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AN ALLOMETRIC STUDY OF PULMONARY MORPHOMETRIC PARAMETERS IN BIRDS, WITH MAMMALIAN COMPARISONS

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[Plates 1–2]

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Comprehensive pulmonary morphometric data from 42 species of birds representing ten orders were compared with those of other vertebrates, especially mammals, relating the comparisons to the varying biological needs of these avian taxa.

The total lung volume was strongly correlated with body mass. The volume density of the exchange tissue was lowest in the charadriiform and anseriform species and highest in the piciform, cuculiform and passeriform species. The surface area of the blood–gas (tissue) barrier, the volume of the pulmonary capillary blood and the total morphometric pulmonary diffusing capacity were all strongly correlated with body mass. The harmonic mean thickness of both the blood–gas (tissue) barrier and the plasma layer were weakly correlated with body mass. The mass-specific surface area of the blood–gas (tissue) barrier (surface area per gram body mass) and the surface density of the blood–gas (tissue) barrier (i.e. its surface area per unit volume of exchange tissue) were inversely correlated (though weakly) with body mass. The passeriform species exhibited outstanding pulmonary morphometric adaptations leading to a high specific total diffusing capacity per gram body mass, consistent with the comparatively small size and energetic mode of life which typify passeriform birds. The relatively inactive, ground-dwelling domestic fowl (*Gallus gallus*) had the lowest pulmonary diffusing capacity per gram body mass.

The specific total lung volume is about 27 % smaller in birds than in mammals but the specific surface area of the blood–gas (tissue) barrier is about 15 % greater in birds. The ratio of the surface area of the tissue barrier to the volume of the exchange tissue was also much greater in the birds (170–305 %). The harmonic mean thickness of the tissue barrier was 56–67 % less in the birds, but that of the plasma layer was about 66 % greater in the birds. The pulmonary capillary blood volume was also greater (22 %) in the birds. Except for the thickness of the plasma layer, these morphometric parameters all favour the gas exchange capacity of birds. Consequently, the total specific mean morphometric pulmonary diffusing capacity for oxygen was estimated to be about 22 % greater in birds than in mammals of similar body mass. This estimate was obtained by employing oxygen permeation constants for mammalian tissue, plasma and erythrocytes, as avian constants were not then available. Recalculations using recent values for the rate of oxygen uptake by avian whole blood indicate that the superiority of the avian pulmonary diffusing capacity for oxygen is even greater, the value for birds exceeding that of mammals by about 82 %. However, because of the small numbers of some of the avian species investigated and the lack of representatives of many important groups of birds, our allometric computations should be regarded as essentially a preliminary basis for comparing the pulmonary morphometric characteristics of birds and mammals.

It is suggested that the greater physiological efficiency of the avian pulmonary system compared with that of mammals can be attributed partly to the pulmonary morphometric differences between these two vertebrate classes. Other major factors are the cross-current relation of parabronchial gas and blood, the auxiliary counter-current relation of air capillary gas and blood, and the bellows action of the air sacs.

1. Introduction

The gas exchange systems of birds and mammals have evolved along remarkably different lines (Hughes 1979). It seems reasonable that a powerful influence on this profound divergence may be sought in the contrasting energetic requirements of these two classes of air-breathing vertebrates. Flight is a highly energetic exercise (Thomas 1980); for example, a budgerigar (*Melopsittacus undulatus*) flying at sea level uses oxygen at almost twice the rate of a mouse of similar mass running hard in a wheel (Tucker 1968*a*; Schmidt-Nielsen 1971). At its most economical speed during steady-state horizontal flight at sea level a budgerigar has to increase

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its oxygen consumption by about 13 times above its standard metabolic rate, and can increase it even further to 20–30 times during maximum effort (Tucker 1968*b*). For a well-trained human athlete this represents continuous heavy work; for example, cycle racing by a man weighing 71 kg requires an increase in metabolic rate of about 13 times times his resting rate (McArdle *et al.* 1981). The ability of some birds to perform this exceedingly strenuous work at high altitudes is altogether exceptional by mammalian standards (Tucker 1972; Berger 1974). At a simulated altitude of 6100 m mice become comatose but house sparrows (*Passer domesticus*) remain active and will actually fly (Tucker 1968*c*). In addition, some birds have a remarkable capacity for continuous flight over immense distances and in some instances they even do this at very high altitudes where the partial pressure of oxygen is extremely low. Among the most notable feats are the 2100 mile non-stop flights of the migrating American golden plover (*Pluvialis dominica*) (Tucker 1968*a*), the pole-to-pole journey of the arctic tern (*Sterna paradisaea*) (Berger 1961), and the trans-Himalayan flight of the bar-headed goose (*Anser indicus*) from sea level to 9200 m (Black *et al.* 1978).

The avian pulmonary design has been regarded as the most efficient gas-exchange system among the air-breathing vertebrates (Duncker 1971*b*; Lasiewski & Calder 1971; Weibel 1973; Scheid 1979), although it is clearly not a prerequisite for flight as bats can also fly though with a mammalian type of lung. The lungs of birds are compact and of constant volume, being ventilated by voluminous air sacs. Gas exchange takes place in the exchange-tissue mantle which surrounds the parabronchial lumina. The air flow in the parabronchi of the paleopulmo is now known to be unidirectional and continuous, whereas that in the neopulmo is believed to oscillate with the phase of respiration. For reviews of the anatomy of the avian lung air sac system see King (1966), King & Molony (1971), and Duncker (1971*b*, 1972, 1974). The physiology of the avian lung has been reviewed by Duncker (1971*b*, 1972), Lasiewski (1972), Fedde (1980), Bouverot (1978), Scheid (1979) and McLelland & Molony (1983).

Although research on the anatomy and physiology of the avian pulmonary system spans several centuries, many structural details are still unknown. In particular, quantitative anatomical data are urgently needed. Lasiewski & Calder (1971), Lasiewski (1972), Piiper & Scheid (1973) and Scheid (1979) have remarked on the scarcity of such information. The anatomy of the gas-exchange apparatus of mammals (see, for example, Dunnill 1962; Tenney & Remmers 1963; Weibel 1963*a*, 1973; Geelhaar & Weibel 1971; Forrest & Weibel 1975; Gehr & Erni 1980; Gehr *et al.* 1980, 1981*a*; Weibel *et al.* 1981*b*; Maina *et al.* 1982*c*), amphibians and reptiles (Szarski 1964; Tenney & Tenney 1970; Meban 1980), and of fish (Hughes & Munshi 1968; Hughes & Weibel 1976; Hughes 1980, 1981) have all been quantitatively investigated to a greater or lesser extent. In contrast, nearly all the comparable quantitative studies on the avian lung have only been preliminary (Duncker 1971*a*, *b*, 1972, 1973; Abdalla 1977; Abdalla & Maina 1981; Maina 1980, 1981, 1982*a*, *c*, *d*; Maina *et al.* 1981; Maina & Settle 1982). Recent exceptions are the thorough reports on the budgerigar (*Melopsittacus undulatus*), violet-eared hummingbird (*Colibri coruscans*) and house sparrow (*Passer domesticus*) by Dubach (1981); on the domestic fowl (*Gallus gallus*, variant *domesticus*) by Abdalla *et al.* (1982); on two anseriform species of bird, namely the wild mallard (*Anas platyrhynchos*) and the greylag goose (*Anser anser*), by Maina & King (1982*b*); on the domestic goose (*Anser anser*) and Canada goose (*Branta canadensis*) by Powell & Mazzone (1983); on eight passeriform species by Maina (1984); on gliding and diving birds by Maina (1987); and on the domestic

form and wild variant (red jungle fowl) of *Gallus gallus*, the domestic form of the muscovy duck (*Cairina moschata*) and the white-breasted water-hen (*Amaurornis phoenicurus*) by Vidyadaran (1987). Furthermore, there has been a detailed investigation of the blood–gas barrier of ten species of bird (Maina & King 1982*a*). An extensive light-microscopic analysis of the lungs of 19 species of bird (Maina *et al.* 1982*a*) has also been made, and the paleo- and neopulmonic regions of the lung of the collared turtle dove (*Streptopelia decaocto*) have been analysed (Maina 1982*b*; Maina *et al.* 1982*b*).

A major weakness in current knowledge of the functional anatomy of the avian lung is that, of about 9000 species of bird, published results of comprehensive quantitative investigations are available only for the 25 species referred to at the end of the previous paragraph. Indeed, the domestic fowl (*Gallus gallus*) is the one species in which almost all aspects of both pulmonary anatomy and physiology have been really thoroughly studied. Consequently, much of our knowledge is based on the domestic fowl, which is by no means an ideal representative of birds in general because of its sheltered and non-flying mode of life (Duncker 1971*a*; Lasiewski 1972). This acute scarcity of comprehensive quantitative data on the avian lung has been the overriding stimulus to our present study.

Comparisons of pulmonary morphometric parameters between 42 species and ten orders of birds are now reported. These avian data are compared with those available for other classes of vertebrates, especially mammals. Allometric functions are calculated for birds in general, and related to comparable functions for mammals. Correlations between the respiratory parameters and energetic requirements of the avian taxa are considered.

2. Materials and methods

The orders, species and number of birds per species and the different investigations done, are shown in table 1. Altogether, 160 individual birds were examined. The birds were believed to be mature and were of mixed sexes. Most of them were completely wild, but a few were captive, domesticated or semi-wild (listed here as feral) (see table 1 under the heading 'state').

After capture the birds were killed immediately (to avoid loss of body mass) by injection of barbiturate into the brachial vein or into the peritoneal cavity in small birds. The birds were then weighed. The trachea was cannulated and the lungs fixed *in situ* by intratracheal infusion with buffered 2.3% (by volume) glutaraldehyde or a combination of 1.5% glutaraldehyde and 0.8% paraformaldehyde (half-strength solution of Karnovsky (1965)). The buffer used was sodium cacodylate or sodium diphosphate when cacodylate was not available, the fixative being adjusted to a pH of 7.4. The osmolarity of the 2.3% glutaraldehyde solution was 350 mOsm† when buffered in sodium cacodylate and 460 mOsm when buffered in sodium diphosphate; that of cacodylate buffered half-strength solution of Karnovsky was also 460 mOsm. Glutaraldehyde fixative gave better fixation in the lungs of the larger birds, whereas half-strength Karnovsky's fixative was more effective for the smaller birds. Fixation was deemed satisfactory for light microscopy when the lumina of the bronchi, atria and blood vessels were patent and the exchange tissue was intact; it was suitable for electron microscopy when the air and blood capillaries were open and separated by an intact blood–gas barrier with well-defined cells.

† One osmole contains one mole of osmotically active particles.

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TABLE 1. SUMMARY OF THE MATERIALS AND INVESTIGATIONS[a]

taxon	n	body mass/g	volume of both lungs, V_L / cm^3	light microscopy[b]	electron microscopy[b]	state of bird[c]
Anseriformes						
Anas platyrhynchos mallard	5	1038±100	30.6±3.73	×	×	f
Anser anser greylag goose	5	3838±182	95.3±5.9	×	×	w
Falconiformes						
Falco tinnunculus common kestrel	2	166.0±5.7	3.11±0.67	×	× (1)	w
Galliformes						
Gallus gallus domestic fowl	12	2141±344	27.0±4.8	—	× (3)	d
Charadriiformes						
Alca torda razorbill	2	487±112.4	18.07±0.25	×	×	w
Cepphus carbo spectacled guillemot	9	737±106	24.1±2.74	×	×	w
Larus argentatus herring gull	2	654±24.7	18.20±1.58	×	×	w
Larus canus common gull	1	302	7.08	×	×	w
Larus ridibundus black-headed gull	6	253±52	7.48±0.89	×	×	w
Columbiformes						
Columba livia rock dove	1	216	7.37	×	×	w
Streptopelia decaocto collared turtle dove	16	189±18	6.46±0.71	×	× (5)	w
Streptopelia senegalensis laughing dove	1	58	1.77	×	×	w
Psittaciformes						
Melopsittacus undulatus budgerigar	6	36.4±6.8	1.025±0.113	×	×	c
Cuculiformes						
Chrysococcyx klaas Klaas' cuckoo	3	26.95±0.13	0.66±0.14	×	×	w
Coliiformes						
Colius striatus speckled mousebird	1	50.5	0.71	×	×	w
Piciformes						
Jynx ruficollis red-breasted wryneck	2	54.3±6.0	1.085±0.01	×	—	w
Pogoniulus bilineatus golden-rumped tinkerbird	1	14.9	0.227	×	×	w

[a] The values are means±s.d.

[b] ×, indicates where an investigation was carried out and, —, where it was not. The number of birds successfully examined by electron microscopy, shown in parentheses, was less than that on which light microscopy was carried out.

[c] State indicates the background of the animal: f, feral; w, wild; d, domestic; c, captive.

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TABLE 1. (*cont.*)

taxon	*n*	body mass/g	volume of both lungs, V_L / cm^3	light microscopy[b]	electron microscopy[b]	state of bird[c]
Passeriformes						
Amblyospiza albifrons grosbeak weaver	5	37.4±3.8	0.97±0.12	×	×	w
Cercotrichas leucophrys[d] white-winged scrub robin	1	15.95	0.384	×	—	w
Chloropeta natalensis yellow flycatcher	1	10.92	0.313	—	—	w
Cisticola cantans singing cisticola	4	15.0±1.9	0.308±0.09	×	×	w
Cossypha caffra robin-chat	2	25.11±0.30	0.584±0.03	× (1)	—	w
Estrilda astrild waxbill	3	6.96±1.16	0.153±0.04	×	—	w
Estrilda melanotis yellow-bellied waxbill	1	5.4	0.129	—	—	w
Hirundo fuligula[d] African rock martin	1	13.7	0.329	×	×	w
Lagonisticta senegala red-billed firefinch	1	8.0	0.223	×	—	w
Laniarius aethiopicus[d] tropical boubou	1	42.8	0.888	×	—	w
Lanius collaris fiscal shrike	6	32.5±1.03	0.717±0.10	×	× (5)	w
Lonchura cucullata bronze mannikin	7	9.4±1.1	0.230±0.3	×	—	w
Nectarinia kilimensis bronze sunbird	2	16.58±0.79	0.495±0.04	× (1)	—	w
Nectarinia reichenowi golden-winged sunbird	3	13.7±1.7	0.363±0.01	×	—	w
Passer domesticus house sparrow	12	25.5±2.02	0.760±0.12	×	—	w
Ploceus baglafecht baglafecht weaver	6	32.5±3.3	0.875±0.07	×	× (4)	w
Ploceus cucullatus black-headed weaver	3	34.9±3.8	0.87±0.16	×	—	w
Ploceus ocularis spectacled weaver	2	26.9±5.5	0.723±0.16	×	—	w
Ploceus xanthops Holub's golden weaver	3	39.3±1.98	1.032±0.07	×	—	w
Prinia subflava tawny prinia	1	9.1	0.213	×	×	w
Serinus canaria canary	6	23.9±2.8	0.709±0.07	—	—	c
Serinus mozambicus yellow-fronted canary	1	13.5	0.273	—	—	w
Sturnus vulgaris common starling	10	72.6±3.4	2.02±0.22	×	×	w
Turdus iliacus redwing	1	51.0	1.19	×	×	w
Turdus olivaceus olive thrush	2	65.1±8.9	1.40±0.14	×	×	w

[d] Not listed by Morony *et al.* (1975), the Latin name being from Gruson (1976).

