

CORRELATIONS BETWEEN STRUCTURE AND FUNCTION IN THE DESIGN OF THE BAT LUNG: A MORPHOMETRIC STUDY

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SUMMARY

1. The lungs of five species of bat *Pipistrellus pipistrellus*, *Miniopterus minor* (Peters), *Tadarida mops* (De Blainville), *Cynopterus brachyotis* (Muller) and *Cheiromeles torquatus* (Horstield) have been analysed by morphometric techniques.

2. The mean body weight (W) ranged from 5 g in *Pipistrellus pipistrellus* to 173 g in *Cheiromeles torquatus*; the lung volume (VL) ranged from 0.3 cm³ in *Pipistrellus* to 10 cm³ in *Cheiromeles*.

3. The volume densities or the main components of the bat lung, namely the parenchyma [$V_v(p,L)$] (the gas exchange region) and the non-parenchyma [$V_v(np,L)$], were closely similar, the $V_v(p,L)$ constituting a mean value of 84.2% and the $V_v(np,L)$ 15.8% in the five species.

4. The VL , the surface area of the blood-gas (tissue) barrier (St), the pulmonary capillary blood volume (V_c), and the total morphometric pulmonary diffusing capacity (DL_{O_2}) were all strongly correlated with body weight. The harmonic mean thickness of the blood-gas (tissue) barrier ($\bar{\tau}t$) and the surface density of the blood-gas (tissue) barrier [$S_v(t,p)$] were poorly correlated with W .

5. The bats had a remarkably higher VL than either birds or terrestrial mammals. The V_c in the bat lung was similar to that in the bird lung but higher than that of the terrestrial mammals. The bats had a more extensive St than either the birds or the terrestrial mammals. In the bats the $\bar{\tau}t$ was thicker than in the birds but thinner than that of the terrestrial mammals. These pulmonary structural adaptations culminated in a higher DL_{O_2} in the bat than either in the birds or in the terrestrial mammals.

6. The superior morphometric properties of the bat lung coupled with the established physiological adaptations may help to explain how the bat lung is capable of providing the immense amount of oxygen demanded by flight.

INTRODUCTION

Bats are unique among mammals in their capacity for continuous flapping flight (Greenhall & Paradiso, 1968; Wimsatt, 1970; Thomas & Suthers, 1972; Dawson, 1975; Yalden & Morris, 1975; Thomas, 1975, 1980; Walker, 1975; Jürgens, Bartels & Bartels, 1981). Bats have thus been able to exploit widely dispersed ecological niches, and consequently show a remarkable adaptive radiation giving rise to about 1000 out of the 4200 mammalian species (Wimsatt, 1970; Thomas & Suthers, 1972; Yalden & Morris, 1975). Windtunnel experiments (Tucker, 1972; Carpenter, 1975; Thomas, 1975) have shown that flapping flight is energetically a very demanding form of exercise, being substantially beyond the energetic capacity of terrestrial mammals of similar size during maximum exercise. For example, a budgerigar flying horizontally at its most economical speed increases its oxygen consumption to about 13 times its standard metabolic rate, which is about 1.5 times the oxygen consumption of a mouse running hard in an exercise wheel (Tucker, 1968*a,b*). In turbulent air or when ascending the bird increases its oxygen consumption for short periods by about 20–30 times, whereas even a good human athlete can achieve for a few minutes an increase of only 15–20 times (Tucker, 1969). Bats have been shown to increase their oxygen consumption during sustained flight by at least 20 times (Bartholomew, Leitner & Nelson, 1964; Carpenter, 1975). In general, the energetics of bat flight appear to be comparable to that of birds (Studier & Howell, 1969; Thomas & Suthers, 1972; Carpenter, 1975; Dawson, 1975; Thomas, 1975; Jürgens *et al.* 1981).

The general anatomy of bats is, of course, fundamentally similar to that of terrestrial mammals (Yalden & Morris, 1975), and in at least one species the general microscopic structure of the pulmonary parenchyma is known to resemble that of other mammals (Maina, King & King, 1982*b*). In contrast, birds have evolved voluminous air sacs which continuously and unidirectionally ventilate the compact, rather rigid lung (for review of anatomy see King, 1966; Duncker, 1971; for physiology see Schmidt-Nielsen, 1975; Scheid, 1979). Moreover the blood–gas relationship in the avian parabronchus is cross-current as opposed to the uniform pool in the pulmonary alveoli of bats and all other mammals (Scheid & Piiper, 1970; Piiper & Scheid, 1973). The cross-current design is functionally superior to the uniform pool, since a higher degree of arterialization can be attained for an equal degree of ventilation (Scheid & Piiper, 1970; Schmidt-Nielsen, 1975; Piiper & Scheid, 1973). Furthermore, examination of the structure of the exchange tissue of the avian lung by morphometric methods indicates that pulmonary parameters such as the thinness of the blood–gas barrier and the surface area of the barrier per gram body weight are superior in birds as compared with mammals generally, leading to a higher anatomical diffusing capacity for oxygen per gram body weight in birds than in mammals (Maina & Settle, 1982).

Despite having an essentially mammalian type of lung, bats nevertheless appear to have an exercise capacity as good as that of birds. The question then arises, might the bat lung possess subtle structural adaptations such as can only be disclosed by morphometric methods? This conclusion was indeed reached by Maina & Nicholson (1982) and Maina *et al.* (1982*b*) from quantitative observations on the lung of a fruit

bat (*Epomophorus wahlbergi*). However, this is the only exhaustive published morphometric study of the bat lung and was limited to a single species.

The present investigation expands our previous work on *Epomophorus* by extending morphometric techniques to the lungs of five additional bat species of widely differing body weights and modes of life. Comparisons are made with corresponding data from the lungs of birds and terrestrial mammals.

MATERIALS AND METHODS

Definitions of symbols used in the tables and text

De_{O_2}	– diffusing capacity (conductance) of the erythrocyte for oxygen.
DL_{O_2}	– total morphometric pulmonary diffusing capacity for oxygen.
Dm_{O_2}	– membrane diffusing capacity for oxygen.
Dp_{O_2}	– diffusing capacity of the plasma layer for oxygen.
Dt_{O_2}	– diffusing capacity of the tissue barrier for oxygen.
Hc	– pulmonary capillary haematocrit.
Kp_{O_2}	– physical coefficient for permeation of the plasma layer by oxygen.
Kt_{O_2}	– physical coefficient for permeation of the tissue barrier by oxygen.
Sa	– surface area of the alveolar epithelium.
Sc	– surface area of the capillary endothelium.
Se	– surface area of the intracapillary erythrocytes.
Sp	– surface area of the plasma layer.
St	– surface area of the tissue (blood–gas) barrier.
Va	– volume of the alveoli.
Vc	– volume of the capillary blood.
Ve	– volume of the erythrocytes.
VL	– volume of the lung.
Vnp	– volume of the non-parenchymatous regions of lungs.
Vp	– volume of the parenchyma (gas exchange) tissue.
Vt	– volume of the tissue of the interalveolar septa.
W	– body weight.
θ_{O_2}	– coefficient for oxygen uptake by whole blood.
τ_{hp}	– harmonic mean thickness of the plasma layer.
τ_{ht}	– harmonic mean thickness of the tissue barrier.
$\bar{\tau}_t$	– arithmetic mean thickness of the tissue barrier.
$V_V(p,L)$	– volume density of the parenchyma, i.e. V_p/VL .
$V_V(np,L)$	– volume density of the non-parenchymatous tissue, i.e. V_{np}/VL .
$S_V(t,p)$	– surface density of the tissue (blood–gas barrier), i.e. St/V_p .

The lungs of 24 wild specimens of adult bats of mixed sexes from five species have been analysed by morphometric techniques. The bats were killed soon after capture by an intraperitoneal injection with barbiturate, and weighed at once. The subsequent procedure for fixation, processing and analysis of the lungs was essentially similar to that adopted by Maina *et al.* (1982b), but the main points here as follows.

