectivity matrix for which the component \( C(n,m) \) is the ratio of the total number of vessels of order \( n \) sprung off from parent vessels of order \( m \) to the total number of vessels of order \( m \). To experimentally obtain the matrix for the average branching pattern in the venous vasculature, we examined the whole tree for all the branches of the casts of orders 1-11.

As a simple numerical example, the tree in Fig. 2D is used to calculate the element \( C(1,m) \), where \( m = 1, 2, 3, \) and 4. There are three vessels of order 2 that give rise to eight vessels of order 1 and one vessel of order 3 that gives rise to one order 1 vessel. Thus, \( C(1,2) = 8/3 \) or 2.67, the average of the three ratios of 3, 3, and 2, over all order 2 vessels with a standard deviation of 0.47; likewise, \( C(1,3) = 1/1 \) or 1. Because there is no order 1 vessel rising from order 1 or 4, \( C(1,1) = 0 \) and \( C(1,4) = 0 \). By similar reasoning, the other components of \( C(n,m) \) and their standard deviations can be derived.

The experimentally obtained connectivity matrix of the pulmonary venous tree of the dog is shown in Table 2. In addition to displaying the global branching pattern of the whole vascular tree, the connectivity matrix provides ample information for calculating the number of branches in each order. For instance, the last column shows that the largest (order 11) vessels in the pulmo-

![Fig. 4](image-url) Average diameter of vessels in each order vs. order number. If \( y \) represents logarithm of diameter and \( x \) represents order number, then \( y = 1.4128 + 0.2307x \) describes results.

![Fig. 5](image-url) Average length of vessels in each order vs. order number. If \( y \) represents logarithm of length and \( x \) represents order number, then \( y = -0.5206 + 0.1920x \) describes results.
nary veins are connected to six vessels of order 10, two vessels of order 8, and no vessels of the other orders. The ninth row shows that none of the order 9 vessels is connected to the largest vessel of order 11, 26 vessels of order 9 (2.2 × 12 = 26, where 12 is the number of vessels of order 10 from Table 3) are connected to vessels of order 10, and three vessels of order 9 (0.091 × 29 = 2.6) are connected to vessels of order 9 from Table 3) are connected to vessels of order 9.

The total number of branches of each order in the venous tree can be computed from the information given in Tables 2 and 3 by using Eq. 3. The computation begins from the largest vessels of order 11, i.e., \( n_{\text{max}} = 11 \) in Eq. 3, and then proceeds successively to \( n = 10, 9, \ldots, 1 \). The results are shown in Table 3. The number of intact vessels and cut-off or broken-off vessels and the total number of branches in each order are also listed in Table 3.

The relationship between the number of branches in each order and the order number is shown in Fig. 6. Here the logarithm of the number of branches (y) in each order is plotted against the order number (x). The regression line is \( y = 6.5602 - 0.5754x \), yielding an average branching ratio of 3.762 over the 11 orders.

Figure 7 plots the total diameter resulting from the summation of the lengths of all vessels in a given order vs. the average branch length for the same order vessels on a log-log scale. Each point on the graph corresponds to a specific branching order. The slope of the regression line gives the fractal dimension of the branch length of the dog's pulmonary venous tree as 2.99.

It is seen from Figs. 7 and 8 that the pulmonary venous system is a fractal structure that provides a mechanism for converting an alveolar-capillary surface area of dimension two into a volume of dimension three. The estimated values of the fractal dimension for vessel diameter and branch length may be useful for developing structure-generating functions. However, our approach for fractal analysis of pulmonary vasculature is derived from the morphometric measurement of one dog's lung casts, which is not sufficient to complete the study of fractal geometry for the pulmonary vascular tree of the dog.

### Table 2. Connectivity matrix

<table>
<thead>
<tr>
<th>Order</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.690±1.207</td>
<td>2.953±1.758</td>
<td>1.517±1.943</td>
<td>1.072±1.740</td>
<td>1.010±1.783</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0.263±0.318</td>
<td>1.716±1.504</td>
<td>1.478±1.503</td>
<td>1.559±1.536</td>
<td>2.383±2.040</td>
<td>2.143±2.669</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>0.359±0.838</td>
<td>1.770±1.120</td>
<td>1.539±1.526</td>
<td>2.159±2.142</td>
<td>2.429±2.615</td>
<td>1.716±2.186</td>
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<tr>
<td>4</td>
<td>0.191±0.440</td>
<td>1.794±1.111</td>
<td>1.889±1.617</td>
<td>2.086±1.687</td>
<td>2.118±1.364</td>
<td>1.091±1.221</td>
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<tr>
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<td>0.216±0.436</td>
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<td>2.086±1.541</td>
<td>2.176±1.811</td>
<td>2.000±1.368</td>
<td>1.727±1.009</td>
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<td>0.415±0.788</td>
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<td>1.861±1.385</td>
<td>1.727±1.009</td>
<td>0.4±0.548</td>
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<tr>
<td>9</td>
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<td>2.2±0.837</td>
<td>0</td>
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</table>

Values are means ± SD. Element \((n, m)\) in row \(n\) and column \(m\) is ratio of total number of branches of order \(n\) that spring directly from parent branches of order \(m\) to total number of branches of order \(m\) in dog's venous tree.