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The lungs were infused by gravity, the cannula being held 25 cm above the animal, which was in a supine position. When the fixative stopped flowing an incision was made caudal to the sternum, and the fixative was allowed to pass freely through the lungs and escape from the air sacs into the body cavities. The trachea was then ligated and the respiratory organs left *in situ*, covered in fixative, for about 20 min. The lungs were removed and immersed overnight in fixative. The extra-pulmonary part of the primary bronchus and the blood vessels were trimmed at the lung hilus, and the adhering fat and connective tissue were removed from the surface of the lung. The volume of one of the pair of lungs for each bird was estimated (there was no significant difference in the volumes of the left and right lung within the experimental limits of the method) by water displacement (Scherle 1970). The total volume of the right and left lungs for each bird was obtained by doubling the volume of the one lung. In each specimen the left lung was used for light microscopy and the right lung for electron microscopy.

(*a*) *Light microscopy*

The large lungs were cut into four slices along the costal sulci; each slice was then cut in half just dorsal to the primary bronchus, to facilitate later processing. The smaller lungs were processed whole. The processing involved dehydration in ethanol at 50%, clearing in xylene or chloroform, and embedding in paraffin wax of melting point 56 °C. Histological sections were cut transversely in relation to the long axis of the lung. For the large lungs, the histological sections were cut at 7 μm from the cranial face of each half-slice and stained with haematoxylin and eosin; the first technically adequate section was used in the analysis. Thus for the large lungs eight transverse histological sections of half slices (giving four complete transverse sections of each lung) were completely analysed. The small lungs were embedded whole, serially sectioned at 7 μm, and stained with haematoxylin and eosin. From each small lung eight transverse histological sections were taken at equal intervals. Some birds had to be excluded from microscopy because fixation was considered to be inadequate, but 38 species (140 individual birds) were investigated (table 2).

The sections were fully analysed field by field, at a magnification of × 100, using a 100-point Zeiss integrating graticule to estimate the volume density (percentage volume proportion within the lung) of the following components: the exchange tissue; the lumina of the parabronchi and secondary bronchi together, including the atria; the walls and lumina of blood vessels larger than capillaries; and the primary bronchus (see Appendix and figure 12). These components were considered to comprise the total volume of the lung. Other possible components like lymphatics and interparabronchial septa were not taken into account, as they occupy infinitesimal volumes (indeed the septa are absent in many species). The parabronchi and secondary bronchi were taken as one component because most of the secondary bronchi have a mantle of exchange tissue around them and therefore resemble parabronchi.

The sufficiency of the number of sections was determined by taking cumulative means. Because the sections were completely analysed field by field, the number of points counted for the three main components of the lung exceeded the number recommended by Weibel (1963*b*) and Dunnill (1968) for a standard error of less than 5%. Usually the primary bronchus did not meet this criterion as its relative volume proportion was very small. The analytical technique of point counting is fully described by Weibel (1979*a*) and has been extensively used in the analysis of biological materials, including the lung (Dunnill 1962; Weibel 1963*a*). The

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TABLE 2. ANALYSIS OF THE VOLUMES OF THE MAIN COMPONENTS OF THE AVIAN LUNG[a]

taxon	*n*	exchange tissue, V_x		lumina of parabronchi and secondary bronchi (including the atria)		blood vessels larger than capillaries		primary bronchus	
		%	cm³	%	cm³	%	cm³	%	cm³
Anseriformes									
Anas platyrhynchos	5	40.55±1.62	12.44±1.05	50.37±1.07	15.46±2.22	6.70±1.06	2.06±0.45	2.38±0.98	0.74±0.37
Anser anser	5	40.37±4.61	38.42±4.26	50.49±4.28	48.61±5.05	6.91±1.22	6.59±1.21	1.73±1.00	1.68±1.07
mean		40.46±0.13	25.43±18.37	50.68±0.44	32.04±23.44	6.81±0.15	4.33±3.20	2.06±0.46	1.21±0.66
Falconiformes									
Falco tinnunculus	2	51.85	1.61	39.03	1.21	7.33	0.23	1.79	0.06
Galliformes									
Gallus gallus	3	46.35±1.60	12.54±2.93	30.56±0.99	8.27±1.93	13.65±1.08	3.69±0.86	9.34±2.07	2.52±0.59
Charadriiformes									
Alca torda	2	32.79±1.46	5.92±0.18	53.43±2.21	9.65±0.53	11.40±0.60	2.06±0.08	2.38±0.11	0.43±0.01
Cepphus carbo	9	33.40±3.83	8.05±1.76	47.92±4.51	11.52±1.34	13.86±4.21	3.33±1.02	4.82±1.20	1.16±0.26
Largus argentatus	2	32.6±8.38	6.01±2.04	60.41±7.25	10.94±0.37	5.56±0.25	1.01±0.04	1.39±0.88	0.25±0.14
L. canus	1	30.85	2.18	61.70	4.37	5.39	0.38	2.06	0.15
L. ridibundus	6	35.83±1.06	2.67±0.29	54.88±2.89	4.11±0.57	7.17±1.71	0.53±0.10	2.12±1.31	0.19±0.06
mean		33.10±1.80	5:14±2.48	55.67±5.58	8.40±3.64	8.68±3.78	1.52±1.23	2.55±1.32	0.45±0.42
Columbiformes									
Columbia livia	1	43.57	3.21	32.26	2.38	14.85	1.09	9.32	0.69
Streptopelia decaocto	16	52.17±5.51	3.36±0.45	29.46±5.56	1.90±0.36	15.53±3.78	1.02±0.29	2.84±0.67	0.19±0.05
S. senegalensis	1	52.26	0.93	40.22	0.71	6.18	0.11	1.34	0.02
mean	49	33±5.0	2.50±1.36	33.98±5.58	1.66±0.86	12.2±5.2	0.74±0.55	4.5±4.2	0.30±0.35
Psittaciformes									
Melopsittacus undulatus	6	46.56±2.15	0.48±0.05	47.46±1.78	0.49±0.07	4.02±0.43	0.04±0.01	1.96±0.79	0.02±0.01

lumina of parabronchi and secondary bronchi (including the atria) | blood vessels larger than capillaries | primary bronchus

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Cuculiformes									
Chrysococcyx klaas	3	53.00±3.38	0.35±0.09	37.03±3.23	0.24±0.03	8.36±1.95	0.06±0.02	0.161±0.44	0.01±0.02
Coliiformes									
Colius striatus	1	50.81	0.39	37.43	0.23	9.78	0.07	1.98	0.02
Piciformes									
Jynx ruficollis	2	45.71±5.58	0.50±0.06	47.65±5.61	0.52±0.07	5.44±0.82	0.06±0.01	1.20±0.80	0.01±0.008
Pogoniulus bilineatus	1	54.20	0.123	35.22	0.08	8.64	0.02	1.94	0.004
mean		49.96±6.00	0.31±0.27	41.44±8.79	0.30±0.31	7.04±2.7	0.04±0.03	1.57±0.52	0.007±0.004
Passeriformes									
Amblyospiza albifrons	5	48.83±2.48	0.47±0.07	44.10±3.13	0.43±0.04	6.17±1.72	0.06±0.02	0.90±0.47	0.008±0.004
Cercotrichas leukophrys	1	42.39	0.16	47.13	0.18	9.48	0.04	1.00	0.004
Cistocola cantans	4	48.61±3.62	0.15±0.03	41.57±4.19	0.13±0.05	7.74±1.32	0.02±0.01	2.08±1.19	0.01±0.004
Cossypha caffra	1	46.50	0.28	44.95	0.27	6.85	0.04	1.70	0.01
Estrilda astrild	3	59.85±4.19	0.09±0.03	30.06±2.73	0.05±0.01	8.40±1.53	0.01±0.002	1.69±0.86	0.003±0.002
Hirundo fuligula	1	51.15	0.17	41.34	0.14	6.69	0.02	0.82	0.003
Lagonosticta senegala	1	56.92	0.13	31.95	0.07	10.02	0.02	1.11	0.002
Laniarius aethiopicus	1	54.57	0.48	37.90	0.34	6.62	0.06	0.91	0.008
Lanius collaris	6	52.99±4.11	0.38±0.05	39.66±4.23	0.28±0.05	6.43±1.57	0.05±0.02	0.92±0.37	0.007±0.002
Lonchura cucullata	7	55.92±2.42	0.13±0.02	33.93±3.0	0.08±0.01	8.64±1.8	0.02±0.01	1.51±0.64	0.003±0.002
Nectarinia kilimensis	1	56.34	0.29	32.62	0.16	8.70	0.04	2.34	0.01
N. reichenowi	3	58.56±3.19	0.21±0.05	31.91±3.36	0.12±0.03	8.67±1.37	0.03±0.01	0.86±0.43	0.003±0.01
Passer domesticus	12	55.68±3.92	0.42±0.09	36.91±3.50	0.28±0.05	6.45±2.48	0.05±0.03	0.96±0.51	0.007±0.004
Ploceus baglafecht	6	49.43±7.01	0.43±0.07	42.38±5.13	0.37±0.06	6.72±2.30	0.06±0.02	1.47±0.50	0.013±0.005
P. cucullatus	3	57.61±5.23	0.49±0.05	35.25±5.32	0.32±0.03	5.67±0.67	0.05±0.01	1.47±0.77	0.01±0.004
P. ocularis	2	47.05±0.20	0.34±0.07	45.04±0.18	0.33±0.07	6.30±0.12	0.05±0.01	1.61±0.51	0.01±0.006
P. xanthops	3	49.13±4.19	0.51±0.07	41.09±3.92	0.42±0.07	7.87±1.07	0.07±0.01	1.91±0.55	0.02±0.005
Prinia subflava	1	51.86	0.11	37.57	0.08	9.08	0.02	1.49	0.003
Sturnus vulgaris	10	51.76±4.25	1.05±0.13	41.16±3.79	0.83±0.13	5.19±0.86	0.11±0.02	1.89±0.63	0.04±0.02
Turdus iliacus	1	45.63	0.54	45.79	0.55	7.11	0.08	1.47	0.02
T. olivaceus	2	55.84±3.53	0.78±0.13	36.38±0.44	0.51±0.04	5.92±2.63	0.08±0.03	1.86±0.14	0.03±0.004
mean		52.22±4.77	0.36±0.24	38.99±5.09	0.28±0.19	7.37±1.36	0.05±0.03	1.43±0.45	0.01±0.009

[a] The investigation was made with a light-microscope. Relative volumes (%) and absolute volumes (cm^3) are means±s.d. The absolute values appertain to the combined volume of the fixed left and right lungs together and are calculated from the relative volumes and the total volume of the lung. The number of specimens per species that were examined is shown under *n*.

absolute volumes of the four components of the lungs were calculated from their volume densities and the combined volume of the left and right lungs together (which constituted the reference volume).

(*b*) *Electron microscopy*

The right lung was cut into four slices along the costal sulci and the slices were then cut into halves just dorsal to the primary bronchus. The half slices were diced and the resulting pieces (about 2 mm^3) were post-fixed in 2% (20 g l^{-1}) osmium tetroxide for about 2 h, stained in 2% (20 g l^{-1}) uranyl acetate with maleic acid, dehydrated in graded ethanol (starting at 50% through absolute) and in acetone or propylene oxide, and embedded in Taab resin. From each half slice a group of 4–10 blocks was prepared. One block was picked at random from each group, and trimmed to eliminate all but the exchange tissue. Ultrathin sections were cut at about 90 nm thickness (silver to gold), mounted on 200 wire-mesh grids, and counterstained with lead citrate. From the first technically adequate section, three micrographs were taken at predetermined corners of the grid squares. A total of 35 micrographs was initially prepared from each bird, but it was ascertained from the cumulative means that 24 micrographs were sufficient, thus a minimum of this number of micrographs was analysed. The pictures were taken at a primary magnification of ×3000 and analysed at a final magnification of about ×7500, which gave a large field but still enabled the essential quantification to be made. A diffraction grating was included in each batch of electron micrographs to calibrate the magnification. Some birds were rejected because fixation was inadequate, 26 species (90 individual birds) being successfully investigated by electron microscopy (tables 3–7 inclusive).

The volume densities of the components of the exchange tissue, i.e. the air capillaries, blood capillaries, tissue and red blood cells, were estimated by point counting using a coherent quadratic lattice grid (Weibel 1969) with 342 points printed on each electron micrograph (figure 13). The surface areas of the components of the exchange tissue were estimated by intersection-counting (see Appendix and figures 13 and 15) (Weibel 1963*b*; Dunnill 1962, 1968). The harmonic mean thicknesses of the blood–gas (tissue) barrier, τ_{ht}, and of the plasma layer, τ_{hp}, were estimated by intercept length measurement (see Appendix and figures 13 and 16) (Weibel & Knight 1964; Weibel 1970–1). The measurements were made with a linear millimetre scale along the lines of the test grid. An intercept in the estimation of τ_{ht} was defined as a line passing from the outer unit membrane of the epithelial cell of an air capillary (i.e. the unit membrane at the gas–tissue interface) to the inner unit membrane of the endothelial cell of a blood capillary (i.e. the unit membrane at the blood plasma – tissue interface), where an air capillary and a blood capillary lay adjacent to each other. When present, the very thin osmiophilic lining complex was included in this measurement, but the complex was often lost during fixation. An intercept for τ_{hp} was a line passing from the inner unit membrane of the capillary endothelial cell to the surface of a red blood cell. The surface area of the plasma layer was estimated as the mean of the surface area of the capillary endothelium (S_c) and that of the red blood cells (S_e) (Weibel 1970–1). The surface density of the blood–gas (tissue) barrier was calculated from its surface area and the volume of the exchange tissue (S_t V_x^{-1}). The absolute values for volumes and surface areas were calculated from the absolute volume of the exchange tissue. The arithmetic mean thickness of the blood–gas (tissue) barrier was estimated using a random short-line test grid (see Appendix and figure 14) (Weibel & Knight 1964).

The morphometric pulmonary diffusing capacity was calculated by the model of Weibel (1970–1), which requires estimation of the conductances to oxygen of three resistances, i.e. the

tissue barrier, the plasma layer and the red blood cell. The physical coefficients (i.e. the permeation coefficients of oxygen through the tissue barrier, K_{tO_2}, and plasma, K_{pO_2}, and the rate of oxygen uptake by whole blood, Θ_{O_2}) which are used in the model are those which have been estimated for mammalian tissue and cited by Weibel (1970–1) (see Appendix); unfortunately the use of mammalian coefficients cannot be avoided at the moment, as strictly equivalent coefficients for birds are lacking†. Because the avian red blood cells are nucleated, the venous haematocrits were adjusted by subtracting the volume of the nucleus (see §3*e*) from that of the red blood cell, thus giving an approximate estimate of the volume of the haemoglobin; the value obtained in this way is more closely comparable to the mammalian venous haematocrit. This modified value was used to adjust the rate of oxygen uptake by whole blood, which is based on a mammalian venous haematocrit of 45% (Weibel 1970–1). This adjustment is essentially similar to that made by Hughes & Weibel (1976) for the nucleated red blood cells of the lungfish (*Lepidosiren paradoxa*).

The terms for the structural components of the avian lung used in the text are from the *Nomina anatomica avium* (Baumel *et al.* 1979). The English names for birds are taken from Gruson (1976). The Latin generic and specific names are based on Morony *et al.* (1975); the latter work closely follows Peter's checklist of the *Birds of the world*, which contains full details of the authors and dates of the Latin names. The names and membership of orders are from Storer (1971).

(*c*) *Statistical methods*

(i) *Regression analysis*

Most of the pulmonary morphometric parameters studied were expected to relate to body mass, and regression lines quantifying such relations were fitted using the following model: $Z_i \approx \mathrm{N}(a + bt_i, \sigma^2)$, where $Z_i = \log_{10} Y_i$, Y_i = random variable denoting parameter value at body mass w_i, w_i = body mass of the i^{th} member of sample, $t_i = \log_{10} w_i$, and a, b, σ^2 are constants to be estimated by least squares from a sample of pairs of values (w_i, y_i), where y_i is an observed value of Y_i.

