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ANGLES OF BRANCHING AND DIAMETERS OF BRANCHES IN THE HUMAN BRONCHIAL TREE

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The principle of minimal work requires that the conducting airways of the human lung should have a maximum radius for minimal resistance to gas flow. At the same time there is a requirement that the airways should have a minimal volume for economy of space. These two opposing requirements have been investigated mathematically, and a method for calculating the angle of branching which produces minimal volume has been derived. The relationship of the radii of the parent and daughter branches to produce minimal resistance has been similarly defined. By measurement of a bronchial cast from a human lung the extent to which the predicted optimum structure is realized in practice has been shown. The change in structure associated with change of function at the transition from conducting airway to diffusion zone has been demonstrated.

The detailed form of biological structures reflects the changes brought about by natural selection and adaptation to the environment, so that form has a survival value. The determinants of form are multifactorial; and while it is possible to enumerate some of these factors, an analysis of their effects on form and function is more difficult. Such an analysis, demonstrating the phenomenon of biological compromise, has been undertaken by several authors (Rashevsky, 1960; d'Arcy Thompson, 1952). It is the purpose of this paper to investigate the form of branching in the human bronchial tree in a theoretical manner, then to compare the results with those actually found.

In the higher vertebrates the lungs are situated within the body cavity. Their function is to exchange gases between the blood and the atmosphere.

The ventilatory aspects of this function take place in two stages. Firstly, gas is transported by a series of branching tubes into the lungs, and then the transported gas is mixed with that already present by gaseous diffusion in the distal airways.

For maximum efficiency a large cross sectional area should be available for diffusion in the gas phase together with a maximum alveolar surface area for exchange of gases with the blood. Any lung volume occupied by conducting airways is not available for alveolar tissue; hence, the maximum capacity for gas exchange cannot be realized. Therefore, the volume of the conducting airways should be as small as possible.

Since the length of the bronchi must be finite, economy of volume could be achieved by having a small diameter. This solution conflicts with a second requirement, that the conducting airways should have a low resistance to flow and thus conform to the biological principle of minimal work. To satisfy this condition the airways should have as large a diameter as possible. Thus the two primary requirements are conflicting and a compromise is necessary. The influence of these two factors on the morphology of the bronchial tree can be investigated.

The theoretical investigation of bronchial tree morphology.

The theory of minimal resistance. Since the human bronchial tree branches by dichotomy, the number of branches N in a generation w is given by

$$N = 2^w. \tag{1}$$

For the purpose of analysis of the size of branches it will be assumed to be a symmetrical system in which all the branches in a given generation are of the same length and diameter.

Let the resistance to flow of gas through one branch in generation w be R_w. Then the reciprocal of the total resistance R of all the branches in parallel is given by

$$\frac{1}{R} = \frac{1}{R_w} \times 2^w, \tag{2}$$

$$R = \frac{R_w}{2^w}. \tag{3}$$

The total resistance of the system R_t is given by the sum of the resistances of each generation since the generations are in series:

$$R_t = \frac{R_0}{2^0} + \frac{R_1}{2^1} + \frac{R_2}{2^2} + \cdots \frac{R_W}{2^W}, \tag{4}$$

where W is the total number of generations. From Poisseuille's equation for laminar flow

$$R_w = \frac{8\eta L_w}{\pi r_w^4}, \tag{5}$$

where L_w and r_w are the length and radius of the bronchus respectively, and η is the viscosity of the air.