### Table 3. Computation of total number of branches in each order of dog's venous tree

<table>
<thead>
<tr>
<th>Order</th>
<th>No. of Intact Vessels</th>
<th>No. of Cut Vessels</th>
<th>No. of Extrapolated Vessels</th>
<th>No. of Vessels (Corrected Total)</th>
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<tr>
<td>11</td>
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<td>1</td>
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<td>2</td>
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<td>78,410</td>
</tr>
<tr>
<td>2</td>
<td>199</td>
<td>903</td>
<td>213,540</td>
<td>214,642</td>
</tr>
<tr>
<td>1</td>
<td>596</td>
<td>1,046</td>
<td>2,474,291</td>
<td>2,475,933</td>
</tr>
</tbody>
</table>

**Figure 6.** Number of branches in each order vs. order number. If \(y\) represents logarithm of number of branches and \(x\) represents order number, then \(y = 6.5602 - 0.5754x\) describes results.
However, our present results serve as a foundation for other morphometric results to follow.

On the basis of the morphometric data of the pulmonary venous vasculature, the total cross-sectional area and vascular volume in every order can be computed along the venous pathway. Figure 9 shows the variation of the total cross-sectional area with the order number in the venous tree. The cross-sectional area of order \( n \) \( (A_n) \) is defined as the product of the area of each vessel and the total number of vessels

\[
A_n = (\pi/4)D_n^2N_n
\]

where \( D_n \) is the average diameter of vessels and \( N_n \) is the total number of vessels of order \( n \). The results shown in Fig. 9 are fitted with an exponential function.

The total blood volume of order \( n \) \( (V_n) \) is given by

\[
V_n = A_nL_n
\]

or

\[
V_n = (\pi/4)D_n^2L_nN_n
\]

where \( L_n \) is the average length of vessels of order \( n \). The calculated venous blood volumes are plotted on a logarithmic scale against their order number in Fig. 10. It is seen that the data may be fitted by a straight line. If \( y \) represents the logarithm of the blood volume and \( x \) represents order number, then

\[
y = -0.2398 + 0.0780x
\]
TABLE 4. Comparison of diameter, length, and branching ratios and number of orders in pulmonary venous tree of dog, cat, and human

<table>
<thead>
<tr>
<th></th>
<th>No. of Orders</th>
<th>DR</th>
<th>LR</th>
<th>BR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dog</td>
<td>11</td>
<td>1.701</td>
<td>1.556</td>
<td>3.762</td>
</tr>
<tr>
<td>Cat</td>
<td>11</td>
<td>1.727</td>
<td>1.533 (4-10)</td>
<td>3.521</td>
</tr>
<tr>
<td>Human</td>
<td>15</td>
<td>1.682 (7-14)</td>
<td>1.679 (7-14)</td>
<td>3.301</td>
</tr>
<tr>
<td></td>
<td>1.493 (1-6)</td>
<td>1.476 (1-6)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

DR, diameter ratio; LR, length ratio; BR, branching ratio. Values of ratios are calculated from total number of orders, except values with numbers in parentheses. Numbers in parentheses refer to order numbers from which ratios have been calculated. [Data for cat are from Yen et al. (24, 25), and data for human are from Horsfield et al. (8, 10).]

represents the order number, then the regression line is

\[ y = -0.2398 + 0.0780x \]

The slope yields an average volume ratio of 1.197 over the 11 orders.

**DISCUSSION**

The morphometric data of the pulmonary venous tree provide three system ratios: the diameter, length, and branching ratios. The concept of system ratio is based on Horton’s law of stream numbers. Horton (7) observed that although the branching ratio is not exactly the same from one order to the next, it will tend to approach a constant throughout the range of orders. Mathematically, Horton’s law states that the number of branches in each order is an exponential function of the order number

\[ N_n = N_1(BR)^{1-n} \]  

where BR is the average branching ratio for the system as a whole. When taking the logarithm of both sides of Eq. 7, we obtain

\[ \log N_n = (\log N_1 + \log BR) - n \log BR \]  

If \( y \) represents the logarithm of the number of branches and \( x \) represents the order number, then Eq. 8 is the least-squares fit regression line for the plotting of the number of branches against the order number. The antilog of the absolute value of the slope of the regression line is defined as the average branching ratio. For the pulmonary venous tree, Eq. 8 is presented in Fig. 6 as \( y = 6.5602 - 0.5754x \) and the branching ratio is 3.762.