For birds, this model was fitted by using the ordinary least-squares method. For mammals, however, it proved necessary to use the method of weighted least squares (see Sprent (1969) for a full description) so as to give some of the data points more importance than others. This was done for the following reason. Some of the parameter values quoted in the literature are not for individual specimens but are arithmetic means for stated numbers of specimens (see table 8); for example, a mean of k specimens is a sample from $\bar{Y}_i = (Y_{i_1} + \ldots + Y_{i_k})/k$ where $\bar{w}_i = (w_{i_1} + w_{i_2} + \ldots + w_{i_k})/k$ is known but the individual data points (w_{i_j}, y_{i_j}) are unavailable. Assuming that the unknown $w_{i_1}, \ldots, w_{i_k}$ do not vary much by comparison with the full range of body masses in the data, then according to the model stated above, $\bar{Z}_i = \log_{10} \bar{Y}_i$ will have approximately the same distribution as Z_i but a reduced variance of $(1/k)\,\sigma^2$; so a sample point $(\bar{w}_i, \bar{y}_i)$ should be given increased importance as compared with a sample point (w_i, y_i), and the method of weighted least squares provides a formal way of taking account of this.

It seems reasonable to examine, for each parameter, the possibility that the regression line for birds may be related to that for mammals, and so a test procedure described by Sprent

† After this work was completed, values of 2.20 and 2.23 ml O_2 min^{-1} $torr^{-1}$ (2.75 and 2.79×10^{-2} ml O_2 s^{-1} $mbar^{-1}$) for Θ_{O_2} have been made available for the mature muscovy duck (*Cairina moschata*) and domestic fowl (*Gallus gallus*) respectively, by Nguyen Phu *et al.* (1986). See also the footnote to p. 25.

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(1969) was carried out to assess this. This procedure was modified to allow for the weighting of the mammalian data, but the modifications do not affect the principles of the approach, which are as follows. The procedure assumes that the data may be described by one of three possible models: model A, which is composed of a pair of unrelated straight lines for birds and mammals; model B, which uses a pair of parallel straight lines, and model C, which consists of a single straight line. The first test decides between models A and B, the simpler model B being preferred only if model A offers no significant improvement at the 5% level of significance. If model B survives this test, a second test is carried out to decide between models B and C. This procedure was used for all the pairs of regression lines considered; in two cases, model A proved significantly better than model B, and in the remaining cases model B proved significantly better than model C, so for no parameter was it reasonable to suppose that a single line could adequately represent both the avian and the mammalian data. The regression lines and the pertinent data are summarized in table 9.

(ii) *Student's t-test*

A few of the parameters studied were not expected to relate to body mass. Some results are quoted of comparisons between different species of birds for such parameters, and the assumption here is that the results for species s are a random sample from a distribution with mean μ_s and variance σ_s^2. Student's t-test is used to compare estimated values of mean μ_s for different species, the numbers of samples of the species in question being in all cases large enough to justify the use of this test.

3. Results

The structure of the parabronchi of the various species differed in detail. The interparabronchial septa were virtually absent in the falconiform, columbiform, psittaciform, cuculiform, coliiform, piciform and passeriform species, minimal or very indistinct in the anseriforms, sometimes apparent in charadriiforms (figure 1) and conspicuous in galliform species. The atria, interatrial septa and atrial muscles were poorly developed in the species which lacked interparabronchial septa, but were well developed in the anseriform, charadriiform and galliform species. The diameter of the parabronchial lumen was usually about half that of the whole parabronchus (i.e. lumen plus the exchange-tissue mantle). The diameter of the whole parabronchus ranged from about 0.34 mm in small passeriforms (e.g. *Estrilda astrild*) to a maximum of about 0.63 mm in *Anser anser*; because of an estimated shrinkage of about 14% during histological processing, these values are smaller than in the living bird. When the interparabronchial septa were not distinct, the parabronchial boundaries could only be identified by the interparabronchial blood vessels.

The air capillaries and blood capillaries formed the exchange tissue (figure 2). The blood–gas (tissue) barrier (figure 3) comprised an epithelial cell, a basal lamina and an endothelial cell, interstitial tissue (e.g. collagen fibrils, fibrocytes, etc.) being generally scarce in birds as in figure 3 (see Maina & King 1982*a*). In some places air capillaries were in contact with air capillaries, and blood capillaries with blood capillaries as in figures 2 and 16, comprising tissue not involved in gas exchange (V_{tn}, see §3).

The detailed results of this investigation are summarized in tables 1–7. The following account draws attention to the main characteristics of each pulmonary morphometric parameter. Any marked differences between species and orders of birds are then pointed out;

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emphasis is placed mainly on the anseriform, charadriiform and passeriform species, which are relatively well represented in this study. The term 'specific value' is used for any value which has been standardized (normalized) against body mass. All the values for areas and absolute volumes are the mean values for the two lungs together.

(*a*) *Lung volume*

The body mass of the species investigated ranged from 5.4 g in the one specimen of the passeriform *Estrilda melanotis* to 3964 g in an individual specimen of the anseriform *Anser anser*. The combined volume of the left- and right-fixed lungs together was obtained in all the birds (42 species, 160 individuals, as in table 1). It ranged from 0.11 cm^3 in a specimen of *Estrilda astrild* to 103 cm^3 in a specimen of *Anser anser*. A strong positive, highly significant, correlation ($r = 0.992$, $p < 0.001$) was found between body mass and lung volume (figure 4). The ratio of lung volume to body mass in the domestic fowl (*Gallus gallus*) was atypically small (figure 4). For this and other reasons noted below, this galliform species has been excluded from the calculation of the allometric (regression) function for lung volume, and from the calculation of all other regression functions.

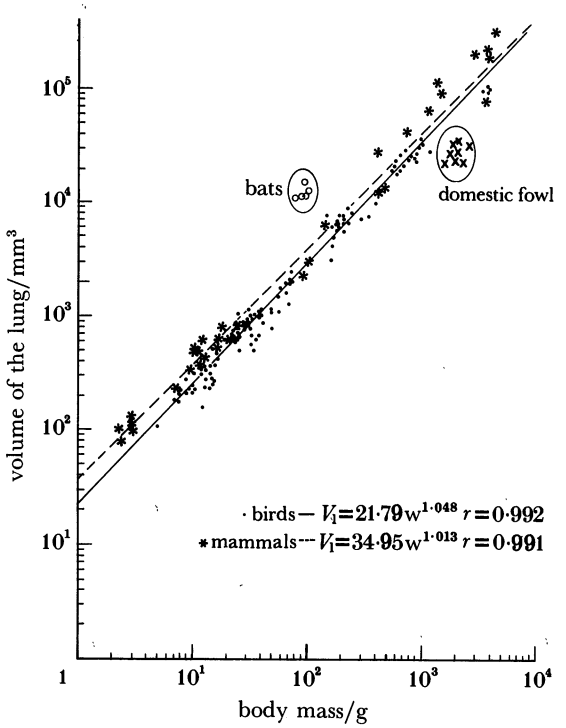

FIGURE 4. Double logarithmic plot of lung volume (V_L) against body mass (W). All the values of V_L appertain to the combined volumes of the left and right lungs together. The lower regression line is based on 160 data points for the 160 individual birds, representing 42 species, summarized in table 1 (after exclusion of the domestic fowl, for which the data points are entered independently on the graph). The upper regression line is based on 40 data points derived from the 40 values published in the literature for V_L, listed in table 8 with references to the literature from which they were taken, for 20 mammalian species within a similar mass range to the birds. As table 8 shows, most of these mammalian values represent individual animals, but some are means because individual values were not reported in the original papers (see §2*c*(i), for statistical treatment). The data points in fact represent 72 individual animals. The values for the five bats (*Epomophorus wahlbergi*, a fruit-eating bat) came from Maina *et al.* (1982*c*), and are entered independently. Lung volume is strongly correlated positively with body mass in both the birds and the mammals (see *r* values on the figure). From a statistical examination of the two regression lines (see §2*c*(ii) and §4*a*(i)) and comparison of the *y*-intercepts it is estimated that the lung volume of the birds in general was about 27% smaller than that of the mammals. However, the values for the bats were remarkably high and those for the domestic fowl exceptionally low.

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TABLE 3. ANALYSIS OF THE VOLUMES OF THE MAIN COMPONENTS OF THE EXCHANGE TISSUE[a]

		air capillaries, V_a		blood capillaries, V_c		tissue of the blood-gas barrier, V_t		tissue not involved in gas exchange, V_{tn}	
taxon	*n*	%	cm^3	%	cm^3	%	cm^3	%	cm^3
Anseriformes									
Anas platyrhynchos	5	59.21±2.45	7.37±0.87	32.98±2.74	4.10±0.35	5.76±0.85	0.72±0.08	2.08±0.56	0.26±0.08
Anser anser	5	62.03±4.04	23.83±2.29	32.43±4.11	12.46±2.59	4.24±0.15	1.63±0.21	1.30±0.23	0.50±0.07
mean		60.62±1.99	15.6±11.64	32.71±0.39	8.28±5.91	5.00±1.07	1.18±0.64	1.69±0.55	0.38±0.17
Falconiformes									
Falco tinnunculus	1	53.02	0.85	25.56	0.41	17.28	0.28	4.14	0.07
Galliformes									
Gallus gallus	3	60.90±6.60	7.64±1.29	27.92±5.54	3.50±1.52	6.30±3.15	0.79±0.37	4.88±1.91	0.61±0.18
Charadriiformes									
Alca torda	2	49.54±1.56	2.94±0.18	36.89±2.69	2.19±0.09	10.19±1.24	0.61±0.09	3.38±0.11	0.2
Cepphus carbo	9	47.49±5.36	3.82±0.86	39.75±5.30	3.20±0.90	9.46±0.57	0.76±0.13	3.30±0.80	0.27±0.08
Larus argentatus	2	53.68±8.46	3.23±1.60	35.92±6.22	2.16±0.36	7.04±0.77	0.42±0.10	3.36±1.48	0.19±0.02
L. canus	1	58.23	1.27	30.45	0.66	8.74	0.19	2.58	0.06
L. ridibundus	6	62.52±3.56	1.67±0.18	28.92±3.07	0.77±0.13	5.96±1.37	0.16±0.04	2.60±0.88	0.07±0.05
mean		54.29±6.17	2.59±1.08	34.39±4.55	1.80±1.07	8.28±1.74	0.43±0.26	3.04±0.42	0.16±0.09
Columbiformes									
Columba livia	1	58.70	1.88	33.63	1.08	5.90	0.19	1.77	0.06
Streptopelia decaocto	5	62.96±4.29	2.12±0.48	22.81±2.94	0.77±0.19	10.42±4.68	0.35±0.03	3.81±0.87	0.13±0.02
S. senegalensis	1	45.13	0.417	34.63	0.320	16.77	0.155	3.46	0.032
mean		55.60±9.31	1.47±0.92	30.36±6.55	0.72±0.38	11.03±5.46	0.23±0.10	3.01±1.09	0.07±0.05

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Psittaciformes									
Melopsittacus undulatus	6	52.47±1.75	0.25±0.02	33.34±2.04	0.16±0.02	11.44±1.54	0.06±0.01	2.75±0.75	0.01±0.004
Cuculiformes									
Chrysococcyx klaas	3	55.09±1.55	0.193±0.06	34.50±0.32	0.121±0.03	8.26±1.43	0.029±0.004	2.15±0.84	0.007±0.001
Coliiformes									
Colius striatus	1	53.75	0.208	36.43	0.141	7.49	0.03	2.33	0.009
Piciformes									
Pogoniulus bilineatus	1	38.21	0.047	39.02	0.048	19.51	0.024	3.25	0.004
Passeriformes									
Amblyospiza albifrons	5	44.84±1.30	0.21±0.04	42.15±2.58	0.20±0.05	9.88±1.20	0.05±0.005	3.13±0.72	0.02±0.0002
Cistocola cantans	4	48.20±10.98	0.07±0.02	38.32±9.59	0.06±0.02	9.92±0.97	0.02±0.002	3.56±0.067	0.005±0.001
Hirundo fuligula	1	45.83	0.08	44.35	0.08	7.74	0.01	2.08	0.004
Lanius collaris	5	45.48±4.90	0.19±0.02	37.13±5.77	0.14±0.02	10.40±2.97	0.04±0.01	2.98±0.86	0.01±0.0003
Passer domesticus	5	45.68±1.59	0.19±0.05	38.04±1.95	0.16±0.04	12.87±1.20	0.05±0.01	3.41±1.45	0.01±0.006
Ploceus baglafecht	4	50.96±8.29	0.22±0.03	36.22±7.85	0.16±0.03	8.99±0.76	0.04±0.01	3.83±0.65	0.02±0.0004
Prinia subflava	1	50.47	0.054	37.38	0.040	9.35	0.010	2.80	0.003
Sturnus vulgaris	10	51.68±2.42	0.54±0.08	32.55±2.94	0.34±0.04	12.55±1.88	0.13±0.03	3.22±0.58	0.03±0.007
Turdus iliacus	1	47.11	0.256	39.33	0.214	11.19	0.061	2.37	0.01
T. olivaceus	2	50.45±6.48	0.39±0.01	39.04±11.62	0.31±0.13	7.81±0.71	0.06±0.01	2.70±0.44	0.02±0.0002
mean		48.47±2.52	0.22±0.15	38.45±3.38	0.17±0.09	10.10±1.84	0.05±0.03	3.01±0.57	0.01±0.01

[a] The observations were made with the electron microscope. The number of specimens is shown under *n* and these apply to tables 4–8 inclusive. Relative volumes (%) and absolute volumes (cm^3) are means±s.d. The absolute volumes appertain to the combined volume of the exchange tissue of the fixed left and right lungs together and are calculated from the relative volumes and the absolute volume of the exchange tissue (table 2). See list of abbreviations for explanation of symbols used.

The function describing the relation between lung volume (cubic millimetres) and body mass (grams) (excluding *Gallus gallus*) was:

$$V_L = 21.79W^{1.05}.$$

The mean lung volume per unit body mass for all the avian species (excluding *Gallus*) was 25.58 $mm^3\ g^{-1}$ (s.d. 4.85); the value for the passeriform species (24.79 $mm^3\ g^{-1}$, s.d. 3.08) was closely similar to that of the non-passeriform species (26.07 $mm^3\ g^{-1}$, s.d. 7.55).

(*b*) *Volumes of lung components*

The results of the light-microscopic analysis of the main components of the avian lung are shown in table 2. The mean volume density of the exchange tissue (V_x) (percentage volume within the lung) was highest (54 %) in the lungs of the piciform and cuculiform species. The mean volume density of the exchange tissue of the passeriforms (51.92 %, s.d. 4.85) was significantly higher ($0.01 > p > 0.001$) than that of the non-passeriform species (42.57 %, s.d. 8.45). It was also significantly higher ($p < 0.001$) than that of the anseriforms and charadriiforms, the latter showing the lowest value of all the orders. The highest volume density was found in the very small passeriform bird *Estrilda astrild*, where the exchange tissue constituted about 60 % of the lung; the lowest value occurred in the charadriiform *Larus canus*, where the exchange tissue constituted only 31 % of the mean volume density. In those species in which the volume of the exchange tissue is relatively large, the increase is apparently achieved mainly at the expense of the lumina of the parabronchi and secondary bronchi, including the atria (table 2). The mean specific volume of the exchange tissue was significantly higher ($0.02 > p > 0.01$) in the passeriform species (12.84 $mm^3\ g^{-1}$, s.d. 2.19) than in the non-passeriform species (11.15, s.d. 3.29).

The volume densities and absolute volumes of the components of the exchange tissue, namely the air capillaries, blood capillaries and tissue, are shown in table 3. When the values for the species were averaged together, the lumina of the air capillaries and blood capillaries comprised about 50 % and 35 %, respectively, of the exchange tissue; the remaining 15 % were distributed between the blood–gas (tissue) barrier and the tissue not involved in gas exchange (the latter composed of the tissue of two adjoining air capillaries or two adjoining blood capillaries).