From (4) and (5)

$$Rt = \frac{8\eta L_0}{\pi r_0^4} + \frac{8\eta}{\pi} \sum_{w=1}^{w=W} \frac{L_w}{2^w r_w^4}. \tag{6}$$

Let the bronchial wall be of thickness a, a small proportion of the total diameter, and of density b. Then the mass of tissue, M_w in one branch of generation w is given by

$$M_w = 2\pi r_w L_w ab. \tag{7}$$

The thickness of the wall is proportional to the radius of the bronchus (Engel, 1947), so

$$a = r_w c, \tag{8}$$

where c is a constant,

From (7) and (8)

$$M_w = 2\pi r_w^2 L_w bc.$$

Let $bc = k$, then

$$M_w = 2\pi r_w^2 L_w k. \tag{9}$$

The total mass, M_t, is given by the sum of M_w for each branch of each generation

$$M_t = 2\pi r_0^2 L_0 k + 2\pi k \sum_{w=1}^{w=W} 2^w r_w^2 L_w, \tag{10}$$

$$2\pi r_0^2 L_0 k = M_t - 2\pi k \sum_{w=1}^{w=W} 2^w r_w^2 L_w, \tag{11}$$

$$r_0^2 = \frac{M_t}{2\pi L_0 k} - \frac{1}{L_0} \sum_{w=1}^{w=W} 2^w r_w^2 L_w, \tag{12}$$

$$r_0^2 = \frac{1}{L_0}\left(\frac{M_t}{2\pi k} - \sum_{w=1}^{w=W} 2^w r_w^2 L_w\right). \tag{13}$$

Substituting for r_0 from (13) into (6) we get

$$Rt = \frac{8\eta L_0}{\pi} \times \frac{L_0^2}{\left[\frac{M_t}{2\pi k} - \sum_{w=1}^{w=W} 2^w r_w^2 L_w\right]^2} + \frac{8\eta}{\pi} \sum_{w=1}^{w=W} \frac{L_w}{2^w r_w^4}. \tag{14}$$

Partial differentiation of R_t with respect to r_w, followed by putting $\partial R_t/\partial r_w = 0$ gives a value of r_w with a maximum or minimum value of R_t. By finding the second derivitive of R_t with respect to r_w in equation (14), the value of R_t has been shown to be a minimum (Rashevsky, 1960). The differentiation gives

$$\frac{\partial R_t}{\partial R_w} = \frac{32\eta}{\pi}\left(\frac{2^w r_w L_w}{\mathrm{r}_0^6} - \frac{L_w}{2^w r_w^5}\right). \tag{15}$$

If $\dfrac{\partial R_t}{\partial r_w} = 0$, then from (15)

$$\frac{2^w r_w L_w}{r_0^6} = \frac{L_w}{2^w r_w^5}; \tag{16}$$

$$r_0^6 = r_w^6 2^{2w}; \tag{17}$$

$$r_w = r_0 2^{-w/3}. \tag{18}$$

Similarly,

$$r_{(w+1)} = r_0 2^{-(w+1)/3}. \tag{19}$$

From (18) and (19)

$$\frac{r_w}{r_{(w+1)}} = \frac{r_0 2^{-w/3}}{r_0 2^{-(w+1)/3}} = \frac{1}{2^{-1/3}} = 3\sqrt{2}, \quad r_{(w+1)} = r_w 2^{-1/3} = 0.794\, r_w. \tag{20}$$

Put into words, when the total mass and the lengths of the branches are defined, the radius of each daughter branch should be 0.794 that of the parent branch for the system to have minimal resistance. Although r decreases as w increases, the total cross sectional area increases. Thus, the cross sectional area of the parent branch, A_w, is given by

$$A_w = 2\pi r_w^2. \tag{21}$$

The cross sectional area of a daughter branch $A_{(w+1)}$ is given by

$$A_{(w+1)} = 2\pi r_{(w+1)}^2. \tag{22}$$

Substituting for $r_{(w+1)}$ from (20) into (22)

$$A_{(w+1)} = 2\pi(r_w 2^{-1/3})^2 = 2\pi r_w^2 \times 2^{-2/3}. \tag{23}$$

From (21) and (23), and considering two daughter branches,

$$\frac{A_w}{2(A_{(w+1)})} = \frac{2\pi r_w^2}{4\pi r_w^2 2^{-2/3}} = \frac{1}{2 \times 2^{-2/3}} = 2^{-1/3} = 0.794. \tag{24}$$

Thus, in each successive generation the radius of each branch should decrease by a factor of 0.794, and the total cross sectional area should increase by $\frac{1}{0.794}$, for minimal resistance under the defined conditions.