Table 1. *The species investigated in this study*

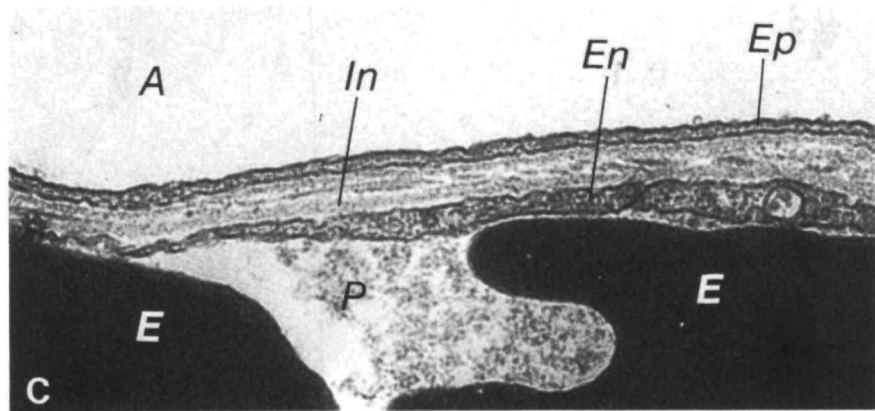
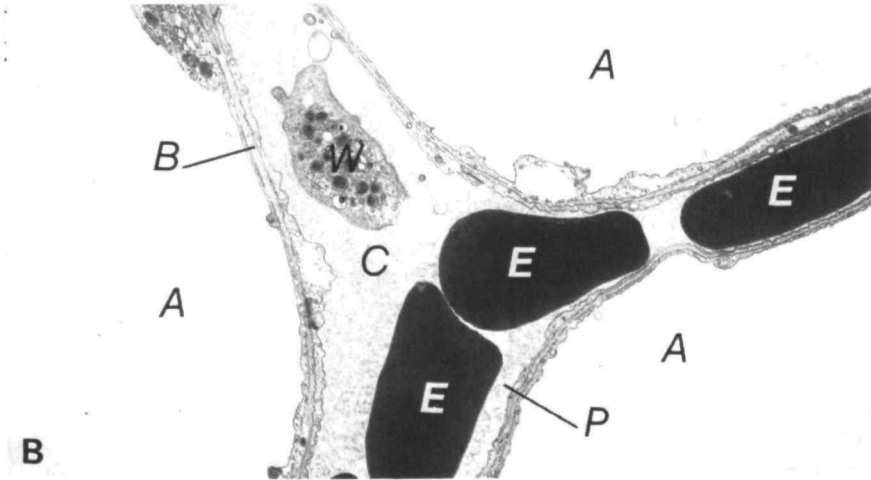
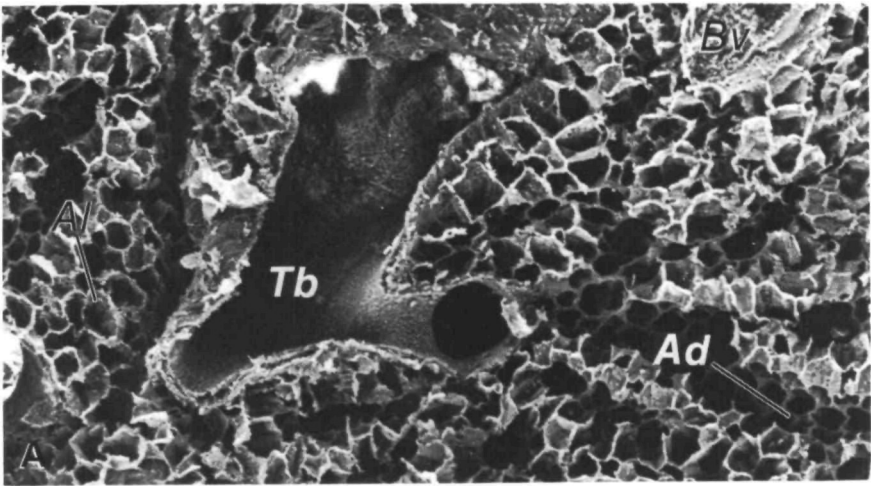
Species	Suborder	Family	Descriptive English names
<i>Pipistrellus pipistrellus</i> *	microchiroptera	vespertilionidae	ordinary bat, pipistrelle
<i>Miniopterus minor</i> †	microchiroptera	vespertilionidae	ordinary bat, long-winged bat
<i>Tadarida mops</i> ‡	microchiroptera	molossidae	free-tailed bat
<i>Cynopterus brachyotis</i> ‡	megachiroptera	pteropodidae	fruit bat, flying foxes, short-nosed fruit bat
<i>Cheiromeles torquatus</i> ‡	microchiroptera	molossidae	free-tailed bat, hairless bat

* *Pipistrellus* was caught in Scotland (U.K.).
† *Miniopterus* was caught in Kenya.
‡ *Tadarida*, *Cynopterus* and *Cheiromeles* was caught in Malaysia.

Immediately after death an incision was made just caudal to the xiphisternum and the diaphragm carefully perforated (avoiding puncturing the lungs) on both sides of the mediastinum; this created a pneumothorax which caused the lungs to collapse. The trachea was then cannulated and the lungs fixed *in situ* by intratracheal infusion with 2.3% glutaraldehyde buffered in sodium cacodylate (pH 7.4, total osmolarity 350 mosmol l⁻¹). The infusion was done by gravity from a height of 25 cm above the supine body. When the fixative stopped flowing the trachea was ligated caudal to the cannula. The volumes of the left and right lungs were estimated by the water displacement method of Scherle (1970).

Electron microscopy

One complete transverse slice was taken from each of the lobes of the lung and diced into small pieces (about 2 mm³) for electron microscopy. These pieces were postfixed in 2% osmium tetroxide, block stained in 2% uranyl acetate in maleic acid, and dehydrated in graded ethanol (starting at 50%) and acetone before infiltration and embedding in Taab resin. Two blocks were taken at random from a group derived from each of the lobes and trimmed to eliminate non-parenchymal tissue; ultrathin sections were cut, counterstained with lead citrate, and examined electron microscopically. Five electron micrographs (from each block) were taken from predetermined corners of the grid squares (to avoid bias) of the first technically adequate section at a primary magnification of ×3000, and the subsequent analysis was performed at about ×7500 with a superimposed quadratic lattice grid. This magnification was found to be optimal as it gave a relatively large field but still enabled the requisite parenchymal components to be identified and quantified. A total of 50 micrographs was analysed for each animal. Point counting was employed to estimate volumes, intersection counting to estimate surface areas, and intercept length measurement to estimate harmonic mean thicknesses (Weibel, 1970/71). The arithmetic mean thickness of the tissue barrier was estimated by a random short line test grid (Weibel & Knight, 1964). The surface density of the tissue barrier was calculated from its surface area and parenchymal volume. The surface area of the plasma layer was estimated as the mean of the surface area of the capillary endothelium (Sc) and that of the erythrocytes (Se) (Weibel, 1970/71). In case of an overlap of erythrocytes only the intersections of the test grid with the outer surface of the erythrocytes (the surface direct



adjacent to the endothelium) were considered, this avoids an overestimate of Se and consequently Sp. As plasma is more of a layer than a surface it was thought reasonable to estimate its surface area (Sp) from the areas of its two boundaries, the endothelium and erythrocytes. The morphometric pulmonary diffusing capacities (conductances) for oxygen of the tissue barrier (D_{tO_2}), plasma (D_{pO_2}), and erythrocyte (D_{eO_2}) were calculated using the physical coefficients for oxygen permeation of the tissue barrier (K_{tO_2}) and plasma layer (K_{pO_2}), and the coefficient for oxygen uptake by whole blood (θ_{O_2}), as estimated for mammalian tissue and cited by (Weibel, 1970/71). The value of θ_{O_2} was adjusted for a venous haematocrit of 60 % reported in a bat by Thomas & Suthers (1972). The membrane diffusing capacity for oxygen (D_{mO_2}) and the total morphometric pulmonary diffusing capacity (DL_{O_2}) were calculated from the individual serial conductances, the model used being that developed by Weibel (1970/71).