(*c*) *Surface areas of resistance barriers*

The surface areas of the resistance barriers of the air–haemoglobin pathway are shown in table 4. The surface area of the air capillaries S_a, was always greater than that of the blood–gas (tissue) barrier, S_t, by about 21 %. This is because the estimation of S_a includes all those areas covered by the epithelial cell, i.e. even those sites where air capillaries lie adjacent to each other. Similarly, the surface area of the blood capillaries, S_c, was also usually greater than S_t. Furthermore, S_c was usually greater than S_a, and this could be because the blood capillaries are generally smaller in diameter and more numerous than the air capillaries, and thus have a larger endothelial surface area. The surface area of the blood–gas (tissue) barrier, S_t, was also strongly positively correlated ($r = 0.977$, $p < 0.001$) with the body mass W (figure 5). The allometric function relating S_t to W was:

$$S_t = 60.6W^{0.883}.$$

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TABLE 4. ANALYSIS OF THE SURFACE AREAS OF THE RESISTANCE BARRIERS OF THE AIR–HAEMOGLOBIN PATHWAY[a]

taxon	S_a	S_t	S_c	S_e	S_p[b]
Anseriformes					
Anas platyrhynchos	3.65±0.38	2.97±0.24	3.31±0.26	3.23±0.68	3.27
Anser anser	11.3±1.6	8.87±1.16	10.4±1.7	9.6±1.4	10.0
mean	7.48±5.41	5.92±4.17	6.86±5.01	6.42±4.50	6.64±4.76
Falconiformes					
Falco tinnunculus	0.61	0.525	0.58	0.28	0.43
Galliformes					
Gallus gallus	2.77±0.44	2.16±0.51	2.42±0.62	3.59±2.2	3.01
Charadriiformes					
Alca torda	1.60±0.27	1.403±0.11	1.82±0.01	1.52±0.06	1.67
Cepphus carbo	2.39±0.55	1.93±0.42	2.79±0.68	1.78±0.85	2.29
Larus argentatus	1.58±0.87	1.46±0.70	1.81±0.59	0.91±0.04	1.36
L. canus	0.714	0.630	0.834	0.636	0.74
L. ridibundus	0.698±0.02	0.606±0.02	0.751±0.05	0.565±0.12	0.66
mean	1.40±0.71	1.21±0.57	1.60±0.84	1.08±0.54	1.34±0.68
Columbiformes					
Columba livia	1.20	0.86	1.06	1.03	1.05
Streptopelia decaocto	1.14±0.31	0.837±0.24	0.931±0.25	0.653±0.29	0.79
S. senegalensis	0.32	0.274	0.367	0.168	0.27
mean	0.89±0.49	0.66±0.33	0.79±0.37	0.68±0.33	0.70±0.40
Psittaciformes					
Melopsittacus undulatus	0.175±0.02	0.151±0.02	0.190±0.02	0.162±0.02	0.18
Cuculiformes					
Chrysococcyx klaas	0.100±0.02	0.086±0.02	0.109±0.04	0.093±0.04	0.59
Coliiformes					
Colius striatus	0.125	0.100	0.147	0.128	0.15
Piciformes					
Pogoniulus bilineatus	0.036	0.033	0.042	0.054	0.05
Passeriformes					
Amblyospiza albifrons	0.18±0.05	0.138±0.02	0.211±0.04	0.194±0.04	0.203
Cisticola cantans	0.048±0.004	0.044±0.007	0.069±0.01	0.060±0.02	0.065
Hirundo fuligula	0.148	0.12	0.152	0.151	0.152
Lanius collaris	0.152±0.01	0.121±0.01	0.155±0.01	0.148±0.03	0.152
Passer domesticus	0.177±0.04	0.170±0.04	0.204±0.04	0.123±0.03	0.164
Ploceus baglafecht	0.151±0.02	0.121±0.01	0.154±0.02	0.123±0.02	0.139
Prinia subflava	0.030	0.026	0.041	0.032	0.03
Sturnus vulgaris	0.418±0.06	0.358±0.06	0.418±0.06	0.310±0.06	0.364
Turdus iliacus	0.172	0.171	0.220	0.155	0.188
T. olivaceous	0.296±0.08	0.237±0.03	0.243±0.12	0.216±0.10	0.230
mean	0.177±0.11	0.151±0.09	0.187±0.10	0.151±0.08	0.169±0.09

[a] The values are given in square metres and are means±s.d. They appertain to both lungs together. See list of abbreviations for an explanation of symbols used.

[b] S_p is calculated as a mean of S_c and S_e.

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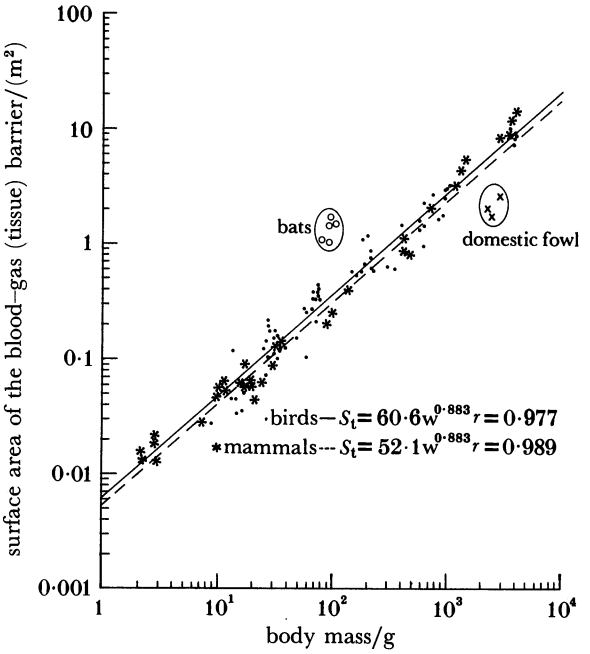

FIGURE 5. Double logarithmic plot of the surface area of the blood–gas (tissue) barrier (S_t) against body mass (W). All the values for S_t appertain to the combined left and right lungs together. The upper regression line is based on 87 data points for the 87 individual birds, representing 25 species, summarized in table 4 (after exclusion of the domestic fowl, for which the data points are entered independently on the graph). The lower regression line is based on 40 data points derived from the 40 values for S_t, listed in table 8 with references to the sources in the literature, for 20 mammalian species within a similar mass range to the birds. As table 8 shows, most of these mammalian values represent individual animals, but some are means because individual values were not reported in the original paper (see §2*c*(i)). The data points in fact represent 72 individual animals. The values for the five bats (*Epomophorus wahlbergi*) come from Maina *et al.* (1982*c*) and are entered independently. The surface area of the tissue barrier is strongly correlated positively with body mass in both the birds and the mammals (see r values on the figure). From a statistical examination of the two regression lines (see §4*a*(iii)) and comparison of the y-intercepts, it is estimated that the surface area of the blood–gas (tissue) barrier of the birds in general was about 15% greater than in the mammals. However, the values for the bats were above the regression line for the birds and those for the domestic fowl were below that for the mammals. (Note that although the units on the Y-axis are in m^2, the units in the equations are in cm^2.)

The mean values of the specific surface area of the blood–gas (tissue) barrier, $S_t W^{-1}$, in the anseriforms (25.9 $cm^2\ g^{-1}$, s.d. 4.0) and in the charadriiforms (25.5 $cm^2\ g^{-1}$, s.d. 3.9) were significantly lower ($0.02 > p > 0.01$) than the mean value for the passeriform species (44.3 $cm^2\ g^{-1}$, s.d. 18.0) (table 5). The highest values of $S_t W^{-1}$ were found in two passeriform species (*Hirundo fuligula*) (87.6) and *Passer domesticus* (63). The lowest values were encountered in the galliform domestic fowl (8.7). A negative correlation ($r = -0.52$, $p < 0.001$) was obtained (figure 6) between the surface area of the blood–gas (tissue) barrier per unit body mass $S_t W^{-1}$, and body mass W. The allometric function relating $S_t W^{-1}$ and W was:

$$S_t W^{-1} = 60.6 W^{-0.117}.$$

(*d*) *Surface density of the blood–gas (tissue) barrier*

Surface density is defined stereologically as the ratio of surface area to the reference volume. The surface density of the blood–gas (tissue) barrier in relation to the volume of exchange tissue (the ratio $S_t V_x^{-1}$) in 26 avian species is shown in table 5. This parameter ($S_t V_x^{-1}$) was negatively

TABLE 5. SOME RATIOS AND PARAMETERS DESCRIBING THE GAS EXCHANGE TISSUE[a]

taxon	S_t/W cm^2/g	S_t/V_x mm^2/mm^3	V_c/S_t cm^3/m^2	V_e cm^3	V_{ec} cm^3	H_c %
Anseriformes						
Anas platyrhynchos	28.7±3.1	239.8±15.4	1.38	2.18±0.20	1.704±0.18	51.9±6.7
Anser anser	23.1±3.7	253±24	1.40	6.50±1.18	5.516±1.04	52.3±5.3
mean	25.9±4.0	246.4±9.3	1.39±0.01	4.34±3.06	3.61±2.70	52.1±0.3
Falconiformes						
Falco tinnunculus	32.4	323.8	0.78	0.15	0.12	36.0
Galliformes						
Gallus gallus	8.70±1.1	172±6	1.62	2.30±1.3	1.79±1.0	63.8±9.1
Charadriiformes						
Alca torda	29.9±9.1	236.5±10.5	1.56	1.15±0.13	0.95±0.08	52.59±3.66
Cepphus carbo	27.0±7.29	240±12.4	1.66	1.36±0.73	1.16±0.63	41±15
Largus argentatus[b]	22.1±9.9	236.26±36.1	1.46	0.55±0.07	0.41±0.09	26.7±7.8
Larus canus	20.8	291.8	1.05	0.29	0.23	41.2
Larus ridibundus	27.6±8.1	238±15	1.27	0.38±0.06	0.34±0.08	47.9±10.5
mean	25.5±3.9	249±24	1.40±0.24	0.75±0.48	0.62±0.41	41.9±9.8
Columbiformes						
Columba livia	39.8	253.8	1.26	0.73	0.59	64.04
Streptopelia decaocto	43.1±11.9	252.5±26.0	0.92	0.36±0.11	0.29±0.08	49.3±5.0
S. senegalensis	47.2	296.2	1.17	0.10	0.08	30.63
mean	43.4±3.7	267.5±24.9	1.12±0.18	0.40±0.32	0.32±0.26	48±17
Psittaciformes						
Melopsittacus undulatus	42.6±9.4	317±13	1.06	0.098±0.02	0.08±0.02	62.0±7.0
Cuculiformes						
Chrysococcyx klaas	31.9±8.0	274.2±14.4	1.41	0.063±0.02	0.052±0.02	56.8±2.1
Coliiformes						
Colius striatus	19.9	259.6	1.41	0.079	0.065	56
Piciformes						
Pogoniulus bilineatus	22.5	272.0	1.46	0.034	0.026	70.8
Passeriformes						
Amblyospiza albifrons	40.7±7.0	314±28	1.45	0.12±0.02	0.10±0.02	57.2±1.6
Cisticola cantans	29.3±5.2	271.4±12.9	1.36	0.03±0.01	0.028±0.007	48.1±5.6
Hirundo fuligula	86.5	352.9	0.67	0.093	0.076	62.42
Lanius collaris	37.37±4.0	300.4±26.3	1.16	0.08±0.02	0.07±0.01	55.1±7.4
Passer domesticus	63±13	388.9±8.1	0.94	0.09±0.02	0.07±0.02	52.4±2.0
Ploceus baglafecht	36.6±3.2	317.4±1.3	1.32	0.08±0.01	0.061±0.006	55.6±11.8
Prinia subflava	29.2	247.2	1.54	0.02	0.017	50.0
Sturnus vulgaris	49.3±6.8	342±20	0.95	0.181±0.03	0.147±0.03	53.0±5.8
Turdus iliacus	33.4	313.5	1.25	0.11	0.09	49.1
T. olivaceus	37.1±10.4	303.2±2.5	1.31	0.16±0.05	0.13±0.05	57.8±3.5
mean	44.3±18.0	315±38	1.20±0.25	0.100±0.05	0.079±0.04	54.1±4.4

[a] The values given are means or means±s.d. and appertain to both lungs together. The ratios are derived from the relevant parameters in tables 2–4 inclusive. H_c is obtained from V_e and V_c.

[b] The values of V_e, V_{ec} and H_c in *Larus argentatus* may be low due to the fact that a small quantity of the fixative was inadvertently injected into the vascular system. See list of abbreviations for an explanation of symbols used.

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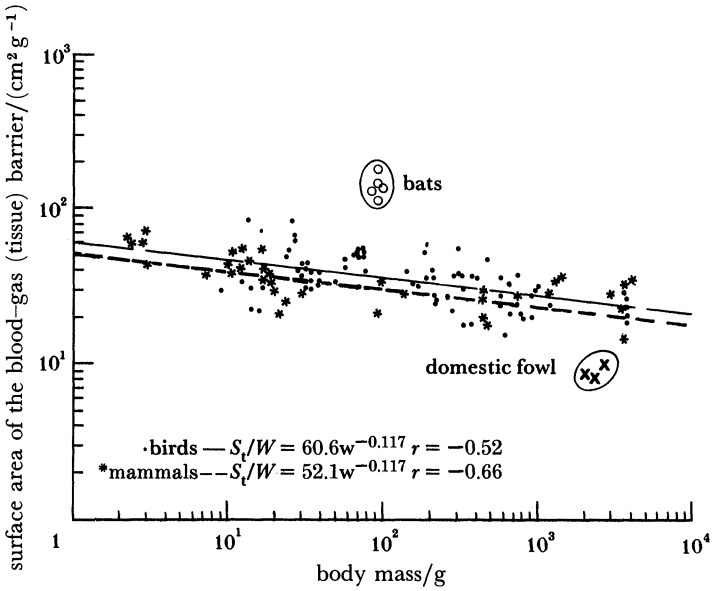

FIGURE 6. Double logarithmic plot of the surface area of the blood–gas (tissue) barrier per gram body mass (S_t/W) against body mass (W). All the values for S_t/W appertain to the combined left and right lungs together. The upper regression line is based on 87 data points for the 87 individual birds, representing 25 species summarized in table 4 (after exclusion of the domestic fowl, for which the data points are entered independently on the graph). The lower (mammalian) regression line and the bat data are derived as stated for figures 4 and 5. The surface area of the barrier per gram body mass is negatively correlated with body mass in both the birds and the mammals, showing that the smaller birds and mammals have a relatively greater value for S_t/W than the larger ones.

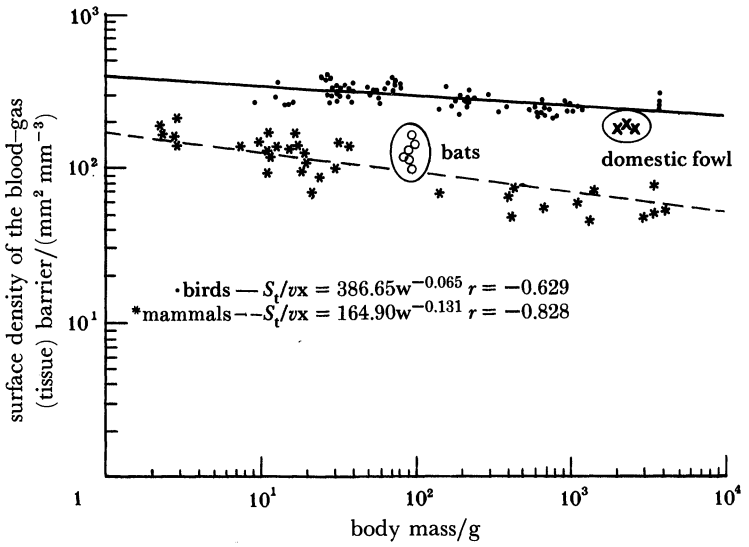

FIGURE 7. Double logarithmic plot of the surface area of the blood–gas (tissue) barrier per unit volume of exchange tissue ($S_t V_x^{-1}$) against body mass (W). The upper regression line (for the birds), and the data for the domestic fowl, are based on table 4. The lower (mammalian) regression line, and the bat data, are derived as for figures 4 and 5. $S_t V_x^{-1}$ is negatively correlated with body mass in both the birds and the mammals. This indicates that the smaller birds and mammals have terminal airways of relatively small diameter. The regression line for the birds is far above that for the mammals, confirming the well-known observation that the air capillaries of birds are of very much smaller diameter than the alveoli of mammals.