The theory of minimal volume. Given three branches of known radii arising from any three points in space A, B and C (Fig. 1a) and meeting at D, then there will be some position of D such that the total volume of the three branches will be minimal. This system has been partly analyzed by Barnett (1957), who considered the special case where ABC (Fig. 1a) is an equilateral triangle and

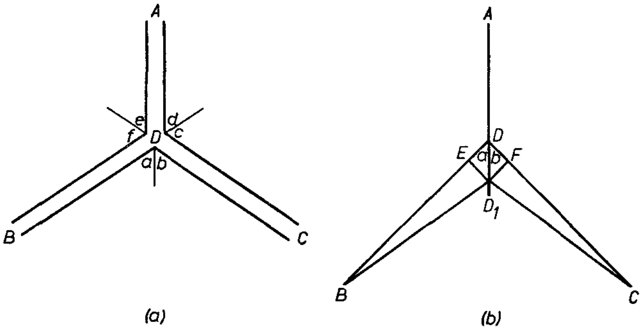

Figure 1. For explanation see text

$AD = \frac{1}{2}BC$. He showed that for minimal volume $\angle a$ is less than $\angle b$ when the radius of branch BD is more than that of branch DC. That is to say, the larger daughter branch deviates least from the line of the parent branch when the system has minimal volume.

The general case (with an exception described later) may be analyzed as follows: Let A, B and C (Fig. 1b) be any three points in space from which come three branches AD, BD and CD meeting at D. Let the lengths and radii of AD, BD and CD be L_1, L_2, L_3 and r_1, r_2 and r_3 respectively.

Now let D be at the position which results in minimal total volume. Then it follows that the rate of change of volume with change in the position of D is zero at this point. Or, if D is moved a very small amount in any direction, the total volume will not change.

Let D move a small distance ΔL_1 along the line of AD to D_1 and points E and F be such that $BD_1 = BE$, and $CD_1 = CF$. Also, $DE = \Delta L_2$ and $DF = \Delta L_3$. In the limit as $\Delta L_1 \to 0$, $\angle D_1ED$ and $\angle D_1FD$ become right angles. If $\angle BDD_1$ be a, and $\angle CDD_1$ be b, then

$$\Delta L_2 = \Delta L_1 \cos a, \tag{25}$$

$$\Delta L_3 = \Delta L_1 \cos b. \tag{26}$$

Now the volume of the system V is given by the sum of the volumes of $AD + BD + CD$,

$$V = L_1\pi r_1^2 + L_2\pi r_2^2 + L_3\pi r_3^2.$$

When D moves to D_1, the volume of AD increases while those of BD and CD decrease, the total remaining unchanged.

Therefore increase in the volume of AD = decrease in the volume $BD + CD$,

$$\Delta L_1 \pi r_1^2 = \Delta L_2 \pi r_2^2 + \Delta L_3 \pi r_3^2. \tag{27}$$

From (25), (26) and (27)

$$\Delta L_1 \pi r_1^2 = \Delta L_1 \cos a \pi r_2^2 + \Delta L_1 \cos b \pi r_3^2, \tag{28}$$