Horton’s law is statistical in nature and provides information on average properties. It can also be applied to measurements of vessel diameter and branch length for the pulmonary venous tree. Because the diameter and length increase with order, the average diameter of vessels \( (D_n) \) and the average length of branches \( (L_n) \) in each order are presented as

\[ D_n = D_1(DR)^{n-1} \]  

and

\[ L_n = L_1(LR)^{n-1} \]  

where DR and LR are the average diameter and length ratios, respectively. Similarly, after taking the logarithm of both sides of the equations, we obtain

\[ \log D_n = (\log D_1 - \log DR) + n \log DR \]  

and

\[ \log L_n = (\log L_1 - \log LR) + n \log LR \]

The exact forms of Eqs. 11 and 12 for the dog’s venous tree are illustrated in Figs. 4 and 5. The diameter and length ratios were calculated as 1.701 and 1.556, respectively.

These three system ratios are the most important parameters in the analysis of pulmonary blood flow. Table 4 shows a comparison of diameter, length, and branching ratios for the pulmonary venous tree of the dog with those of cats and humans. It can be seen that our data are similar, in certain aspects, to the data from cats and humans.

The differences between these studies may partly stem from the definition of order 1 vessels. Branches averaging 29 \( \mu m \) in diameter are taken to be order 1 in the present study on the dog, which corresponds exactly with the order 3 vessels in the human venous tree (8). However, regarding the order 1 definition by Yen et al. (27, 28), the order 2 branches in humans are better represented by the order 1 in cats, which was pointed out by both authors (9, 27). Thus, in response to this interpretation, the dog’s venous tree has 12 DDS orders compared with 11 orders in the cat venous tree and 14 orders in the human venous tree.

When the morphometric data of the pulmonary venous tree are combined with the morphometric data of the arterial tree and capillary bed and the elasticity data of those blood vessels, a theoretic analysis of blood flow in the lung can be completed. Zhuang et al. (30) have presented such an analysis for the cat and predicted the resistance distribution in the lung. This resistance is influenced by both the morphometry and distensibility of the pulmonary vascular system. For a steady blood flow in a rigid tube, the pressure-flow relationship is described by Poiseuille’s equation, which applied for each vessel of order \( n \) is

![Fig. 11. Computed Poiseuille's resistance of venous branches in each order vs. order number. Each point corresponds to specific branching order.](image-url)
\[ \Delta P_n = (128 \mu_n L_n / \pi D_n^4 N_n) Q_n \]  
(13)

or

\[ \Delta P_n = R_n Q_n \]  
(14)

where \( \Delta P_n \) is the pressure drop at order \( n \), \( \mu_n \) is the apparent viscosity of the blood, \( Q_n \) is the total flow in order \( n \), and \( R_n \) is defined as Poiseuillean resistance of order \( n \) and is given by the terms within parentheses in Eq. 13. Obviously, the Poiseuillean resistance considers only the morphometric aspects of the vessels.

To calculate the Poiseuillean resistance in each order, the apparent viscosity values of blood should be estimated first. According to the results determined by Yen and Fung (25) in model experiments and calculations, an apparent viscosity of 4.0 cp is assumed in large vessels. The apparent viscosity of blood in small vessels of orders 1–3 is obtained by interpolation as 2.5, 3.0, and 3.5 cp, respectively.

With these data the Poiseuillean resistance from orders 1–11 in the dog’s venous tree was computed, and the results are shown in Fig. 11. It is seen that most of the resistance occurs in the small vessels of diameters <100 \( \mu m \) and that the resistance in the small vessels is 55% of the cumulative Poiseuillean resistance in the venous system.

In addition to the Poiseuillean resistance, the blood volume distribution within the venous bed provides a functional analysis for pulmonary circulation. The results of Fig. 10 show that blood volume increases with order number, and the average vascular volume in order \( n \) \( (V_n) \) is presented as

\[ V_n = V_1 (VR)^{n-1} \]  
(15)

where VR is the average volume ratio. The best fit relationship between the average blood volume and the order number is also illustrated in Fig. 10. The equations result in the vascular volume ratio of 1.197 for the pulmonary venous tree of the dog. The cumulative venous volume is 22 ml in the dog’s right lung, where 50% of the total venous volume resides in the largest three orders of the venous tree.

Results obtained from measurements of vascular volume in the lung (6, 9, 10, 20) are quite variable. These wide variations may be related to the different physiological states and experimental conditions for data measurement. Horsfield (9) studied the cast model of the human pulmonary venous tree and showed that the total venous volume was 73 ml, compared with an arterial volume of 86 ml (excluding the main pulmonary artery). Compared with this result, the 22-ml volume of blood in the venous tree in the dog’s right lung is reasonable.

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REFERENCES