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correlated (figure 7) with body mass ($r = -0.629$, $p < 0.001$). The allometric (regression) line relating these two parameters was:

$$S_t V_x^{-1} = 386.6 W^{-0.065},$$

$S_t V_x^{-1}$ being expressed in square millimetres per cubic millimetres. The value of $S_t V_x^{-1}$ in the passeriforms (315, s.d. 38) was significantly higher than that for both the anseriforms (246.4, s.d. 9.3, $p < 0.001$) and the charadriiforms (249, s.d. 24, $0.01 > p > 0.001$). The highest values of $S_t V_x^{-1}$ were found in two passeriform species, i.e. 389 in *Passer domesticus* and 353 in *Hirundo fuligula*.

(*e*) *Pulmonary blood volume*

The estimated volumes of blood in the pulmonary vessels which were larger than capillaries, and in the capillaries themselves (V_c), are given in tables 2 and 3, respectively. The pulmonary capillary blood volume, V_c (table 3), was strongly correlated ($r = 0.984$, $p < 0.001$) with body mass (figure 10). The allometric (regression) function relating these two parameters was

$$V_c = 5.84 W^{0.933},$$

V_c being expressed in cubic millimetres. The values for the domestic fowl were well below the allometric (regression) line for the rest of the birds (figure 10).

Table 5 reports the ratios of pulmonary capillary volume to the surface area of the blood–gas (tissue) barrier, $V_c S_t^{-1}$ (this ratio being comparable to 'capillary loading', see §4*a*(viii). The mean value for this ratio ($cm^3 m^{-2}$) in the passeriforms (1.20, s.d. 0.25) was significantly lower ($0.05 > p > 0.02$) than the value for the anseriforms (1.39, s.d. 0.01), but was not significantly different ($0.5 > p > 0.1$) from that of the charadriiforms (1.40, s.d. 0.24).

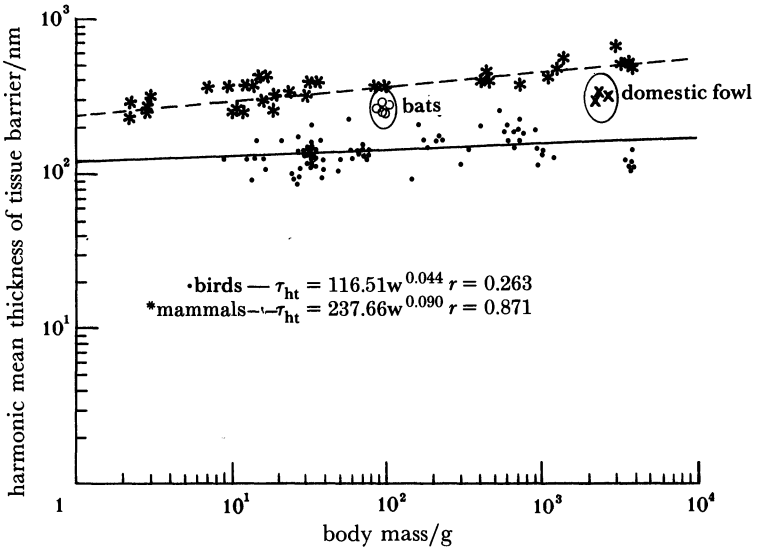

FIGURE 8. Double logarithmic plot of the harmonic mean thickness of the blood–gas (tissue) barrier (τ_{ht}) against body mass (W). The lower regression line (the birds) and the data for *Gallus*, are based on table 6. The upper (mammalian) regression line and the bat data are derived as for figures 4 and 5. In both the birds and the mammals the harmonic mean thickness of the tissue barrier was positively correlated with body mass. The avian line was well below that of the mammals, suggesting that the tissue barrier was much thinner in the birds. Comparison of the lines indicates that the tissue barrier in the lightest birds may be about 56% thinner than that of a mammal of the same body mass; in the heaviest animals the difference appears to become greater.

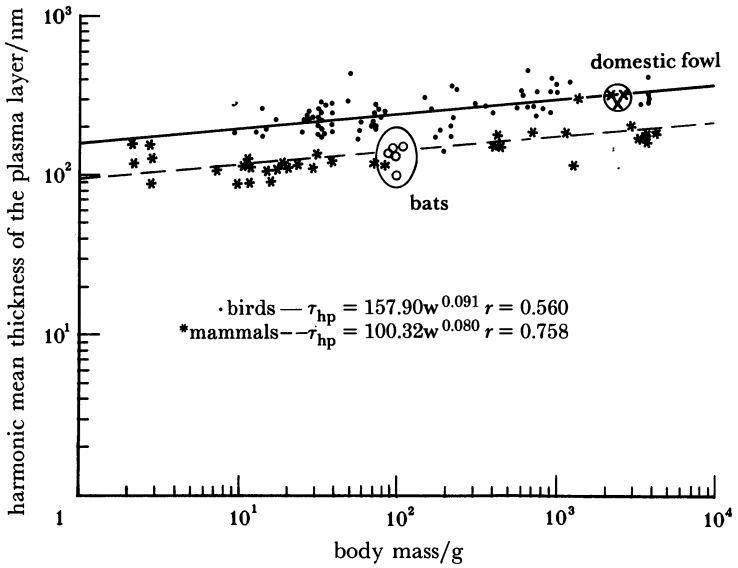

FIGURE 9. Double logarithmic plot of the harmonic mean thickness of the plasma layer (τ_{hp}) against body mass (W). The upper regression line (birds) and the data for the domestic fowl, are based on table 6. The lower (mammalian) line and the bat data, are derived as for figures 4 and 5; however, as values for τ_{hp} were not available for the rats, the line is based on 38 data points representing 61 animals. In both the birds and the mammals τ_{hp} was positively correlated with body mass. The avian line is well above the mammalian, suggesting that the plasma layer was considerably thicker in the birds. From a statistical examination of the two regression lines (see §4a(vi)) and comparisons of the y-intercepts it is estimated that τ_{hp} was bout 66 % thicker in the birds than in the mammals.

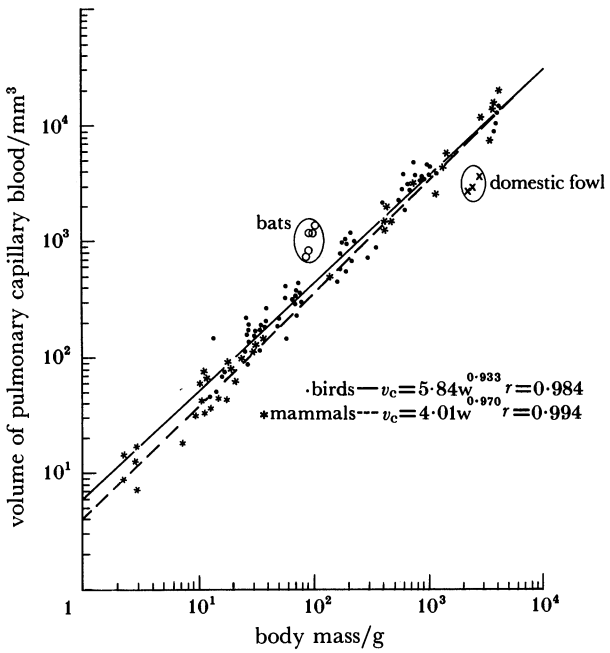

FIGURE 10. Double logarithmic plot of the pulmonary capillary blood volume (V_c) against body mass (W). The values for V_c appertain to the combined left and right lungs together. The upper (avian) regression line is based on 87 data points from 25 species summarized in table 3 (after exclusion of the domestic fowl, for which the data are entered independently on the graph). The lower (mammalian) regression line, and the bat data, are derived as for figures 4 and 5. In both the birds and the mammals V_c was strongly correlated positively with body mass. From a statistical examination of the two regression lines (see §4a(viii)) and comparison of the y-intercepts, it is estimated that V_c in the birds in general was about 22 % greater than in the mammals. However, the values for the bats are well above the regression line for the birds.

Also shown in table 5 are the volumes of the red blood cells (V_e), the volumes of their cytoplasm (V_{ec}, their nuclei being excluded), and the pulmonary capillary haematocrit (H_c, the volume density of the erythrocytes in the pulmonary capillary blood). H_c was lowest (27 %) in the charadriiform *Larus argentatus* (a value which may have been a slight underestimate due to the accidental injection of a small volume of fixative into the pulmonary artery). It was almost as low (31 %) in the columbiform *Streptopelia senegalensis*. The highest value was 71 % in the piciform *Pogoniulus bilineatus* (table 5). Scanning of the data suggests that this parameter does not appear to be correlated with body mass (table 5). The nucleus of the red blood cells constituted about 19 % of the volume of the red cell (this being the mean value for all species). The rest of the cell was composed of cytoplasm with a few organelles, constituting V_{ec} in table 5.

(*f*) *Thickness of blood–gas (tissue) barrier*

Table 6 shows the harmonic mean thicknesses of the blood–gas (tissue) barrier (τ_{ht}) and the plasma layer (τ_{hp}) and the arithmetic mean thickness of the tissue barrier ($\bar{\tau}_t$). A weak positive correlation ($r = 0.263$, $0.05 > p > 0.02$) was observed between the harmonic mean thickness of the blood–gas (tissue) barrier (τ_{ht}) and body mass (figure 8). The allometric (regression) function relating to the two parameters was

$$\tau_{ht} = 116.5 W^{0.044},$$

τ_{ht} being in nanometres and W in grams. The values for the domestic fowl were well above the allometric (regression) line for all the other birds (figure 8).

The harmonic mean thickness of the blood–gas (tissue) barrier of the passeriform species (0.126 μm, s.d. 0.03) was not significantly different from the values for the anseriforms (0.123 μm, s.d. 0.01, $p > 0.5$) and charadriiforms (0.168 μm, s.d. 0.04, $0.5 > p > 0.1$). The thickest blood–gas (tissue) barrier was observed in the galliform domestic fowl (0.318, s.d. 0.02) and in the charadriiform *Alca torda* (0.230, s.d. 0.04). Of note is the relatively thick barrier found in the falconiform *Falco tinnunculus* (0.210 μm), an energetic bird capable of hovering, but this one specimen may not be representative of the species. The thinnest barrier was observed in the passeriforms *Hirundo fuligula* (0.090 μm) and *Passer domesticus* (0.096 μm, s.d. 0.007).

On the electron micrographs sporadic attenuation of the blood–gas (tissue) barrier, i.e. corrugation, could be discerned. Corrugation was quantitatively reflected both in the minimum harmonic mean thickness (τ_{ht} min.) in table 6, estimated for some species, and in the ratio of the arithmetic mean thickness of the blood–gas (tissue) barrier to its harmonic mean thickness ($\bar{\tau}_t \tau_{ht}^{-1}$ in table 6). Measurements of the volume densities of the three main components of the blood–gas (tissue) barrier in some species showed that the endothelium formed the greatest proportion (67 %) of this barrier, and the epithelial cell and basal lamina constituted 12 % and 21 %, respectively.

The harmonic mean thickness of the plasma layer (τ_{hp}) was correlated with body mass ($r = 0.560$, $p < 0.001$, see figure 9). The allometric (regression) function describing τ_{hp} (nm) and body mass (W) in grams was:

$$\tau_{hp} = 157.90 W^{0.091}.$$

In all groups except the galliforms and columbiforms the plasma layer was much thicker than the tissue barrier (on average, by about 80 %).

Table 6. Analysis of the thickness of the blood–gas (tissue) barrier and the plasma layer[a]

taxon	τ_{ht}	τ_{ht}/min	τ_{hp}	$\bar{\tau}_t$	$\bar{\tau}_t \tau_{ht}^{-1}$
Anseriformes					
Anas platyrhynchos	0.133±0.014	0.062±0.007	0.369±0.033	0.903±0.132	6.79
Anser anser	0.118±0.016	0.050±0.007	0.322±0.052	0.887±0.199	7.85
mean	0.123±0.01	0.056±0.01	0.346±0.03	0.895±0.01	7.32
Falconiformes					
Falco tinnunculus	0.210	0.099	0.252	1.662	7.91
Galliformes					
Gallus gallus	0.318±0.02	—	0.306±0.02	1.34±0.04	3.90
Charadriiformes					
Alca torda	0.230±0.04	—	0.254±0.01	0.803±0.13	3.49
Cepphus carbo	0.193±0.017	—	0.280±0.03	0.850±0.08	4.40
Largus argentatus	0.153±0.02	0.075±0.007	0.399±0.10	1.275±0.36	8.33
L. canus	0.116	—	0.272	0.684	5.90
L. ridibundus	0.146±0.032	0.071±0.016	0.306±0.09	0.925±0.23	6.34
mean	0.168±0.04	0.073±0.003	0.302±0.06	0.907±0.22	5.69±1.87
Columbiformes					
Columba livia	0.161	—	0.197	0.804	4.99
Streptopelia decaocto	0.218±0.06	—	0.160±0.023	0.801±0.44	3.67
S. senegalensis	0.227	—	0.166	0.986	4.34
mean	0.202±0.04	—	0.174±0.02	0.864±0.11	4.33
Psittaciformes					
Melopsittacus undulatus	0.117±0.02	0.068±0.01	0.260±0.03	0.976±0.09	8.34
Cuculiformes					
Chrysococcyx klaas	0.157±0.02	—	0.236±0.001	0.679±0.114	4.33
Coliiformes					
Colius striatus	0.148	—	0.265	0.761	5.14
Piciformes					
Pogoniulus bilineatus	0.165	—	0.191	1.010	6.12
Passeriformes					
Amblyospiza albifrons	0.121±0.01	—	0.201±0.03	0.584±0.08	4.83
Cisticola cantans	0.122±0.01	—	0.219±0.04	0.608±0.07	4.98
Hirundo fuligula	0.090	—	0.172	0.613	6.81
Lanius collaris	0.170±0.05	—	0.216±0.5	0.638	3.75
Passer domesticus	0.096±0.007	0.052±0.007	0.217±0.02	1.034±0.086	10.77
Ploceus baglafecht	0.151±0.011	—	0.215±0.024	0.762±0.05	5.05
Prinia subflava	0.124	—	0.197	0.675	5.44
Sturnus vulgaris	0.141±0.009	0.065±0.005	0.226±0.02	1.124±0.107	7.97
Turdus iliacus	0.120	0.060	0.457	1.012	8.43
T. olivaceus	0.127±0.02	—	0.234±0.06	0.599±0.07	4.72
mean	0.126±0.03	0.059±0.001	0.235±0.08	0.765±0.21	6.27±2.18

[a] The values except the ratio $\bar{\tau}_t \tau_{ht}^{-1}$ are means (μm) ±s.d. For explanation of symbols please see list of abbreviations.