Light microscopy

The remaining parts of the lobes were cut in 7 μ m serial transverse paraffin sections. Three sections were taken from each lobe at predetermined equidistant intervals, stained with haematoxylin and eosin and analysed for the volume density of the parenchyma (tissue involved in gas exchange) and of the non-parenchyma by point counting using a 100 point Zeiss integrating graticule at $\times 200$ magnification. The absolute volumes of these two components could then be calculated from the volume of the lungs.

RESULTS

The results are summarized in Tables 2–8. In *Cheiromeles torquatus* and *Cynopterus brachyotis* the alveoli constituted 91 % and 92 % respectively of the parenchyma, while the lowest value (81 %) was observed in *Pipistrellus pipistrellus*, the mean for all five species being 87 %. The mean volume densities of the pulmonary blood capillaries and the tissue of the interalveolar septa in the five species of bat were 7 % and 6 % respectively. The components of the parenchyma, and the blood gas barrier are shown in Fig. 1.

The surface areas of the resistance barriers constituting the air haemoglobin pathway, namely the blood–gas (tissue) barriers (St), alveolar epithelium (Sa), capillary endothelium (Sc), and the erythrocytes (Se), are shown in Table 4. St is functionally a

Fig. 1. (A) A scanning electron micrograph of the bat lung showing the non-parenchymatous region represented by a terminal bronchus (*Tb*), a large blood vessel (*Bv*) and the alveolar duct (*Ad*). The parenchyma consists of alveolar sacs and alveoli (*Al*). Critical point dried material. $\times 330$. (B) A transmission electron micrograph of the pulmonary parenchyma of the bat lung showing alveoli (*A*) separated by an interalveolar septa which consists of blood capillaries (*C*). The air and blood gas exchange media are separated by a blood–gas (tissue) barrier (*B*). The capillaries contain erythrocytes (*E*). *W*, white blood cell; *P*, plasma layer. $\times 7000$. (C) A high power transmission electron micrograph showing the blood–gas barrier. The tissue barrier consists of an epithelial cell (*Ep*), which is normally overlaid with a thin surfactant layer (which was not preserved in this preparation), an interstitium (*In*) and an endothelial cell (*En*). *P*, plasma; *A*, alveoli; *E*, erythrocyte. $\times 21\ 000$. All preparations are from *Tadarida mops*.

Table 2. Body weight (W), lung volume (VL), volume density [$V_v(p, L)$] and absolute volume (V_p) of the parenchyma and volume density [$V_v(np, L)$] and absolute volume (V_{np}) of the non-parenchymatous regions of the lungs of five species of bat

Species	N	W (g)	VL (cm ³)	$V_v(p, L)$ (%)	V_p (cm ³)	$V_v(np, L)$ (%)	V_{np} (cm ³)
<i>Pipistrellus pipistrellus</i>	2	5.1 ± 0.8	0.31 ± 0.07	85.3 ± 1.0	0.26	14.7 ± 1.0	0.05
<i>Miniopterus minor</i>	5	9.1 ± 0.9	0.65 ± 0.07	82.6 ± 2.0	0.54	17.4 ± 2.0	0.11
<i>Tadarida mops</i>	5	24.0 ± 2.2	2.3 ± 0.3	84.6 ± 2.2	1.95	15.4 ± 2.2	0.35
<i>Cynopterus brachyotis</i>	7	36.7 ± 4.1	2.9 ± 0.3	84.0 ± 2.9	2.44	16.0 ± 2.9	0.46
<i>Cheiromeles torquatus</i>	5	172.7 ± 12.5	10.1 ± 0.6	84.4 ± 0.9	8.53	15.6 ± 0.9	1.58

The absolute values appertain to both lungs together.

Values are means ± s.d.

The symbols in this and subsequent tables are explained in the Methods sections.

Table 3. Volumes of the components of the parenchyma and pulmonary haematocrit

Species	N	V_a (cm ³)	V_c (cm ³)	V_t (cm ³)	V_e (cm ³)	Hc (V_e/V_c) (%)
<i>Pipistrellus pipistrellus</i>	2	0.21 ± 0.05	0.03 ± 0.004	0.02 ± 0.001	0.02 ± 0.006	66.7
<i>Miniopterus minor</i>	5	0.46 ± 0.05	0.04 ± 0.007	0.04 ± 0.004	0.03 ± 0.004	75
<i>Tadarida mops</i>	5	1.71 ± 0.03	0.14 ± 0.01	0.10 ± 0.03	0.07 ± 0.01	50
<i>Cynopterus brachyotis</i>	5*	2.24 ± 0.3	0.08 ± 0.02	0.12 ± 0.02	0.05 ± 0.02	63
<i>Cheiromeles torquatus</i>	5	7.72 ± 0.5	0.45 ± 0.1	0.27 ± 0.1	0.29 ± 0.1	64.4

* Out of seven specimens of *Cynopterus brachyotis* only five were fixed well enough for electron microscopy.

The values of N in this table apply to the subsequent tables.

The values appertain to both lungs together and are means ± s.d.

more meaningful parameter than S_a as it takes into account only those areas of the alveolar epithelium where gas exchange actually takes place. It was felt that S_t , which can be directly determined, was a much more accurate estimate of the morphometric pulmonary diffusing capacity rather than estimating S_t as the mean of S_a and S_c (Weibel, 1970/71). In this study the values of S_t , S_a and S_c are given in Table 5 and the difference in estimating S_t both ways is clearly apparent. It consistently appears in this study, and our previous ones, that the indirect way of estimating S_t leads to an overestimate of the surface area available for gas exchange and consequently that of the diffusing capacity. Obviously S_a will always be higher than S_t when these values are estimated together on the same preparations.

Ratios of some parameters of the components of the parenchyma are shown in Table 6. *Pipistrellus pipistrellus* and *Tadarida mops* had the highest values (respectively 63 and 56 cm² g⁻¹) for the surface area of the blood-gas (tissue) barrier per unit body weight (S_t/W); the lowest values were observed in *Cheiromeles torquatus* (33.3 cm² g⁻¹) and *Cynopterus brachyotis* (30 cm² g⁻¹). The ratio $S_v(t,p)$ expresses the surface density of the blood-gas (tissue) barrier and thus indicates the relative alveolar diameter (see Discussion). The highest value of $S_v(t,p)$ was observed in a specimen of *Pipistrellus pipistrellus* (153 mm² mm⁻³), and the lowest (31 mm² mm⁻³) in a specimen of *Cynopterus brachyotis*. The ratio V_c/S_a has been defined as capilla

Table 4. Surface areas of the resistance barriers that constitute the air-haemoglobin pathway in the lungs of five species of bat

Species	St	Sa	Sc	Se
<i>Pipistrellus pipistrellus</i>	0.032 ± 0.004	0.118 ± 0.06	0.033 ± 0.001	0.038 ± 0.005
<i>Miniopterus minor</i>	0.044 ± 0.005	0.054 ± 0.007	0.048 ± 0.005	0.035 ± 0.007
<i>Tadarida mops</i>	0.130 ± 0.02	0.172 ± 0.02	0.146 ± 0.02	0.139 ± 0.01
<i>Cynopterus brachyotis</i>	0.107 ± 0.02	0.162 ± 0.03	0.115 ± 0.02	0.086 ± 0.02
<i>Cheiromeles torquatus</i>	0.568 ± 0.05	0.70 ± 0.10	0.576 ± 0.07	0.846 ± 0.41

The values appertain to both lungs together and are means (m²) ± s.d.