$$r_1^2 = \cos a r_2^2 + \cos b r_3^2, \tag{29}$$

$$\cos a = \frac{r_1^2}{r_2^2} - \frac{\cos b r_3^2}{r_2^2}. \tag{30}$$

Similarly it can be shown (Fig. 1a) that

$$\cos c = \frac{r_2^2}{r_3^2} - \frac{\cos d r_1^2}{r_3^2}, \tag{31}$$

and

$$\cos e = \frac{r_3^2}{r_1^2} - \frac{\cos f r_2^2}{r_1^2}. \tag{32}$$

But since $d = a$, $b = e$ and $c = f$, by substitution in (31) and (32) we get

$$\cos c = \frac{r_2^2}{r_3^2} - \frac{\cos a r_1^2}{r_3^2}, \tag{33}$$

and

$$\cos b = \frac{r_3^2}{r_1^2} - \frac{\cos c r_2^2}{r_1^2}. \tag{34}$$

Now let

$$\frac{r_1^2}{r_2^2} = P, \quad \frac{r_2^2}{r_3^2} = Q \quad \text{and} \quad \frac{r_3^2}{r_1^2} = R.$$

Then (30), (33) and (34) can be expressed as

$$\cos a = P - \frac{\cos b}{Q}; \tag{35}$$

$$\cos b = R - \frac{\cos c}{P}; \tag{36}$$

$$\cos c = Q - \frac{\cos a}{R}. \tag{37}$$

From (35) and (36) we get

$$\cos a = P - \frac{1}{Q}\left(R - \frac{\cos c}{P}\right), \tag{38}$$

and from (37 and (38)

$$\cos a = P - \frac{1}{Q}\left[R - \frac{1}{P}\left(Q - \frac{\cos a}{R}\right)\right], \tag{39}$$

$$\cos a = P - \frac{R}{Q} + \frac{1}{P} - \frac{1}{QPR}\cos a. \tag{40}$$

But $QPR = 1$.

Therefore

$$2\cos a = P - \frac{R}{Q} + \frac{1}{P}; \tag{41}$$

$$\cos a = \frac{1}{2}\left(P + \frac{1}{P} - \frac{R}{Q}\right). \tag{42}$$

Similarly it can be shown that

$$\cos b = \frac{1}{2}\left(R + \frac{1}{R} - \frac{Q}{P}\right). \tag{43}$$

Knowing the radii r_1, r_2 and r_3 we can thus compute the angle of branching for minimal volume of the system. If $r_1 > r_2 > r_3$ (i.e., the parent branch is the largest, and r_2 is the radius of the larger daughter branch), then $\cos a > \cos b$ and $b > a$.

Thus the larger branch deviates least from the line of the parent branch when the system occupies minimal volume.

In a symmetrical system with minimal resistance, equation (20) implies $r_2 = r_3 = 0.794\, r_1$. By solving (42) and (43) with $r_1 = 1$, $r_2 = 0.794$, $r_3 = 0.794$, we get $a = b = 37°\ 28'$. This is the angle of branching for minimal volume in a system with minimal resistance.

This analysis is satisfactory in most cases but when, owing to the degree of variation of the radii in practice, the total cross sectional area decreases at a dichotomy, the situation becomes unreal. Thus, if $r_1^2 > (r_2^2 + r_3^2)$, the minimal volume is given by the system shown in Figure 2a. The line AD has disappeared, and hence there are no angles.

This situation can be analyzed if we assume that AD is of a given length, with BD and CD being variable. Let ABC (Fig. 2b) be any three points as before and AD remain constant. The point D moves through the arc of a circle with A at the center, and there will be some position of D, say D_1, such that the volume of branch BD + branch CD is minimal. Let D move a small arc, ΔD, to D_2. The point F is on CD_2 such that the $CF = CD_1$ and D_2F represents ΔL_3, the increase in L_3.