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(*g*) *Morphometric pulmonary diffusing capacities*

Table 7 summarizes the estimates of morphometric (anatomical) diffusing capacities. A strong correlation of the mean total D_{LO_2} with body mass ($r = 0.978$, $p < 0.001$) was observed (figure 11). The allometric function relating the two parameters (table 9) was:

$$D_{LO_2} = 1.031 W^{0.888} \times 10^{-4},$$

D_{LO_2} being expressed in S.I. units as ml O_2 (s mbar)$^{-1}$, and body mass (W) in grams. S.I. units can be converted into conventional units, i.e. ml O_2 (min mmHg)$^{-1}$ by dividing by 1.2501×10^{-2} (see Appendix). The value of D_{LO_2} for the domestic fowl was below the allometric (regression) line for the rest of the birds (figure 11). D_{LO_2} was always smaller than D_{mO_2} (the membrane diffusing capacity). Of the three serial resistances constituting the air–haemoglobin pathway (i.e. the blood–gas (tissue) barrier, the plasma layer and the red blood cell

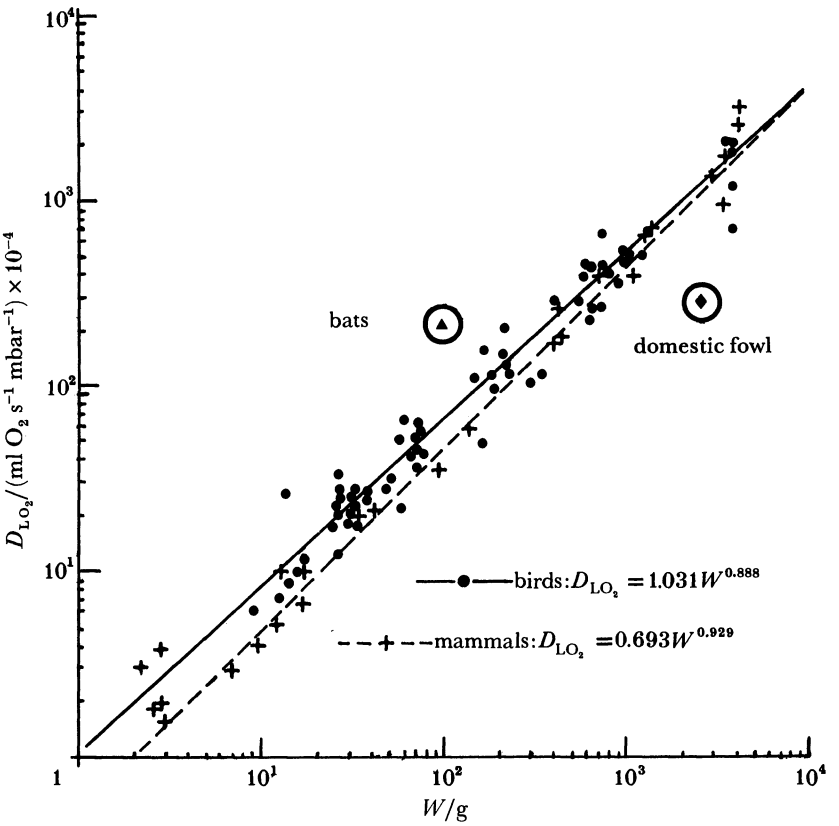

FIGURE 11. Double logarithmic plot of the mean total morphometric pulmonary diffusing capacity (D_{LO_2}) against body mass (W). The values for D_{LO_2} appertain to the combined left and right lungs together. The upper (avian) regression line is based on 87 data points from 25 species summarized in table 7 (excluding the domestic fowl, for which a mean data point is entered independently on the graph). The lower (mammalian) regression line and the bat data, are derived as for figures 4 and 5, except that only 32 data points (though still representing 72 individual animals) are available for this regression line. There is a strong positive correlation between D_{LO_2} and body mass in both the birds and the mammals. From a statistical examination of the two regression lines (see §4*a* (ix)) and comparison of the *y*-intercepts, it is estimated that D_{LO_2} in the birds in general was about 22% greater than in the mammals. However, the mean value for the bats is above the regression line for the birds. The values for the domestic fowl are well below the mammalian regression line. In figure 17 the values for avian D_{LO_2} have been recalculated using a recently reported constant for avian Θ_{O_2} (see footnote to p. 11).

TABLE 7. THE MORPHOMETRIC PULMONARY DIFFUSING CAPACITIES OF THE THREE MAIN RESISTANCE BARRIERS OF THE AIR–HAEMOGLOBIN PATHWAY[a]

taxon	venous haematocrit (%)[b]	D_{tO_2}	D_{pO_2}	D_{eO_2}	D_{mO_2}	D_{LO_2}
Anseriformes						
Anas platyrhynchos	41[(1)]	0.930	0.424	0.062	0.289	0.050
Anser anser	44[(2)]	3.26	1.506	0.211	1.018	0.172
mean		2.10	0.965	0.137	0.654	0.111
Falconiformes						
Falco tinnunculus	39.63[(3)]	0.103	0.080	0.006	0.024	0.0048
Galliformes						
Gallus gallus	31.5[(4)]	0.279	0.488	0.041	0.168	0.0318
Charadriiformes						
Alca torda	43.9[(5)]	0.256	0.309	0.038	0.139	0.0290
Cepphus carbo	44.6[(6)]	0.419	0.394	0.058	0.198	0.0432
Larus argentatus	44.6[(6)]	0.407	0.161	0.033	0.110	0.0245
Larus canus	43.9[(5)]	0.224	0.126	0.012	0.080	0.0101
Larus ridibundus	43.9[(5)]	0.180	0.102	0.011	0.062	0.0113
mean		0.297	0.218	0.030	0.118	0.0236
Columbiformes						
Columba livia	54.43[(7)]	0.221	0.249	0.025	0.116	0.0201
Streptopelia decaocto	49.0[(8)]	0.168	0.236	0.014	0.096	0.0117
S. senegalensis	49.0[(8)]	0.050	0.076	0.006	0.030	0.0051
mean		0.146	0.187	0.015	0.081	0.0123
Psittaciformes						
Melopsittacus undulatus	44.94[(9)]	0.054	0.032	0.003	0.020	0.0024
Cuculiformes						
Chrysococcyx klaas	44.94[(10)]	0.026	0.020	0.002	0.011	0.0016
Coliiformes						
Colius striatus	44.94[(10)]	0.028	0.030	0.003	0.014	0.0021
Piciformes						
Pogoniulus bilineatus	44.94[(10)]	0.008	0.012	0.0008	0.005	0.0007
Passeriformes						
Amblyospiza albifrons	44.94[(10)]	0.048	0.047	0.003	0.024	0.0029
Cisticola cantans	44.94[(10)]	0.015	0.014	0.001	0.007	0.0009
Hirundo fuligula	51.87[(11)]	0.055	0.041	0.003	0.023	0.0026
Lanius collaris	44.94[(10)]	0.033	0.033	0.003	0.016	0.0022
Passer domesticus	43.5[(12)]	0.074	0.035	0.003	0.024	0.0025
Ploceus baglafecht	44.94[(10)]	0.033	0.031	0.002	0.016	0.0021
Prinia subflava	44.94[(10)]	0.009	0.009	0.0007	0.004	0.0006
Sturnus vulgaris	44.94[(10)]	0.105	0.076	0.006	0.027	0.0051
Turdus iliacus	48.2[(13)]	0.059	0.019	0.004	0.014	0.0031
T. olivaceus	48.2[(13)]	0.074	0.056	0.006	0.032	0.0051
mean		0.051	0.036	0.003	0.020	0.0027

[a] The units of conductances are ml O_2 (per second per millibar) (1 bar = 10^5 Pa). D_{pO_2}, D_{eO_2}, D_{mO_2} and D_{LO_2} are means of the maximum and minimum values calculated from the relevant data, given in the preceding tables, using the maximum and minimum physical constants. The values for each of the five conductances appertain to the combined left and right lungs together. The individual mass-specific conductances can be calculated from the details

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cytoplasm), the red blood cell contributed about 90% of the total pathway resistance, this being evident from table 7 (resistance being the reciprocal of conductance). The mean specific total morphometric diffusing capacity ($D_{LO_2} W^{-1}$) of the passeriform species was 0.083, s.d. 0.04 ml O_2 and this was significantly higher ($0.05 < p < 0.02$) than that of both the anseriforms (0.046, s.d. 0.002) and charadriiforms (0.049, s.d. 0.013) (1 bar = 10^5 Pa) (tables 1 and 7). The highest specific D_{LO_2} was observed in the passeriform *Hirundo fuligula* (0.190) and the lowest in the domestic fowl (0.015, s.d. 0.004).

4. Discussion

(a) *Principal morphometric pulmonary parameters: comparisons of birds with other vertebrates*

The understanding of the functional anatomy of the avian lung has been hampered by lack of comprehensive quantitative data in the literature. In this study we attempted to investigate as many species of birds as possible. However, because of the difficulty in obtaining such material and occasional imperfections of fixation, in some orders only one or two specimens were examined; nevertheless, the results from these have been included because of the total lack of such data in the literature, though they may not be reliably representative of their species.

The structure of the lung is adapted to the oxygen demands of an animal, which reflect various factors such as body mass and mode of life. Thus the horse and dog show a greater oxygen consumption per unit body mass than the cow and man, respectively; the specific gas-exchange surface (surface area of the blood–gas tissue barrier per unit body mass) of the former two species is larger by a factor corresponding to their higher oxygen consumption (Weibel 1979*b*).

The 42 species of bird examined in this study occupy widely different habitats, requiring in some instances a highly energetic mode of life as in martins (*Hirundo*), and in other instances a much less demanding performance as in the ground-dwelling domestic fowl. Morever, the species examined varied greatly in body mass, ranging from a mere 5.4 g in *Estrilda melanotis* to 3964 g in a specimen of *Anser anser*; for reasons of scaling (for example, Tenney & Remmers 1963; Hughes 1974; Schmidt-Nielson 1975*b*), such variations in body mass will be reflected in diverse metabolic rates. For all these reasons, the oxygen consumption per unit body mass should vary among these avian species. It could be predicted that such variations would in turn be reflected in their pulmonary morphometric parameters. The following discussion will attempt to show that the morphometric data obtained in this study confirm this prediction.

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of body mass given in table 1. The minimum and maximum values can be calculated from the relevant data and physical constants given in the Appendix. Symbols are defined in the list of abbreviations. The units can be converted into ml O_2 min^{-1} $torr^{-1}$ by dividing by a constant (1.2501×10^{-2}).

[b] Sources of the venous haematocrit: (1) *Anas*, Altman & Dittmer (1970) – mean value of two males and two females; (2) *Anser*, Albritton (1952) – value reported for an unnamed goose; (3) *Falco*, Balasch *et al.* (1976) – mean for eight falconiform species of bird; (4) *Gallus*, Sturkie & Textor (1960) and Lucas & Jamroz (1961) – mean of the values given by these authors; (5) *Alca*, *Larus canus*, and *Larus ridibundus*, Balasch *et al.* (1974); (6) *Larus argentatus* and *Cepphus*, mean of the values given by Clausen *et al.* (1971) and Balasch *et al.* (1974); (7) *Columba livia*, Carpenter (1975*a*); (8) *Streptopelia decaocto* and hence *S. senegalensis*, own estimates; (9) *Melopsittacus*, mean value of 16 small passeriform species given by Palomeque *et al.* (1980*a*); (10) For the rest of the birds (i.e. cuculiform, coliiform, piciform and passerine species) a mean value of 16 passerine species (Carpenter 1975*a*) was used except for the following species: *Hirundo*, mean value of three apodiform species (Palomeque *et al.* 1980*b*); *Passer*, mean of the values given by Palomeque *et al.* (1980 *a*) and Baumann & Baumann (1977); *Turdus iliacus* and *T. olivaceus*, mean of the values given by Carey & Morton (1976) for a bird of the same genus (*Turdus migratorius*) and Palomeque *et al.* (1980*a*) for *Turdus merula*. See list of abbreviations for explanation of symbols.

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TABLE 8. MAMMALIAN PULMONARY MORPHOMETRIC DATA FROM WHICH ALLOMETRIC FUNCTIONS WERE CALCULATED AND COMPARED WITH THOSE FOR THE BIRDS[a]

	W/g	V_L cm^3	S_t m$^{2(b)}$	$\frac{S_t V_x}{}$ mm^2 mm^{-3}	V_c cm^3	τ_{ht} µm	τ_{hp} µm	$\frac{D_{LO_2} m_{LO_2}}{}$ (s mbar)$^{-1}$
shrews								
Sorex minutus[(1)]	2.88	0.11	0.0205	207.1	0.0111	0.26	0.09	0.00019
S. species[(1)]	9.95	0.33	0.04415	148.7	0.0312	0.37	0.09	0.00038
Neomys fodiens[(1)]	16.87	0.60	0.09045	167.5	0.0592	0.29	0.09	0.00096
Suncus etruscus[(1)]	2.21	0.10	0.0150	166.7	0.0139	0.23	0.16	0.00030
	2.24	0.08	0.01345	186.81	0.0085	0.28	0.12	0.00017
	2.85	0.13	0.0185	158.12	0.017	0.24	0.16	0.00038
	2.92	0.10	0.0129	143.33	0.0071	0.31	0.13	0.00015
Crocidura juvenata[(1)]	7.37	0.22	0.02705	136.62	0.0179	0.37	0.11	0.00028
C. russula[(1)]	11.90	0.36	0.0533	164.5	0.0332	0.36	0.09	0.00055
	12.41	0.42	0.05115	135.32	0.0354	0.35	0.11	0.00058
C. poensis[(1)]	15.90	0.50	0.0589	130.89	0.0424	0.41	0.11	0.00069
	17.97	0.47	0.0579	136.88	0.0427	0.43	0.11	0.00071
C. flavescens[(1)]	32	1.06	0.1375	144.1	0.127	0.37	0.14	0.00194
	37.0	1.19	0.1420	132.59	0.142	0.38	0.13	0.00170
C. giffardi[(1)]	92.5	2.30	0.2018	97.5	0.241	0.35	0.13	0.00396
	100	3.0	0.2506	92.82	0.248	0.34	0.13	0.00414
Mus musculus								
white mouse[(2)]	19	0.60	0.0648	119.91	0.077	0.32	0.12	
	20	0.60	0.0590	109.2	0.075	0.31	0.11	
	21	0.7	0.0432	68.57	0.060	0.31	0.11	0.00213[b]
	24	0.8	0.0619	85.90	0.099	0.34	0.12	
	30	1.0	0.0888	98.61	0.110	0.33	0.11	
Mus wagneri								
Japanese waltzing mouse[(2)]	10.5	0.5	0.0521	93.78	0.059	0.25	0.12	
	11.0	0.5	0.0562	124.78	0.041	0.26	0.12	
	11.6	0.50	0.0525	116.7	0.066	0.25	0.13	0.00097[b]
	11.6	0.50	0.0646	119.54	0.071	0.26	0.13	
	18.3	0.60	0.0682	94.79	0.088	0.26	0.13	
Rattus rattus								
white rat[(3)]								
($n = 8$)	140.0	6.34	0.398	69.66	0.480	0.37	—	0.00679
($n = 3$)	457.0	13.4	0.801	66.42	1.48	0.40	—	0.01830
Cavia porcellus								
guinea pig[(4)]								
($n = 15$)	429	13.04	0.0825	70.30	1.46	0.42	0.187	0.01790
Oryctolagus cuniculus								
rabbit[(5)]								
($n = 5$)	3560	79.2	5.28	74.07	7.15	0.50	0.180	0.09170
Helogale pervula								
dwarf mongoose[(3)]	418	27.4	1.158	46.96	1.20	0.398	0.158	0.01700
	441	22.9	1.327	64.39	1.98	0.418	0.155	0.02600
	724	41.4	2.125	57.02	3.01	0.366	0.189	0.04100
Mungos mungo								
banded mongoose[(3)]	1140	63.3	3.275	57.49	2.53	0.409	0.181	0.03800
Genetta tigrina								
genet cat[(3)]	1330	111.2	4.53	45.26	4.40	0.485	0.117	0.06400
	1415	86.8	5.334	68.28	5.66	0.527	0.303	0.07300
Nesotragus moschatus								
suni[(3)]	3000	208.7	8.545	45.49	11.72	0.654	0.203	0.13900
	3600	210.0	9.275	49.07	13.11	0.469	0.161	0.17300

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TABLE 8. (*cont.*)

	W/g	V_L cm^3	S_t m$^{2(b)}$	$\frac{S_t V_x}{}$ mm^2 mm^{-3}	V_c cm^3	τ_{ht} µm	τ_{hp} µm	$\frac{D_{LO_2} m_{LO_2}}{}$ (s mbar)$^{-1}$
Madoqua kirkii dik dik[3]	4100	314.6	14.16	50.01	19.35	0.446	0.187	0.257 00
Macaca irus monkey ($n = 6$)	3710	184.0	12.50	75.48	15.0	0.50	0.180	0.205 00

[a] These 20 mammalian species were selected because their body masses were similar to those of the birds which we investigated. The values for volumes appertain to the combined left and right lungs together. The symbols are defined in the list of abbreviations.