Table 5. Ratios describing some functional parameters of the lungs of five species of bat

Species	St/W (cm ² g ⁻¹)	Sv(t, p) (mm ² mm ⁻³)	Vc/Sa (cm ³ m ⁻²)	VL/W (cm ³ g ⁻¹)
<i>Pipistrellus pipistrellus</i>	63.2 ± 17.8	124.73 ± 39.6	0.32 ± 0.19	0.060 ± 0.003
<i>Miniopterus minor</i>	49.6 ± 4.5	81.34 ± 7.8	0.71 ± 0.09	0.071 ± 0.007
<i>Tadarida mops</i>	56.1 ± 8.6	73.6 ± 18.4	0.80 ± 0.07	0.097 ± 0.017
<i>Cynopterus brachyotis</i>	30.02 ± 6.7	44.42 ± 9.3	0.50 ± 0.12	0.082 ± 0.007
<i>Cheiromeles torquatus</i>	33.31 ± 1.4	64.3 ± 5.5	0.63 ± 0.13	0.059 ± 0.007

The values appertain to both lungs together and are means ± s.d.

Table 6. Harmonic and arithmetic mean thicknesses of the blood-gas (tissue) barrier and plasma layer in the lungs of five species of bat

Species	tht	thp	$\bar{\tau}t$	$\bar{\tau}t/tht$
<i>Pipistrellus pipistrellus</i>	0.206 ± 0.03	0.213 ± 0.02	1.19 ± 0.10	5.78
<i>Miniopterus minor</i>	0.216 ± 0.01	0.165 ± 0.02	1.45 ± 0.13	6.71
<i>Tadarida mops</i>	0.221 ± 0.01	0.170 ± 0.02	1.43 ± 0.15	6.47
<i>Cynopterus brachyotis</i>	0.282 ± 0.03	0.097 ± 0.04	1.52 ± 0.28	5.39
<i>Cheiromeles torquatus</i>	0.202 ± 0.01	0.190 ± 0.07	1.40 ± 0.13	6.93

The values are in μm and are means ± s.d.

loading (Perry, 1978; Gehr *et al.* 1980) and expresses the degree of exposure of blood to air, a lower ratio indicating a higher degree of exposure (Perry, 1978). The lowest value of Vc/Sa was found in *Pipistrellus pipistrellus* (mean 0.32 cm³m⁻²). Relatively high values of Vc/Sa (means 0.80 and 0.71 cm³m⁻²) were observed in *Tadarida mops* and *Miniopterus minor* respectively.

Table 6 gives the harmonic and arithmetic mean thicknesses of the blood-gas (tissue) barrier and the plasma layer. The thinnest harmonic mean thickness of the tissue barrier, tht, (0.184 μm) was found in a specimen of *Pipistrellus pipistrellus*; the thickest barrier (0.313 μm) was found in a specimen of *Cynopterus brachyotis*. The lowest and the highest values of the arithmetic mean thickness ($\bar{\tau}t$) of the blood-gas (tissue) barrier (1.12 and 1.81 μm) were again observed respectively in a specimen of *Pipistrellus pipistrellus* and a specimen of *Cynopterus brachyotis*.

In Table 7 are shown the morphometric pulmonary diffusing capacities of the three

Table 7. *Morphometric pulmonary diffusing capacities of the resistance barriers of the air-haemoglobin pathway in the lungs of five species of bat*

Species	Dt _{O₂}	Dp _{O₂}	De _{O₂}	Dm _{O₂}	DL _{O₂}
<i>Pipistrellus pipistrellus</i>	0.52 ± 0.13	1.35 ± 0.66	0.07 ± 0.01	0.37 ± 0.12	0.06 ± 0.003
<i>Miniopterus minor</i>	0.68 ± 0.10	1.04 ± 0.12	0.09 ± 0.02	0.41 ± 0.05	0.07 ± 0.01
<i>Tadarida mops</i>	2.06 ± 0.31	3.48 ± 0.84	0.31 ± 0.03	1.28 ± 0.22	0.24 ± 0.02
<i>Cynopterus brachyotis</i>	1.31 ± 0.39	5.75 ± 3.29	0.18 ± 0.05	1.01 ± 0.25	0.15 ± 0.04
<i>Cheiromeles torquatus</i>	9.26 ± 0.31	14.46 ± 3.81	1.01 ± 0.27	5.55 ± 0.62	0.72 ± 0.17

The values (mlO₂ min⁻¹ mmHg⁻¹) appertain to both lungs together and are means ± s.d.

The values of Dp_{O₂}, De_{O₂}, Dm_{O₂} and DL_{O₂} are means of the maximum and minimum values.

barriers constituting the air-haemoglobin pathway; also shown are the membrane diffusing capacity and the total morphometric pulmonary diffusing capacity. The highest mean values of the specific (weight normalized) total morphometric pulmonary diffusing capacity, DL_{O₂}/W (mlO₂ min⁻¹ mmHg⁻¹ kg⁻¹), were found in *Pipistrellus pipistrellus* and *Tadarida mops* (11.53 and 10.2 mlO₂ min⁻¹ mmHg⁻¹ kg⁻¹ respectively). The lowest mean values of DL_{O₂}/W were found in *Cheiromeles torquatus* (4.18) and *Cynopterus brachyotis* (4.19 mlO₂ min⁻¹ mmHg⁻¹ kg⁻¹).

DISCUSSION

The structure of the lung is adapted to meet the oxygen demands of an animal, which in turn will reflect various factors such as body weight and mode of life. Bats are excellent fliers in terms of speed, distance and manoeuvrability (Hartman, 1963; Krzanowski, 1964; Griffin, 1970; Vaughan, 1970; Schmidt-Nielsen, 1975, 1979; Yalden & Morris, 1975; Walker, 1975; Norberg, 1976; Snyder, 1976; Bouverot, 1978). It has been shown that bats have developed specializations of the oxygen transport system in the form of a relatively large heart, high haematocrit, high haemoglobin concentration, a high oxygen capacity and low oxygen affinity of the blood (Hartman, 1963; Thomas & Suthers, 1972; Snyder, 1976; Jürgens *et al.* 1981). However, Snyder (1976) observed that the haematological parameters of *Cynopterus brachyotis* are within the range of the values reported for non-flying mammals and even lower than those of the laboratory mouse; he nevertheless observed that this species of bat had a heart weight 60% greater than that expected of a non-flying mammal and comparable to that of a bird. In the present study it will be shown that the bat lung is morphologically well adapted for gas exchange; furthermore there are indications that individual species seem to be adapted according to their small or large size and their energetic or non-energetic life style.

Lung volume

Jürgens *et al.* (1981), on the basis of measurements of lung weight, concluded that bats had proportionately larger lungs than small terrestrial mammals. Our morphometric observations confirm that bats do indeed have immensely large lungs compared with those of both birds and terrestrial mammals (Fig. 2, Table 5). The mean lung

Volume in the five species of bats examined here per gram body weight (VL/W) was $0.074 \text{ cm}^3 \text{ g}^{-1}$. In contrast, the mean VL/W for eight species of shrews examined by Gehr *et al.* (1980) was only $0.030 \text{ cm}^3 \text{ g}^{-1}$; the VL/W in the violet-eared hummingbird was $0.043 \text{ cm}^3 \text{ g}^{-1}$ (Dubach, 1981). Thus, the specific lung volume (i.e. volume per gram body weight) of our bats was 2.5 times greater than that of the shrews and