In the limit, as $\Delta D \to 0$, D_1D_2 becomes a tangent to the arc, $\angle D_1ED_2$ becomes a right angle, and $\angle c = \angle d$. Then

$$\Delta L_3 = \Delta D \cos c = \Delta D \cos d = \Delta D \cos (90 - b) = \Delta D \sin b;$$

$$\Delta L_3 = \Delta D \sin b. \quad (44)$$

Similarly it can be shown that

$$\Delta L_2 = \Delta D \sin a. \quad (45)$$

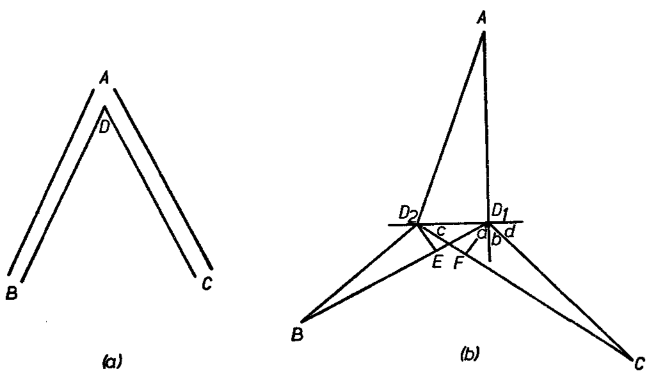

Figure 2. For explanation see text

Now when D moves from D_1 to D_2 the total volume remains constant because the rate of change of volume at D_1 is zero. Hence the increase in the volume of CD equals the decrease in the volume of BD

$$\Delta L_3 \pi r_3^2 = \Delta L_2 \pi r_2^2. \quad (46)$$

Substituting for ΔL_2 and ΔL_3 in (46) from (44) and (45) we get

$$\Delta D \sin b \pi r_3^2 = \Delta D \sin a \pi r_2^2, \quad (47)$$

$$\frac{\sin b}{\sin a} = \frac{r_2^2}{r_3^2}. \quad (48)$$

Thus, if the parent branch is considered to be of a given length, the ratio of the cross sectional areas of the daughter branches is equal to the inverse of the ratio of the sines of their respective angles of branching when the system has minimal volume.

It has been shown for any bronchial dichotomy that for minimal flow resistance there is an ideal ratio between the radii of the branches concerned, and that for minimal volume of the system the angles of branching are a function of the cross sectional areas of the branches. The next section describes the measurement of these parameters on a cast of the bronchial tree in order to see how closely, in practice, they meet the theoretical requirements.

The practical investigation of bronchial morphology.

Methods and materials. The trachea and lungs were removed intact at autopsy from a young man who had died from a nonrespiratory disease. The lungs were fixed in 2 per cent formalin in a position slightly less than full inspiration and a cast of the lumen of the bronchi made using a resin and monomer mixture which polymerises without shrinkage. Concentrated hydrochloric acid was then used to dissolve the tissues away, leaving the intact cast. The method is described in detail elsewhere (Horsfield, Cumming and Hicken, 1966).

Measurements of the diameters of branches were made by placing the points of a pair of dividers across the branch, and then viewing them under a low power microscope with an eye piece grid calibrated to 0.04 mm. Readings were recorded to the nearest 0.1 mm.

The angles of branching were measured by viewing through a rotatable disc of perspex on which were etched two diameters at right angles to each other. On the periphery, an angular scale was marked in degrees. The cast was set up and firmly clamped so that the three branches making up the angle being measured lay in a plane parallel to the disc and as close to it as possible. The point of meeting of the branches, the center of the disc and the observer's eye lay on a line at right angles to their planes so as to avoid parallax. By rotating the disc so that one of the lines across the diameter was aligned with each branch in turn, it was possible to read the angles of branching from the peripheral scale. Readings were recorded to the nearest degree.

The choice of angles to be measured. This study was part of a larger one on normal bronchial anatomy in which every branch down to 0.7 mm. in diameter was measured. All branches measured were allocated an identification number and listed in numerical order. By starting at a random position in the list and taking every fifth branch which had intact daughter branches, 100 random branches were chosen. The diameters of these and their daughter branches were measured, as were the angles between them.

In addition, since these included no branches of 4 mm. diameter or greater, the 16 branchings of the main bronchi down to broncho-pulmonary segment level were similarly measured and included. Thus 116 dichotomies with 232 angles were studied.