[b] S_t was here calculated as the mean of S_a and $\overline{S_c}$ (Weibel 1970–1), and for calculating the volume density of the blood–gas tissue barrier ($S_t V_x^{-1}$) the parenchyma was assumed to constitute 90% of the lung (Weibel *et al.* 1981*b*).

[c] Mean values. For *Mus musculus* and *Mus wagneri*, values for D_{LO_2} were not available for individual animals. Number of animals investigated for *Rattus rattus*, *Cavia porcellus*, *Oryctolagus cuniculus* and *Macaca irus* is denoted by *n*. Units in ml O_2 s^{-1} mbar^{-1} can be converted into ml O_2 min^{-1} torr^{-1} by dividing by a constant (1.2501×10^{-2}). Sources of data: (1) Gehr *et al.* (1980); (2) Geelhaar & Weibel (1971); (3) Gehr *et al.* (1981*a*); (4) Forrest & Weibel (1975); (5) Weibel (1973).

In this investigation various pulmonary morphometric parameters have been correlated with body mass. Up to now, this has only been attempted once, by Lasiewski & Calder (1971) from scanty data that they had largely derived from the literature. Body mass is a very variable parameter depending on many factors, including season, sex and the availability of food (Clark 1979); nevertheless, it has been used extensively in the literature as a basis for standardization (normalization) of many anatomical and physiological parameters.

Passeriform species constitute the majority of the small species of bird (Lasiewski & Dawson 1967; Palomeque *et al.* 1980*a*). They have a higher basal metabolic rate than non-passeriform species of similar body mass (Lasiewski & Dawson 1967; Lasiewski & Calder 1971; Palomeque *et al.* 1980*a*). For example, the resting oxygen consumption of the passeriform fish crow (*Corvus ossifragus*) is about twice that of a non-passeriform bird, or a terrestrial mammal, of the same body mass (Bernstein & Schmidt-Nielsen 1972). The metabolic rate of a non-passeriform bird is much the same as that of a mammal of similar body mass (Lasiewski & Dawson 1967; Schmidt-Nielsen 1975*a*). These varying metabolic characteristics raise the question, are there corresponding morphometric variations in the lung?

The morphometric parameters of the lungs of the passeriform species do appear to be better adapted for gas exchange than those of the non-passerine species, as will be shown below. There are also indications that individual species seem to be especially adapted according to their size, and a particularly energetic life-style. It will also be suggested that, in general, there are some substantial differences between the morphometric parameters of the lungs of birds and those of mammals; comparisons with other vertebrates are made where data allow.

Except where otherwise stated, we have excluded the domestic fowl (*Gallus gallus* var. *domesticus*) from data representing birds in general. This is because, as stated in the Results, we have found that the measurements for this species are consistently atypical.

(i) *Lung volume*

A strong positive correlation ($r = 0.992$) was observed between lung volume and body mass in the species of birds examined in this study (figure 4). Lasiewski & Calder (1971) noted a strong positive correlation between 'the total lung volume' (i.e. lung air-sac system) of birds

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and body mass on the basis of data from five species of bird. A strong positive correlation between the volume of the lung and body mass has been established in mammals by Tenney & Remmers (1963), Weibel (1972) and Gehr *et al.* (1981 *a*). A similar correlation between lung volume and body mass has been observed by Tenney & Tenney (1970) in species of Amphibia and Reptilia, though in the latter order lung volume was more strongly correlated with metabolic rate than with body mass. It has long been believed that the specific lung volume in birds is less than that of a mammal of similar body mass (Burton & Smith 1967; Schmidt-Nielsen 1975*a*; Dejours 1981). However, this proposition was challenged by Lasiewski & Calder (1971) after computation of allometric functions based on lung mass measurements. It was also questioned by Dubach (1981) on the basis of a study of the volumes of the lungs of three species of bird. The mean volume of the lung per unit body mass ($V_L W^{-1}$) for all the birds examined in this study was about 0.026 $cm^3\ g^{-1}$. This just falls within the range of a group of mammals cited by Gehr & Erni (1980), namely 0.02 $cm^3\ g^{-1}$ in the rabbit (*Oryctolagus cuniculus*) to 0.08 $cm^3\ g^{-1}$ in the wildebeest (*Connochaetes taurinus*). Figure 4 shows the allometric (regression) lines for the lung volume of our birds and that for the mammals (within a similar range of body masses) investigated by Gehr *et al.* (1981 *a*). The line for the birds lies somewhat below that for the mammals, indicating that the lung volumes of the birds tend to be relatively smaller than those of the mammals. Statistical examination has shown ($p < 0.01$) that the regression lines for birds and mammals represent distinct populations (table 9), but may be assumed to be parallel with a common slope of 1.03. If this assumption is adopted, then for the birds the *y*-intercept corresponding to a mass of 1 g becomes 23.4 mm^3 and that for the mammals 32.0 mm^3. Thus V_L in the birds generally would appear to be about 27 % smaller than in the mammals of similar body mass. As was pointed out by Lasiewski & Calder (1971), if the volume of the air-sacs of birds, as well as that of their lungs, is taken into account, birds obviously have a very much larger respiratory volume than mammals of similar body mass.

TABLE 9. SUMMARY OF AVIAN (A) AND MAMMALIAN (M) ALLOMETRIC REGRESSION FUNCTIONS; ALSO SHOWN ARE CORRELATION COEFFICIENTS (r) AND 95 % CONFIDENCE INTERVALS OF COEFFICIENTS (a) AND EXPONENTS (b)[a]

	function[b]	correlation coefficient (r)	95 % confidence intervals (a)	(b)	relation[c]
1.	(A) $V_L = 21.79 W^{1.05}$	0.992	19.73, 24.06	1.026, 1.070	distinct populations
	(M) $V_L = 34.95 W^{1.01}$	0.991	27.03, 45.19	0.967, 1.060	($p < 0.01$)
2.	(A) $S_t = 60.6 W^{0.883}$	0.977	48.90, 75.17	0.840, 0.926	distinct populations
	(M) $S_t = 52.1 W^{0.883}$	0.989	40.82, 66.50	0.839, 0.926	($p < 0.05$)
3.	(A) $S_t V_x^{-1} = 386.65 W^{-0.065}$	−0.629	353.76, 422.59	−0.0825, −0.0471	distinct populations
	(M) $S_t V_x^{-1} = 164.90 W^{-0.131}$	−0.828	139.41, 195.05	−0.1611, −0.1006	($p < 0.01$)
4.	(A) $\tau_{ht} = 116.51 W^{0.044}$	0.263	97.58, 139.12	0.0083, 0.0789	distinct populations
	(M) $\tau_{ht} = 237.66 W^{0.090}$	0.871	215.65, 261.92	0.0728, 0.1076	($p < 0.01$)
5.	(A) $V_c = 5.84 W^{0.933}$	0.984	4.85, 7.03	0.896, 0.970	distinct populations
	(M) $V_c = 4.01 W^{0.970}$	0.994	3.25, 4.95	0.932, 1.008	($p < 0.01$)
6.	(A) $D_{LO_2} = 1.031 W^{0.888}$	0.978	0.838, 1.270	0.846, 0.929	distinct populations
	(M) $D_{LO_2} = 0.693 W^{0.929}$	0.992	0.549, 0.873	0.887, 0.971	($p < 0.01$)

[a] The symbols are defined in the list of abbreviations. The 95 % confidence intervals on (b) are symmetrical but those on (a) are not, since the latter are obtained by taking antilogs of the symmetrical limits on the log–log fits.

[b] Units: W, g; V_L, mm^3; S_t, cm^2; $S_t V_x^{-1}$, $mm^2\ mm^{3-1}$; τ_{ht}, nm; V_c, mm^3; D_{LO_2}, ml O_2 (s mbar)$^{-1} \times 10^{-4}$.

[c] Based on Sprent (1969). The intervals for the avian and mammalian coefficients (a) overlap slightly in functions 5 and 6 and substantially in function 2. However, the more sensitive tests described by Sprent demonstrate that the lines are not coincident in functions 5 and 6 ($p < 0.01$) or function 2 ($p < 0.05$).

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(ii) *Volume densities of the components of the lung*

The mean relative volume density of the exchange tissue of the lungs of the passeriform species (51.92%) was significantly higher than that of the non-passeriform species (43.57%). The volume densities of the exchange tissue obtained by Dubach (1981) in *Passer domesticus* and *Melopsittacus undulatus* were 58 and 51% respectively; similar values were obtained in this investigation for these two species (i.e. 56 and 47%). Our mean values for this parameter in columbiform (49.3%), anseriform (40.5%) and passeriform (51.9%) species of bird are similar to those obtained by Duncker (1972) on a smaller number of species from these orders (i.e. 49, 36 and 51%, respectively). The values of the volume densities of the blood vessels larger than capillaries in our study were 14.9% in *Columba livia*, 7.3% in the passeriform species, and 6.9% in *Anser anser*. These values are somewhat different from those obtained by Duncker (1972) in the same or similar birds, i.e. 8.4% in *Columba livia* and 11.7% in the Canada goose (*Branta canadensis*). Further comparisons of the results of our light microscopic analysis with Duncker's (1972) are not possible, as Duncker combined the lumina of the secondary with that of the primary bronchus: in our study the lumina of the parabronchi were combined with those of the secondary bronchi, because many of the secondary bronchi resemble parabronchi in having a mantle of exchange tissue. Such secondary bronchi (i.e. those with a mantle) would be functionally similar to parabronchi, and also it is difficult to distinguish them from parabronchi with absolute certainty on histological sections.

The volume densities of the main components of the exchange tissue (i.e. of the lumina of the air capillaries and blood capillaries and of the tissue), reported by Dubach (1981), were respectively 54.1, 36.8 and 9.2% for *Passer domesticus* and 67.3, 26.1 and 6.6% for *Melopsittacus undulatus*. Our values were 46, 38 and 16% in *Passer* and 53, 33 and 14% in *Melopsittacus* (table 3). Duncker's (1973) values for these three components of the exchange tissue in *Gallus gallus*, respectively, were 56, 28 and 16%; Vidyadaran's (1987) values were also exactly 56, 28 and 16%; ours were 61, 28 and 11%.

(iii) *Surface area of the blood–gas (tissue) barrier*

The surface area of the blood–gas (tissue) barrier, S_t, of the species examined (figure 5) was strongly correlated positively with body mass ($r = 0.977$). Similarly the surface area of the alveoli in mammalian lungs was observed to be strongly correlated with body mass (Weibel 1972, 1973; Gehr *et al.* 1981*a*). However, the allometric (regression) line of S_t for the birds (figure 5) was a little above that for the mammals examined by Gehr *et al.* (1981*a*), with body masses falling within a similar range to that of our birds, and this suggests that the birds in general may have had a slightly greater surface area than the mammals. Statistical examination has shown ($p < 0.05$) that the regression lines for the birds and mammals represent distinct populations (table 9), but may be assumed to be parallel, with a common slope of 0.882. If this assumption is adopted, then for the birds the y-intercept corresponding to a mass of 1 g becomes 60.96 cm^2 and that for the mammals 52.28 cm^2. Thus S_t in the birds would appear to be about 15% greater than in the mammals of similar body mass.

In the present study a negative (inverse) correlation between the surface area of the blood–gas (tissue) barrier per unit body mass ($S_t\ W^{-1}$) against body mass was found (figure 6). This clearly suggests that the smaller birds, most of which were passeriforms, had a more extensive $S_t\ W^{-1}$ than the bigger ones. This would be consistent with the reasoning (Tenney &

Remmers 1963; Schmidt-Nielsen 1980) that in general the smaller the animal, whether it be a bird or a mammal, the higher is its oxygen requirement per unit body mass. As already noted, passeriform species have a higher metabolic rate than non-passeriform birds of similar size; also, they appear to have a higher body temperature than the other birds, as calculated from the data given by King & Farner (1969).

The lowest value for the surface area of the blood–gas (tissue) barrier per unit body mass, $S_t W^{-1}$, was observed in *Gallus gallus* (8.7 $cm^2 g^{-1}$). The highest values were observed in the passeriform species, the two outstanding instances being 87 $cm^2 g^{-1}$ in *Hirundo fuligula* and 63 $cm^2 g^{-1}$ in *Passer domesticus*. The value of $S_t W^{-1}$ for *Hirundo fuligula* is virtually the same as that of 87 $cm^2 g^{-1}$ obtained for the violet-eared hummingbird (*Colibri coruscans*) by Dubach (1981). The values of $S_t W^{-1}$ reported in our study for *Passer domesticus* and *Melopsittacus undulatus* (63 and 42 $cm^2 g^{-1}$, respectively) agree reasonably closely with those obtained by Dubach (1981) for the same species (59 and 48 $cm^2 g^{-1}$, respectively).

In Amphibia and Reptilia the pulmonary surface area was directly correlated with body mass (Tenney & Tenney 1970). As would be expected from the relatively low oxygen consumption of ectothermic vertebrates (Schmidt-Nielsen 1980), the values of $S_t W^{-1}$ in reptiles and fish are relatively low. Thus values of 3.18 and 5.27 $cm^2 g^{-1}$ were found in two species of lizard, *Tupinambis nigropunctus* and *Varanus exanthematicus* (Perry 1981); in the lungfish (*Lepidosiren paradoxa*) the value was 0.85 $cm^2 g^{-1}$ (Hughes & Weibel 1976); in the gills of the tench (*Tinca tinca*) it was 2.28 $cm^2 g^{-1}$ (Hughes 1972). In general, the more active species of fish had a larger specific gill surface area than sluggish species (Hughes 1966). The values for $S_t W^{-1}$ in ectothermic vertebrates are below the lowest obtained for any of our birds; that is, 8.7 $cm^2 g^{-1}$ in *Gallus*.

(iv) *Surface density of the blood–gas (tissue) barrier*

The surface density of the blood–gas (tissue) barrier (surface area of the tissue barrier per unit volume of the gas exchange tissue, $S_t V_x^{-1}$ in the avian lung is an indicator of the relative diameter of the air capillaries. The lowest value (172 $mm^2 mm^{-3}$) was observed in *Gallus gallus*, whereas relatively high values were observed in the passeriform species, the highest being 389 $mm^2 mm^{-3}$ in *Passer domesticus*. The negative correlation ($r = -0.629$) between this parameter ($S_t \cdot V_x^{-1}$) and body mass (figure 7) shows that the small, generally more metabolically active, species of bird have air capillaries of smaller diameter, thus facilitating the 'packing' of a relatively more extensive blood–gas (tissue) barrier into each unit volume of exchange tissue. The concept that the parameter $S_t V_x^{-1}$ is a useful indicator of the relative diameter of the terminal airways in mammals was touched on by Weibel (1979*b*) and Gehr *et al.* (1980) and discussed in detail for the bat by Maina *et al.* (1982*c*). Direct confirmation of this concept for birds has been obtained in three species. Thus the minimum diameter of the air capillaries in the passeriform *Sturnus vulgaris* was 4 μm (Maina *et al.* 1981) and $S_t V_x^{-1}$ was 342 $mm^2 mm^{-3}$ (table 5). In the collared turtle dove (*Streptopelia decaocto*) the minimum diameter of the air capillaries was 6.8 μm (Maina 1982 *b*) and $S_t V_x^{-1}$ was 253 $mm^2 mm^{-3}$ (table 5). In the lung of the domestic variant of *Gallus gallus* the minimum diameter of the air capillaries was 8 μm (Maina 1982*c*) and $S_t V_x^{-1}$ was only 172 $mm^2 mm^{-3}$ (table 5).