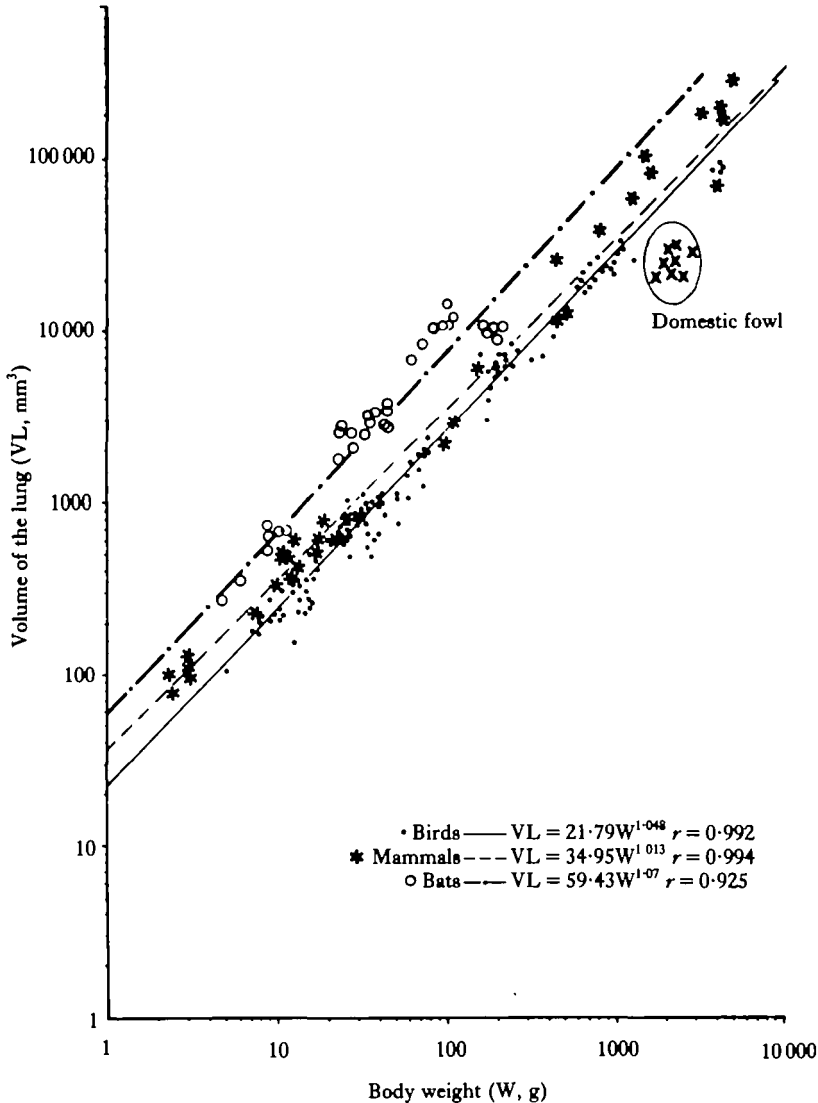


Fig. 2. Double logarithmic plot of lung volume (VL) against body weight (W). The values of VL pertain to the combined volumes of the left and right lungs. The bird line is based on 148 data points for the 148 individual birds representing 41 species examined by Maina (1982). The data points for the domestic fowl are entered separately. The terrestrial mammal line was based on 40 data points for the value of VL in some 20 terrestrial mammalian species examined by Gehr *et al.* (1981), falling within the same weight range as the birds. The bat line is based on 29 specimens from six species; the values of the fruit bat *Epomophorus wahlbergi* incorporated in the calculation of the regression line were reported in detail in Maina, King & King (1982b). The bats have a remarkably larger lung volume than the mammals and the birds. The mammals in turn have a larger lung volume than the birds. In the three groups of animals VL is very strongly correlated with W.

almost twice that of the hummingbird. Even more remarkable was the fruit bat *Epomophorus wahlbergi*, which had a specific lung volume of $0.13 \text{ cm}^3 \text{ g}^{-1}$ (Maina *et al.* 1982b), i.e. about 4.3 times greater than the shrews.

Tenney & Remmers (1963), however, in their plot of lung volume against body weight in a large number of mammalian species, included a value for an unnamed species of bat which fell slightly below the common regression line. This discrepancy could possibly be due to species differences or to the technique used for fixing and measuring lung volume. Tenney & Remmers removed the lungs immediately after death and kept them inflated at a pressure of 20 cm of water until they were dry. Unfortunately this technique gives no assurance that the volume of the dried lungs was similar to their volume *in situ*. Comparison of their values with those obtained here is therefore inconclusive.

Surface area of the blood-gas (tissue) barrier

Three of our five species of bats exhibited relatively high values of the surface area of the blood-gas (tissue) barrier per gram body weight (St/W). Thus the mean values of St/W obtained in *Pipistrellus pipistrellus*, *Miniopterus minor* and *Tadarida mops* were respectively 63, 50 and $56 \text{ cm}^2 \text{ g}^{-1}$. These values are substantially higher than the values of 26, 26, 43, 29 and $46 \text{ cm}^2 \text{ g}^{-1}$ obtained by Maina (1982) and Maina & King (1982) in anseriform, charadriiform, columbiform, piciform and passeriform avian species respectively. They are also much higher than the mean value of $33 \text{ cm}^2 \text{ g}^{-1}$ reported by Gehr *et al.* (1980) for eight species of shrew. On the other hand, the relatively low values of St/W in *Cynopterus brachyotis* ($30 \text{ cm}^2 \text{ g}^{-1}$) and *Cheiromeles torquatus* ($33 \text{ cm}^2 \text{ g}^{-1}$) are closely similar to the mean values for the shrews (Gehr *et al.* 1980; Weibel, 1979). The value of St/W found in the violet-eared hummingbird was $87 \text{ cm}^2 \text{ g}^{-1}$ (Dubach, 1981), and this exceeds all of the five bat species in the present study. However, the highest values of St/W reported so far in any vertebrate ($138 \text{ cm}^2 \text{ g}^{-1}$) occurred in the fruit-bat *Epomophorus wahlbergi* (Maina *et al.* 1982b). The plot (Fig. 3) suggests that bats may prove to have a more extensive blood-gas (tissue) barrier than birds in general or terrestrial mammals of comparable size, though undoubtedly examination of more species of bats is called for.

The relatively high values of St/W in *Tadarida mops* could be associated with the capacity for fast and sustained flight in molossid bats (Vaughan, 1966, 1970; Yalden & Morris, 1975). The values of St/W in *Pipistrellus pipistrellus* are higher than those of *Tadarida* though Vaughan (1966) observed that vespertilionid bats exhibit slower flight close to the ground. The insectivorous bats like *Pipistrellus pipistrellus* have, however, to be more manoeuvrable and fly continuously in search of food (Vaughan, 1970). *Pipistrellus pipistrellus* is one of the smallest bats (Yalden & Morris, 1975). This, and the need for sustained flight when feeding, may account for the high value of St/W in this species of bat.

Tenney & Remmers (1963) reported the value of the alveolar surface area in an unnamed species of bat to be similar to that of terrestrial mammals. To estimate alveolar surface areas they used relatively thick sections $100 \mu\text{m}$, which were photographed at low power (presumably using a light microscope). Analysis of tissues at low magnifications gives an underestimate due to lack of resolution (Dunnill, 1962). The value for the bat obtained by Tenney & Remmers (1963) is not therefore comparable with our study.