Results. The following abbreviations will be used in describing the results:

D_1	The diameter of the parent branch;
D_2 and D_3	The diameters of the daughter branches where $D_2 \geqslant D_3$;
a	The angle of branching of the branch with diameter D_2;
b	The angle of branching of the branch with diameter D_3.

Diameters. In a symmetrical system the two daughter branches would be identical, but in the bronchial tree this is not so. A measure of the asymmetry is given by the ratio D_3/D_2, the distribution of which is shown in Figure 3a.

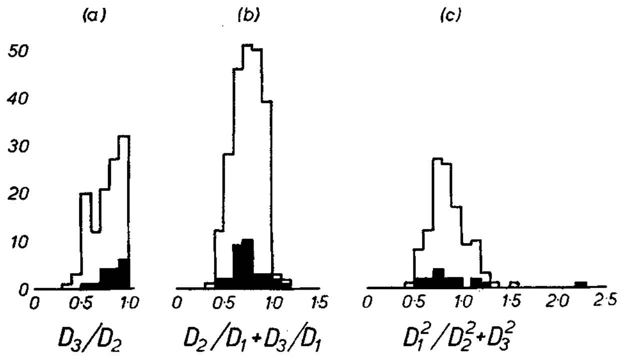

Figure 3a. Distribution of the ratios of the diameter of the smaller daughter branch to the diameter of the larger at a dichotomy

Figure 3b. Distribution of the ratios of the diameters of the daughter branches to the diameter of the parent branch at a dichotomy

Figure 3c. Distribution of the ratios of the cross sectional area of the parent branch to the summed area of the daughter branches at a dichotomy. (In Fig. 3a, 3b and 3c the main branches are shown in black)

This ratio is unity when the branches are of equal diameter and less than unity when they are unequal, being smaller the more unequal they are. In 27.6 per cent the diameter is greater than 0.9 and in 69.0 per cent it is greater than 0.7. The smallest value in this study was 0.37, though even smaller ones can be found.

We have shown that the ratios D_2/D_1 and D_3/D_1 should be 0.79 for minimum resistance. Figure 3b shows the distribution which ranges from 0.3 to 1.12 with a mean of 0.76. In five cases the daughter branch was larger than the parent (i.e., $D_2/D_1 > 1$).

Similarly for minimal resistance, the cross sectional area of the parent branch should be 0.79 that of the summed cross sectional area of the daughter branches. Figure 3c shows the distribution of $D_1^2/(D_2^2 + D_3^2)$, with most values lying between 0.4 and 1.14, though two are higher. The mode lies between 0.7 and 0.8 and the mean is 0.88. In 25 cases the ratio is greater than unity indicating a decrease in cross sectional area at that dichotomy.

Although the selection of the 16 main branches was not random, their inclusion has not greatly affected the distributions. In Figures 3, and Figure 4a they are shown in black on the histograms.

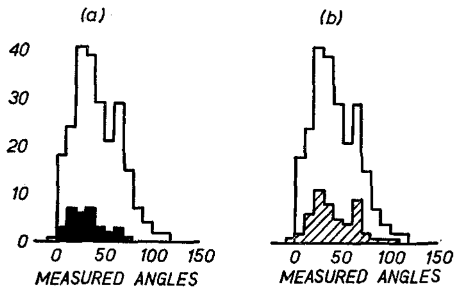

Figure 4a. Distribution of the angles of branching. The main branches are shown in black

Figure 4b. Distribution of the angles of branching. The hatched area shows the angles where the summed cross sectional area decreased at a dichotomy

Angles of branching. For minimal volume, the smaller daughter branch should come off at the greater angle ($b > a$), and where the diameters are equal the angles should be equal ($b = a$). Of the 102 angles where $D_2 > D_3$, in 79, $b > a$ and in 23, $a > b$. In one of the latter the angle was $-2°$. Of the 14 angles where $D_2 = D_3$, a and b were equal in none and differed by more than 20° in seven cases. The distribution of angles is shown in Figure 4a, there being a wide range from $-2°$ to 112° with a mean of 41° 26′. This is close to the ideal angle of 37° 28′ for minimal resistance.