Surface density of the blood-gas (tissue) barrier

The surface area of the blood-gas (tissue) barrier per unit volume of parenchyma, $S_v(t,p)$, shows how much of the barrier has been packed into a unit containing volume. A large diffusing surface area can be achieved by an increase in either the lung volume, or the lung partitioning, or both (Tenney & Remmers, 1963; Geelhaar & Weibel, 1971; Weibel, 1979). The value $S_v(t,p)$ is an indicator of the relative sizes of the terminal gas exchange units. The values of $S_v(t,p)$ in mammalian lungs are in general relatively lower than those of the avian species (Fig. 4). For instance the mean value of $S_v(t,p)$ in the eight species of shrew examined by Gehr *et al.* (1980) was

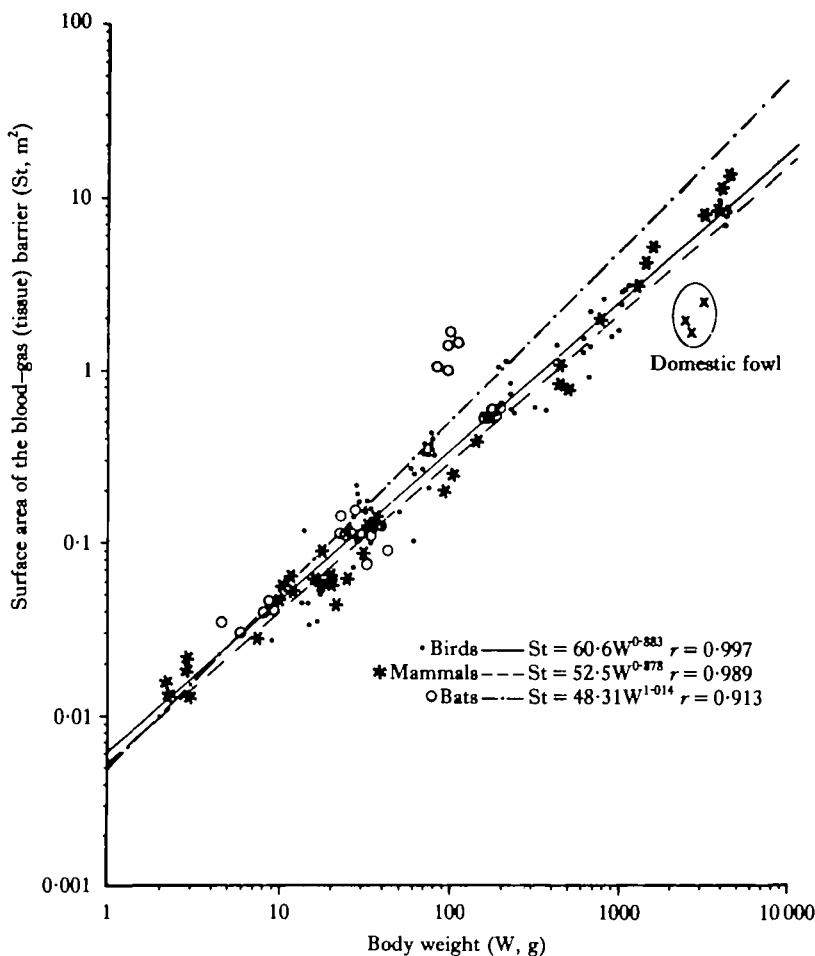


Fig. 3. Double logarithmic plot of the surface area of the blood-gas (tissue) barrier (St) against body weight (W). The values of St pertain to the combined left and right lungs. The bird line is based on 87 data points for the 87 individual birds representing 25 species examined by Maina (1982), this number is lower than that given in Fig. 1 due to unsatisfactory degree of fixation for electron microscopy. The mammalian line is based on the species as in Fig. 1. The bat line is based on the five species which are the subject of this study and *Epomophorus wahlbergi* reported in Maina, King & King (1982b). St in the bats is higher than in the birds and the terrestrial mammals. St is strongly correlated with body weight in these three groups of animals.

$121 \text{ mm}^2 \text{ mm}^{-3}$; this value was the same as that found in the lung of the metabolically active Japanese waltzing mouse (*Mus wagneri*) by Geelhaar & Weibel (1971). In birds, the value of $S_v(t,p)$ in *Gallus domesticus* was $179.5 \text{ mm}^2 \text{ mm}^{-3}$ (Abdalla *et al.* 1982). The hummingbird *Coribri coruscans* has a value as high as $389 \text{ mm}^2 \text{ mm}^{-3}$ (Dubach, 1981). The air capillaries of the avian lung are extremely small, being only $3\text{--}10 \mu\text{m}$ in diameter (Duncker, 1972), whereas the diameters of mammalian alveoli range from about $28 \mu\text{m}$ in a bat to about $1800 \mu\text{m}$ in the dugong (Tenney & Remmers, 1963). Maina *et al.* (1982b) suggested that on the basis of data from *Epomophorus*, of which the mean value of $S_v(t,p)$ was $121 \text{ mm}^2 \text{ mm}^{-3}$, bats may generally have relatively small alveoli. Although this generalization agrees with the observations of Tenney & Remmers (1963), it is not upheld by the values of $S_v(t,p)$ obtained from the larger population of bats examined here (Fig. 4). Thus, although *Pipistrellus* had a value of $125 \text{ mm}^2 \text{ mm}^{-3}$, the mean for all five species was only $78 \text{ mm}^2 \text{ mm}^{-3}$. This aspect needs to be investigated further, either by direct measurements of alveolar diameters or estimation of $S_v(t,p)$ in more species of bat.

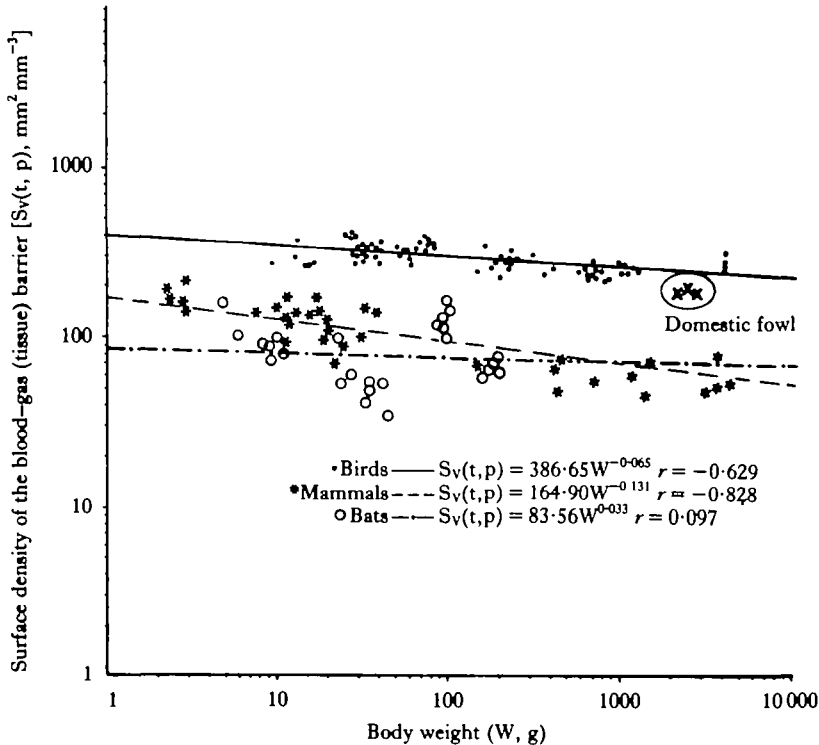


Fig. 4. Double logarithmic plot of the surface area of the blood-gas (tissue) barrier per unit volume of exchange tissue [$S_v(t,p)$] against body weight (W). The regression lines for the bats, terrestrial mammals and birds are based on the specimens and species stated in Fig. 2. $S_v(t,p)$ is negatively correlated with body weight in the birds, terrestrial mammals and the bats. $S_v(t,p)$ appears to be relatively lower in the bats than in both the birds and terrestrial mammals. This would generally indicate that the bats have larger alveoli than the terrestrial mammals and that the alveoli of the bats are remarkably larger than the air capillaries of the birds (see text). The negative correlation between $S_v(t,p)$ and W in these groups of animals suggest that smaller animals generally have small terminal respiratory units which would be a form of adaptation as small respiratory units are presumed to have a higher partial pressure for oxygen (see text).

Harmonic mean thickness of the blood-gas (tissue) barrier

This parameter (τ_{ht}) is the most appropriate estimator of the barrier conductance to oxygen (Weibel & Knight, 1964; Weibel, 1970/71, 1973; Hughes, 1980). The thinner the barrier, the greater will be its conductance to oxygen. The smallest τ_{ht} hitherto reported in a mammalian lung was $0.230 \mu\text{m}$ in a specimen of the shrew (*Suncus etruscus*) by Gehr *et al.* (1980).