However, if we group the angles according to the diameter of the parent branch (Table 1), we find that the smaller peripheral bronchi branch at greater angles. Thus the number of each diameter included will influence the mean value obtained.

Down to $D_1 = 2$ mm. the mean angles show little variation, being between 30° and 36°. Between $D_1 = 1$ mm. and $D_1 = 2$ mm. the mean angle increases to 43°, and when $D_1 < 1$ mm. the mean angle is 50°. It will be seen that the mean of the ratios D_2/D_1 and D_3/D_1 also increases, being 0.87 when $D_1 < 1$ mm.

Where $D_1^2 < (D_2^2 + D_3^2)$ the ideal angles for minimal volume were calculated for the measured diameters. This was done for 182 angles, 50 being excluded.

TABLE 1

Diameter in millimeters	Mean angle	Mean $D_2/D_1 + D_3/D_1$	Number measured
>4	32	0.76	32
3–4	30	0.82	8
2–3	36	0.77	62
1–2	43	0.74	122
<1	50	0.87	8

The histogram in Figure 4b shows the angles where $D_1^2 > (D_2^2 + D_3^2)$ shaded. The relationship between the measured and the calculated angles is shown in Figure 5. There is a wide scatter with a correlation coefficient of 0.31. However, the mean values are similar (measured 41° 54′, and calculated 39° 48′) and the correlation is highly significant ($0.01 > p > 0.001$).

The remaining 50 angles were analyzed by the second method in which for minimal volume

$$\frac{D_2^2}{D_3^2} = \frac{\sin b}{\sin a}.$$

These are plotted in Figure 6. The mean of D_2^2/D_3^2 is 1.74 and the mean of $\sin b/\sin a$ is 1.71, with a correlation coefficient of 0.56, and $0.01 > p > 0.001$.

Discussion. Down to bronchi of 1 mm. diameter the mean values of D_2/D_1 and D_3/D_1 do not show much change, varying between 0.74 and 0.82. These correspond quite well to the ideal value of 0.79 for minimal resistance.

With respect to minimal volume the results confirm the general rule that the smaller branch comes off at the greater angle. The angles measured show a wide scatter about the calculated ideal angles; nevertheless, there is a highly significant correlation between the two, and less than 2° difference in their mean values.

The second method shows a highly significant correlation between D_2^2/D_3^2 and $\sin b/\sin a$, and mean values differ by only 0.03.

If the angles are grouped according to the diameter of the parent branch, it is seen that both the ratios D_2/D_1 and D_3/D_1, and the angle of branching, increase distally. Down to 1 mm. diameter the mean angles vary between 30° and 43°

compared with the ideal of 37° 28′, and the mean ratios from 0.74 to 0.82, compared with the ideal of 0.79. When the parent branch is less than 1 mm. diameter, the mean ratios D_2/D_1 and D_3/D_1 increase to 0.87 and the mean angle of branching to 50°. This is clearly diverging from the principle of minimal resistance, but minimal volume is still maintained since the ideal angle when $D_2 = D_3 = 0.87\ D_1$ is 52°.