In the bats examined here the smallest τ_{ht} ($0.184 \mu\text{m}$) was observed in one of the specimens of *Pipistrellus pipistrellus*, this value being the thinnest barrier reported in any mammalian lung so far. It is apparent from Fig. 5 that the bats have a thicker τ_{ht} than the active birds, but a thinner τ_{ht} than the terrestrial mammals. The τ_{ht} in the lungs of flightless species of birds was generally thicker than that of the bat. Thus, τ_{ht} in *Gallus domesticus* was $0.314 \mu\text{m}$ (Abdalla *et al.* 1982), $0.320 \mu\text{m}$ in *Numida meleagris* (Abdalla & Maina, 1981), and $0.385 \mu\text{m}$ in *Meleagris gallopavo* (Dubach, 1981).

Volume of pulmonary capillary blood

The volume of the pulmonary capillary blood is an important parameter since it

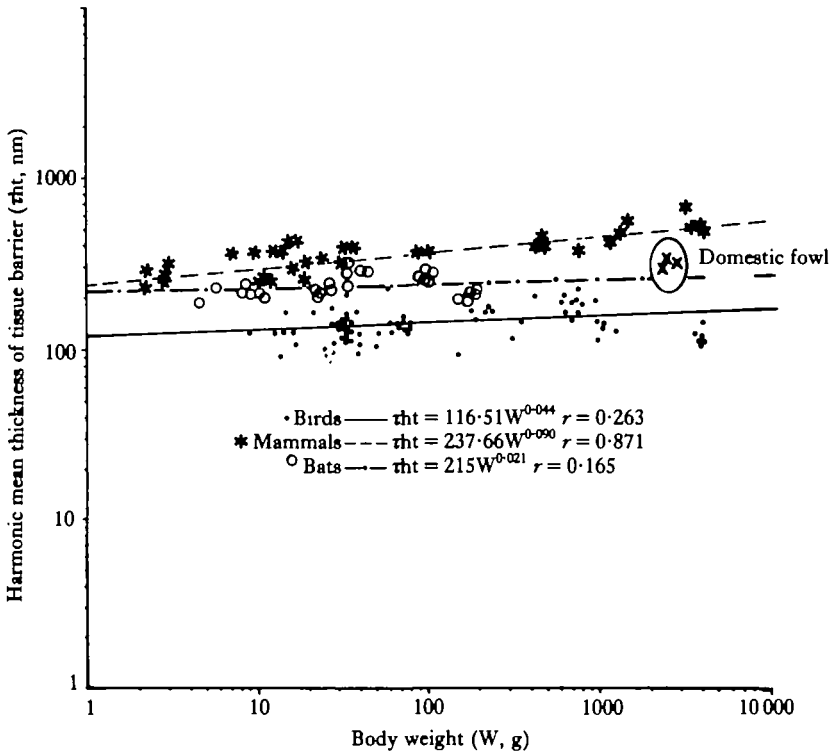


Fig. 5. Double logarithmic plot of the harmonic mean thickness of the blood-gas (tissue) barrier (τ_{ht}) against body weight (W). The regression lines for the bats, birds and terrestrial mammals are based on the specimens and species stated in Fig. 2. The bats had a thicker blood-gas (tissue) barrier than the birds but the barrier in the bats was thinner than in the terrestrial mammals. The τ_{ht} is generally weakly correlated with W in the animals. The blood-gas (tissue) barrier in the domestic fowl is thicker than in the active (wild) species of birds, and is apparently as thick as in the bats.

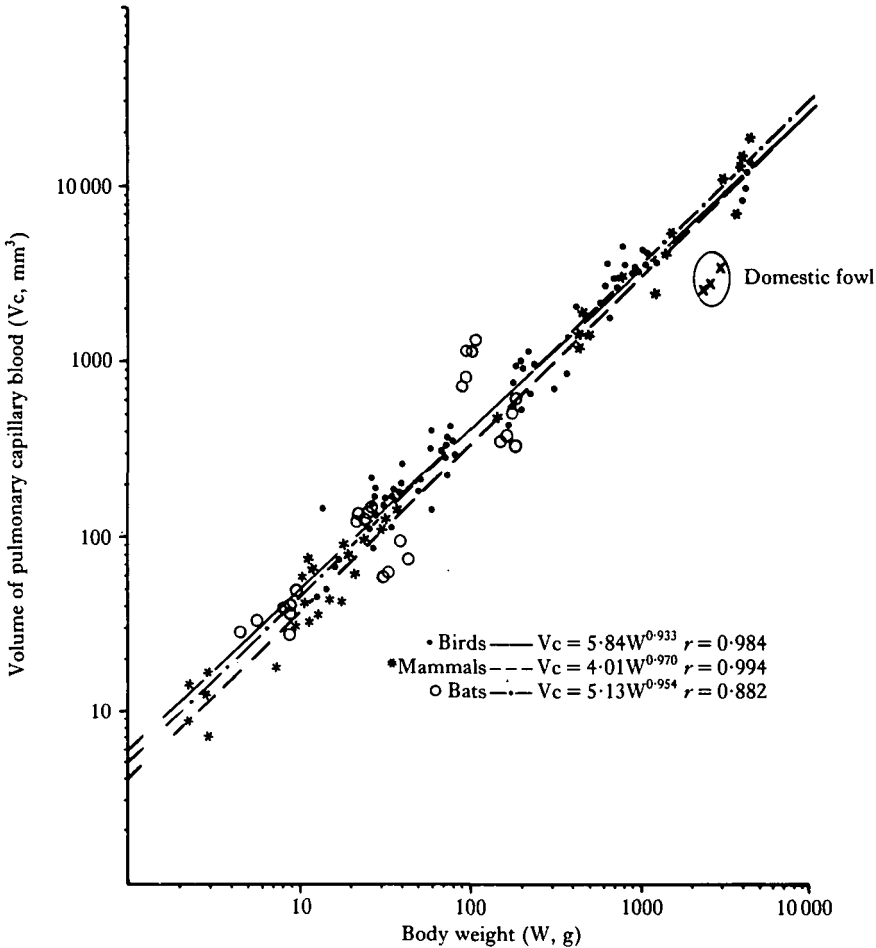


Fig. 6. Double logarithmic plot of the pulmonary capillary blood volume (V_c) against body weight (W). The values of V_c appertain to the combined left and right lungs. The number of birds, terrestrial mammals and bats on which the regression lines are based are as in Fig. 2. V_c in the bats is apparently higher than in the terrestrial mammals but very little different from that in the birds. V_c is strongly correlated with W in these three groups of animals.

influences the total morphometric pulmonary diffusing capacity for oxygen. Fig. 6 indicates that a bat does have a larger amount of blood in the gas exchange tissue (par enchyma) than a terrestrial mammal of the same body weight. However, the volumes of the pulmonary capillary blood in the bat and bird appear to be much the same. Duncker (1973) remarked that the relatively large volume of blood in the avian lung may be a possible reason for its high degree of efficiency; such an observation may also apply to the bat lung.