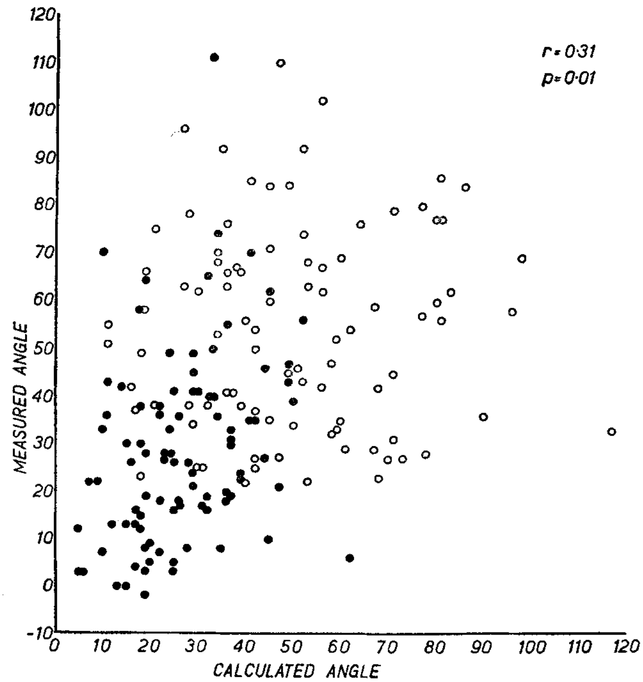

Figure 5. The relationship between the measured angle and that calculated for minimal volume where the summed cross sectional area increased at a dichotomy. The closed circles represent the angle made by the larger daughter branch at each dichotomy, and the open circles the angle made by the smaller branch

These changes in pattern in the distal part of the bronchial tree are in keeping with the known facts, for the three most distal generations of bronchioles tend to be about 0.5 mm. diameter (Weibel, 1963). When all three branches are of equal diameter, D_2/D_1 and D_3D_1 become unity and the ideal angle of branching is 60°. Inspection of the periphery of the cast used for the present study under a dissecting microscope shows that the angles are of this order, though no measurements have been made.

We are now in a position to consider these findings in relation to the total function of the bronchial tree. The bronchi down to terminal bronchioles (0.6 mm. in diameter) are concerned with conducting gas from the atmosphere down to the lung units where gas exchange occurs. This is brought about by mass movement down the pressure gradient which occurs when the chest expands, a process involving the expenditure of muscular energy. Minimal resistance to flow is important here, and it has been shown that the bronchial diameters accord with this principle.

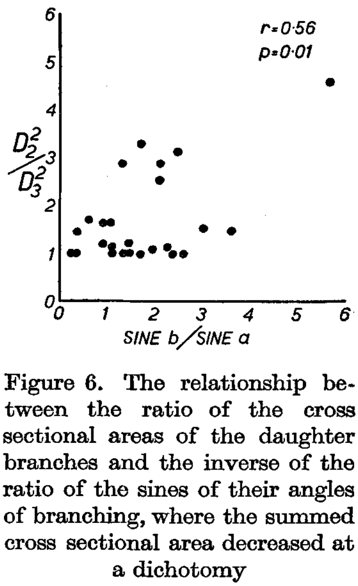

Figure 6. The relationship between the ratio of the cross sectional areas of the daughter branches and the inverse of the ratio of the sines of their angles of branching, where the summed cross sectional area decreased at a dichotomy

Gas exchange occurs in the lung unit, or acinus, distal to the terminal bronchiole, and the mixing of gas within the acinus is by molecular diffusion. Thus there will be an intermediate zone, probably between bronchi of 1 mm. diameter and 0.6 mm. diameter, where both mass movement and diffusion contribute significantly to gas movement.

In the acinus it is advantageous to have the maximum total cross sectional area available for molecular diffusion. Since the ratios D_2/D_1 and D_3/D_1 approach unity, the total cross sectional area doubles at each division, instead of increasing by a factor of $3\sqrt{2}$ which is the ideal for regions of mass flow. Thus, where mass movement gives way to diffusion as the means of gas transport, i.e., where the bronchi are less than 1 mm. diameter, the value of D_2/D_1 increases towards unity, a value more appropriate for molecular diffusion. The angle of branching also increases distally, thus maintaining the principle of minimal volume throughout.

It has thus been shown that the morphology of the bronchial tree is appropriate to the function of mass flow in the upper part, and to molecular diffusion in the distal part, while occupying the minimal volume compatible with these functions.

There are doubtless many other determinants of form in the human lung, but these remain to be elucidated.

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