Total morphometric pulmonary diffusing capacity

The total morphometric pulmonary diffusing capacity for oxygen (DL_{O_2}) estimates the maximum possible conductance in the lung under perfect conditions of ventilation and perfusion over the entire barrier (Weibel, 1970/71; Siegwart, Gehr, Gil █

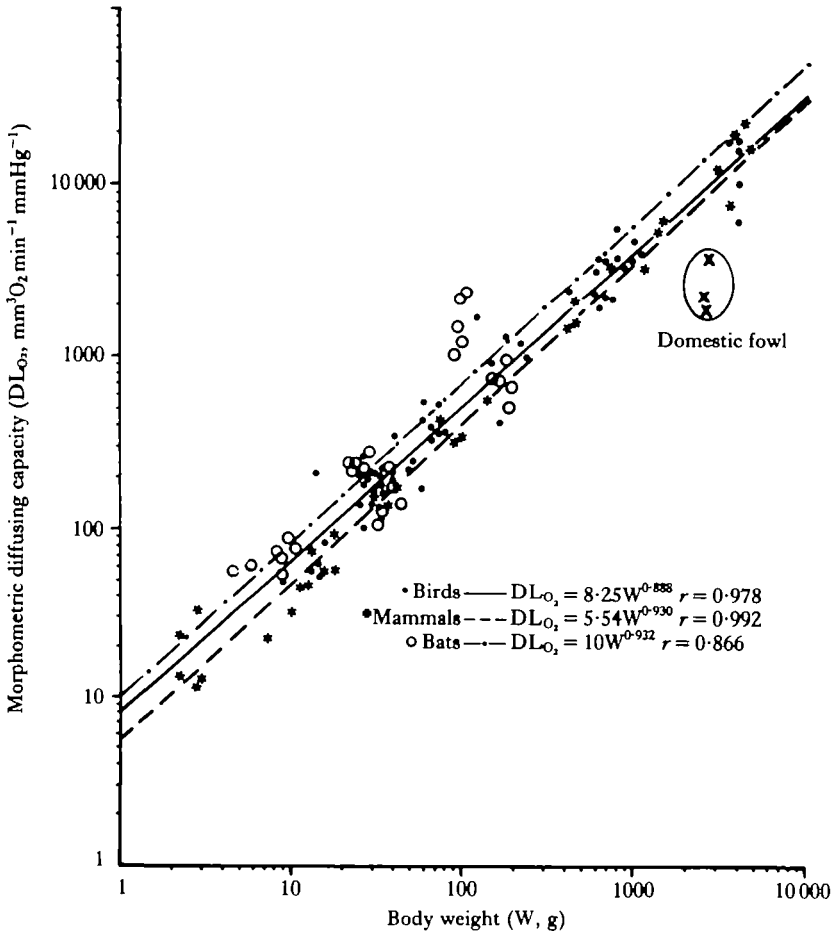


Fig. 7. Double logarithmic plot of the mean total morphometric pulmonary diffusing capacity (DL_{O_2}) against body weight (W). The values of DL_{O_2} pertain to the combined left and right lungs. The regression lines for the bats, birds and terrestrial mammals are based on the specimens and species as stated in Fig. 2. DL_{O_2} is higher in the bats than in both birds and terrestrial mammals. This is as a result of V_L , St and V_c being fairly high in bats in addition to the relatively small θ ; St , V_c and θ are utilized in calculating DL_{O_2} . DL_{O_2} is strongly correlated to body weight in these three groups of animals. DL_{O_2} in the domestic fowl is remarkably low.

Weibel, 1971), although such conditions are seldom realised even during strenuous exercise. The physiologically-estimated pulmonary diffusing capacity is thus always lower than that estimated morphometrically. Apparently the physiological pulmonary diffusing capacity has not been estimated for any bat.

In the six species of bat which have so far been examined, the highest value of DL_{O_2}/W ($20 \text{ mlO}_2 \text{ min}^{-1} \text{ mmHg}^{-1} \text{ kg}^{-1}$) was found in *Epomophorus* (Maina *et al.* 1982b). In the species investigated in the present study, the highest value was found in a specimen of *Pipistrellus pipistrellus* ($13 \text{ mlO}_2 \text{ min}^{-1} \text{ mmHg}^{-1} \text{ kg}^{-1}$). Relatively high values of DL_{O_2}/W were also found in *Tadarida mops*, the mean for this species being $10 \text{ mlO}_2 \text{ min}^{-1} \text{ mmHg}^{-1} \text{ kg}^{-1}$. The lowest values of DL_{O_2}/W in our five species (mean $4.2 \text{ mlO}_2 \text{ min}^{-1} \text{ mmHg}^{-1} \text{ kg}^{-1}$) were found both in *Cynopterus*

Table 8. Summary of the allometric (regression) functions $y = aW^b$ (y being a pulmonary variable; a , the y -intercept; W , body weight; and b the slope – the scaling factor between y and W) and correlation coefficients (r) of the main pulmonary components in six species* of bats

		r
VL	$= 59.45W^{1.07}$	0.925
St	$= 48.31W^{1.01}$	0.913
Vc	$= 5.13W^{0.954}$	0.882
S _v (t, p)	$= 83.56W^{0.033}$	0.097
tht	$= 215W^{0.021}$	0.165
DL _{O₂}	$= 10W^{0.932}$	0.866

Units: VL, mm³; St, cm²; Vc, mm³; S_v(t, p), mm²mm⁻³; tht, nm; DL_{O₂}, mm³O₂min⁻¹mmHg⁻¹; W, g.

* The values of the fruit bat *Epomophorus wahlbergi* reported in Maina, King & King (1982b) were incorporated with those of the bats examined here, in the calculation of these regression functions.

The symbols are defined in the Methods section.

brachyotis and *Cheiromeles torquatus*. However, the values of DL_{O₂}/W even in *Cynopterus* and *Cheiromeles* are slightly higher than the mean value of 4 mlO₂ min⁻¹ mmHg⁻¹ kg⁻¹ in the eight species of shrew examined by Gehr *et al.* (1980). Fig. 7 clearly shows that the DL_{O₂} of the bats so far examined is higher than that of both birds and terrestrial mammals. This is mainly as a result of the extensive and thin blood-gas (tissue) barrier, and the higher pulmonary capillary blood volume in the bats. When these morphological features of the bat lung are combined with the haematological adaptations which have been found in several species of bat, they appear to constitute effective adaptations for transferring the large amount of oxygen required by flight.

The molossid bats tend to be regarded as the most advanced bats (Griffin, 1970; Yalden & Morris, 1975). These insectivorous bats are speedy and enduring flyers, a chiropteran version of swallows and swifts (Vaughan, 1970). It might be expected that the energetic demands of this mode of life would entail an advanced level of respiratory specialization. Among our bats, the molossid *Tadarida mops* did have a relatively high morphometric diffusing capacity for oxygen. On the other hand the lowest value occurred in *Cheiromeles torquatus*, another molossid species. Among the six species of bat which we have now examined, by far the most outstanding respiratory adaptations have been found in the fruit bat *Epomophorus wahlbergi*. The big fruit bats have often been regarded as relatively 'primitive'. However, the body conformation of *Epomophorus* has been adapted to house lungs which are extraordinarily large and have a most extensive area for gas exchange, features which culminate in a morphometric diffusing capacity for oxygen of exceptional magnitude; on the other hand, *Cynopterus brachyotis* had a very low DL_{O₂}. Both of these pteropodid species are said to travel long distances to and from their feeding sites (Yalden & Morris, 1975), but *Cynopterus* seems to be entirely incapable of hovering (Snyder, 1976). The haematological parameters for *Cynopterus* differ very little from those of a terrestrial mammal (Snyder, 1976). Jepsen (1970) cast doubt on the concept of 'primitiveness', which includes being 'less highly organized anatomically', and noted that the debat

nds to be 'short on information'. We hope that data on the respiratory characteristics of bat species may broaden the basis for discussion.

It is notable that the volume proportions of the parenchyma and non-parenchyma in the bats which we have investigated are fairly constant and are similar to those of the lungs of the terrestrial mammals (Burri & Weibel, 1971; Gehr & Erni, 1980). The volume proportions of the main components of the parenchyma (alveoli, blood capillaries and the tissue of the interalveolar septa) in the bat lung are also similar to those reported for terrestrial mammals (Gehr, Bachofen & Weibel, 1978; Gehr *et al.* 1980; Gehr & Erni, 1980). In birds it has been found (Maina, 1982; Maina, Abdalla & King, 1982a) that the volume proportion of the exchange tissue is higher in the more active species of bird. The results of the present study of the bat lung are consistent with the suggestion by Maina *et al.* (1982b) that these basic proportions of the mammalian lung have become uniformly optimized in the course of evolution, whereas the avian lung has been sufficiently adaptable to permit even these basic proportions to be varied. Both orders possess enough flexibility for detailed refinements of the exchange surface. But for bats, confronted by immense energetic demands imposed by flight, this alone must have been insufficient: their sole remaining resource was greatly to increase the size of the lung as a whole.

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