Our value of $S_t V_x^{-1}$ for *Passer domesticus* (389 $mm^2 mm^{-3}$) slightly exceeded Dubach's (1981) (326 $mm^2 mm^{-3}$), but the value we obtained for *Melopsittacus undulatus* (317 $mm^2 mm^{-3}$) is fairly close to hers (301 $mm^2 mm^{-3}$). Our value for domestic *Gallus gallus* (172 $mm^2 mm^{-3}$) was

lower than that reported by Duncker (1972) for this species (192 mm^2 mm^{-3}), but identical to that obtained by Vidyadaran (1987). In general, there seems to be an acceptable degree of agreement about this parameter in the species examined so far.

A negative (inverse) correlation ($r = -0.828$) between $S_t V_x^{-1}$ and body mass also emerges from the literature on mammalian species within a similar mass range to the birds examined here (figure 7, table 8). As for the birds, this negative correlation indicates that the smaller mammals will have alveoli of relatively small diameter. This relation is apparent from comparisons of the shrew and horse (Weibel 1979*b*). Furthermore, Tenney & Remmers (1963), working on a wide range of mammalian lungs, showed that alveolar diameters were inversely correlated with oxygen consumption (V_{O_2}); this again indicates that small mammals such as the shrew, bat and mouse, which have a higher specific V_{O_2}, have relatively small alveoli.

Inspection of figure 7 shows that the regression line for $S_t V_x^{-1}$ in the birds is well above that for the mammals, which indicates that the terminal airways of the birds in general are of much smaller diameter than those of the mammals. Statistical examination has shown ($p < 0.01$) that the two lines represent distinct populations (table 9), and a test described by Sprent (1969) shows ($p < 0.01$) that the lines may not be assumed to be parallel. However, comparison of the lines indicates that the lightest bird would have a value about 170% larger than that for a mammal of the same body mass. The value in our heaviest bird would be 305% larger than in a mammal of the same body mass.

Weibel *et al.* (1981*a*), Taylor *et al.* (1981) and Gehr *et al.* (1981*a*) have reported a paradox in that, when animals of about the same body mass but different metabolic needs were compared, morphometric $D_{L O_2}$ was strongly related to the oxygen needs of an organism. But on comparing mammals over a wide range of greatly differing body masses they found that $D_{L O_2}$ related more closely to body mass than to oxygen consumption. One reason which Weibel *et al.* (1981*a*) offered to explain this paradox is that the partial pressure gradient for oxygen from alveolar surface to the red cells could depend on the diameter of the terminal airways. Essentially, small and metabolically active animals, such as the Japanese waltzing mouse (Geelhaar & Weibel 1971) and the shrew and bat (Tenney & Remmers 1963), have small alveoli. Weibel *et al.* (1981*a*) have suggested that the pressure gradient of oxygen (the driving force for oxygen) from these small air spaces to blood could be higher than that in the larger alveoli of the bigger animals. Avian air capillaries are very small in diameter, ranging from 3 to 10 μm, according to Duncker (1972), whereas mammalian alveoli are about 35 μm in diameter in the shrew (Tenney & Remmers 1963), 47–117 μm in some other species examined by Tenney & Remmers (1963), 122 μm in the dog (Siegwart *et al.* 1971) and 250 μm in man (Weibel 1963*a*). Following this line of argument, the driving force for oxygen should be far higher in the bird lung than in the lung of even the smallest mammals. The influence of this driving force is not taken into account in the calculation of the morphometric diffusing capacity for oxygen, but nevertheless is likely to be a factor in the superior efficiency of the respiratory system of birds as compared with mammals.

The design of the avian pulmonary system is such that the volume of the lung does not change appreciably with every respiratory cycle (Duncker 1971*a*). This has made possible the drastic reduction in the diameter of the air capillaries, as the forces of surface tension do not have to be overcome during inspiration.

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(v) *Harmonic mean thickness of the blood–gas (tissue) barrier*

In the birds examined in the present investigation the thickest barrier, expressed as the harmonic mean thickness (τ_{ht}), was observed in domestic *Gallus gallus* (0.318 μm). The thinnest barriers were generally found in the passeriform species (table 6), remarkably thin barriers being encountered in *Hirundo fuligula* (0.090 μm) and *Passer domesticus* (0.096 μm). Dubach (1981) found τ_{ht} to be 0.118 μm in *Passer domesticus*, 0.118 μm in *Melopsittacus undulatus*, 0.346 μm in *Gallus domesticus* and 0.133 μm in *Anas platyrhynchos*; except for *Passer domesticus* (in which Dubach's value is 23% thicker), these are closely similar to our values, which were 0.096, 0.117, 0.318 and 0.133 μm, respectively, in these four species. By far the thickest barrier encountered in any avian species was found in a specimen of a Humboldt penguin (*Spheniscus humboldti*) by Maina & King (1987). In a non-quantitative study, Welsch & Aschauer (1986) had already called attention to an unusually thick barrier in the emperor penguin (*Aptenodytes forsteri*); in the Humboldt penguin the harmonic mean thickness of the barrier was indeed 0.530 μm. As suggested by Welsch & Aschauer, a thick barrier in these most highly specialized diving birds can be attributed to the need to increase the mechanical stability of the barrier against the effects of compression during diving. The two large auks in table 6 (*Alca torda* and *Cepphus carbo*) are also specialized pursuit divers and resemble penguins in using their wings to fly under water at relatively high speeds; their mean barrier thickness (0.212 μm) exceeds the means of all the other orders or families listed in table 6 (see Maina 1987), but is less than half that of the Humboldt penguin.

The mean τ_{ht} for all the 25 species of birds which we examined in this project (excluding *Gallus gallus*) was 0.150 μm. This was very much smaller than that of the 37 mammalian species (0.444 μm) examined by Gehr *et al.* (1981 *a*) and the eight mammalian species (0.61 μm) examined by Meban (1980). The harmonic mean thickness of the lungs of ten amphibian and ten reptilian species (Meban 1980) were 1.70 and 1.01 μm, respectively. In a preliminary study Perry (1981) has reported values of 0.36 and 0.70 μm, respectively for the lungs of two species of lizard, namely the teju (*Tupinambis nigropunctus*) and the savanna monitor (*Varanus exanthematicus*). The τ_{ht} for the lungfish (*Lepidosiren paradoxa*) was reported to be 0.86 μm (Hughes & Weibel 1976), and that for the water–blood barrier of a bony fish (the tench, *Tinca tinca*) was found to be 2.47 μm (Hughes 1972). The relatively great thickness of the barrier through which oxgyen has to pass in some of these ectothermic vertebrates may be correlated with the fact already noted that generally their oxygen consumption is lower than that of endothermic homeotherm vertebrates. In addition, some of these ectothermic air-breathing animals utilize accessory organs such as the skin for gas exchange.

The thickest and the thinnest blood–gas (tissue) barriers (τ_{ht}) reported for mammalian species (table 8) are 0.72 μm in the pig (Meban 1980) and 0.23 μm in a specimen of the shrew *Suncus etruscus* (Gehr *et al.* 1980). The thinnest blood–gas (tissue) barriers in all vertebrates examined so far have been found in the hummingbird *Colibri coruscans* (0.099 μm) by Dubach (1981), and in our study in *Hirundo fuligula* (0.090 μm) and in *Passer domesticus* (0.096 μm).

The harmonic mean thickness is the most appropriate estimator of the resistance of a barrier to oxygen diffusion (Weibel & Knight 1964; Weibel 1973). The diffusing capacity of the lung will vary inversely with the thickness of the blood–gas (tissue) barrier and directly with the surface area of the barrier. These are two major morphometric features which can be adapted in order to increase the efficiency of gas exchange in a lung. Thus it is not surprising that the

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thinnest tissue barriers (τ_{ht}) and the most extensive specific surface areas of the tissue barrier ($S_t\ W^{-1}$, square millimetres per gram) have been found in the small, metabolically very active passeriform and trochilid species.

In figure 8, the regression line for the birds is well below that for the mammals, showing that birds have a much thinner barrier than mammals. Statistical examination has shown ($p < 0.01$) that the regression lines for the birds and the mammals represent distinct populations (table 9) and a test described by Sprent (1969) shows ($p < 0.05$) that the lines may not be assumed to be parallel. However, comparison of the lines indicates that our lightest bird had a value for τ_{ht}, which we estimate to be about 56% less than that of a mammal of the same body mass. The difference becomes greater as body mass increases, so that τ_{ht} in our heaviest birds is estimated to be about 67% less than in a mammal of the same body mass.

The values of the minimum harmonic mean thickness of the blood–gas (tissue) barrier (table 6) were highest in *Falco tinnunculus* (0.099 μm) and lowest in *Anser anser* (0.050 μm) and *Passer domesticus* (0.052 μm). This parameter indicates the degree to which the barrier can be sporadically attenuated without losing its structural integrity. Clearly the total area of the regions of 'minimum thickness' is of comparative functional importance; it could be estimated, but up to now this has not been attempted in any vertebrate.

(vi) *Harmonic mean thickness of the plasma layer*

A substantial discrepancy between our observations and those of Dubach (1981) occurred in the harmonic mean thickness of the plasma layer in *Passer domesticus* and *Melopsittacus undulatus*. Thus our values for τ_{hp} in these two species were 0.217 and 0.260 μm, respectively; Dubach's (1981) values were 0.016 and 0.018 μm, lower by a factor of about 14. Using the same stereological technique as ours, Vidyadaran (1987) obtained a value of τ_{hp} in the domestic fowl of 0.300 μm, s.d. 0.06, which was virtually identical to ours in this species (0.306, s.d. 0.02). The possible sources of this discrepancy are discussed at the end of this account under Critique of the Methodology. The discrepancy is further reflected in the diffusing capacity of the plasma D_{pO_2}, and also in the membrane diffusing capacity (D_{mO_2}) and the total diffusing capacity (D_{LO_2}), τ_{hp} being utilized in the calculation of all these values.

A positive correlation ($r = 0.560$) between τ_{hp} and body mass (figure 9) was observed in our birds. A positive correlation ($r = 0.758$) between τ_{hp} and body mass is also apparent in the mammals examined by Gehr *et al.* (1981*a*), with body masses falling within a similar range to our birds (figure 9). Inspection of figure 9 shows that the regression line for birds is well above that of mammals, indicating that the harmonic mean thickness of the plasma layer may be substantially greater in birds generally than in mammals. Statistical examination has shown that the regression lines for the birds and mammals represent distinct populations, but may be assumed to be parallel, with a common slope of 0.084. If this assumption is adopted, then for the birds the y-intercept corresponding to a mass of 1 g becomes 163 nm and that for mammals 98 nm. Thus τ_{hp} in birds is estimated to be about 66% thicker than in the mammals of similar body mass.

(vii) *Arithmetic mean thickness of the blood–gas tissue barrier*

The value of the arithmetic mean thickness, $\bar{\tau}_t$ was highest in *Falco tinnunculus* (1.66 μm) and in *Gallus gallus* (1.24 μm). The mean for all our birds (excluding *Gallus*) was 0.866 μm, that for the passeriforms alone being 0.775 μm (table 6). Much lower values of $\bar{\tau}_t$ were reported by

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Dubach (1981), including those for three avian species which we also examined, namely the domestic fowl (0.494 μm), *Passer domesticus* (0.218 μm) and *Melopsittacus undulatus* (0.210 μm); our values for the domestic fowl, *Passer domesticus*, and *Melopsittacus undulatus* were 1.24, 1.034 and 0.976, respectively, i.e. 2.5–5 times higher than Dubach's values. Vidyadaran (1987), using the same stereological methods as ours, obtained a value of 0.459 μm for the domestic fowl, i.e. essentially the same as Dubach's value. (See Critique of the Methodology for further discussion.)

The parameter arithmetic mean thickness of the blood–gas barrier ($\bar{\tau}_t$) expresses the tissue mass of the blood–gas (tissue) barrier in the lung, and thus reflects the oxygen consumption of the tissue of the barrier itself (Weibel & Knight 1964; Weibel 1973). The mean values of $\bar{\tau}_t$ for the many mammalian species examined by Weibel and his co-workers and Meban (1980) was 1.50 μm; those for Amphibia and Reptilia (Meban 1980) were 2.22 and 2.02 μm, respectively. Apparently, the volume of the tissue mass of the barrier is substantially lower in birds than in the other air-breathing vertebrates, thus minimizing the amount of oxygen utilized by the barrier tissues.

The relative thinness of the avian blood–gas (tissue) barrier is due to a great reduction of its interstitial connective tissue elements. Fibroblasts, collagen and elastic fibres comprise the 'fibrous skeleton of the lung parenchyma' in mammals (Gehr *et al.* 1978). The reduction of the fibrous skeleton in the avian lung emphasizes the remarkable ability, noted by Macklem *et al.* (1979), of the extremely small avian air capillaries to resist collapse. An exception to this reduction of the fibrous skeleton of the avian blood–gas (tissue) barrier appears to occur in deep-diving penguins. Thus Welsch & Aschauer (1986) observed relatively abundant collagen fibrils in the basal lamina of the emperor penguin. On the other hand, in the Humboldt penguin, which is not such a deep diver, collagen fibrils seldom occur in the basal lamina (Maina & King 1987), although the barrier is the thickest measured in any avian species.

Electron micrographs of the avian exchange tissue generally show marked variations in the thickness of the blood–gas (tissue) barrier which suggest that the barrier may be corrugated. It is claimed (Weibel 1973; Meban 1980) that such qualitative corrugations of the barrier are reflected quantitatively in the ratio of $\bar{\tau}_t$ to τ_{ht}. A ratio of about 3:1 reported in mammals by Weibel (1973) and Meban (1980) was held to indicate corrugation. On the other hand, the lower ratios in reptiles and amphibians (1.1:1 to 2.3:1) are thought to indicate less corrugation in these two vertebrate classes (Meban 1980). Because the mean ratio of $\bar{\tau}_t:\tau_{ht}$ in the birds examined here was 6:1, this line of reasoning suggests that the avian barrier is much more

Description of plate 1

Figure 1. Paraffin section of the parabronchi, cut transversely and obliquely, of the black-headed gull (*Larus ridibundus*). The atria (small arrows) are well developed. Abbreviations: BV, interparabronchial blood vessels lying in interparabronchial septa which are not prominent; M, mantle of exchange tissue; L, lumen of parabronchus. Stained by haematoxylin and eosin. Magn. ×150.

Figure 2. Electron micrograph of the exchange tissue of the black-headed gull (*Larus ridibundus*). Abbreviations: Ac, air capillary; Bc, blood capillary; C, cytoplasm of red blood cell; N, nucleus of red blood cell. Arrows show regions where blood capillaries contact blood capillaries, comprising tissue not involved in gas exchange. Magn. ×5500.

Figure 3. Electron micrograph of the blood–gas (tissue) barrier of the domestic fowl (*Gallus gallus*). Abbreviations: Ac, air capillary; Bc, cytoplasm of red blood cell; Bl, basal lamina; En, relatively thick endothelial cell; Ep, very thin epithelial cell; P, blood plasma; Sl, osmiophilic lining complex. Magn. ×30400.

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FIGURES 1–3. For description see opposite.

(*Facing p.* 36)

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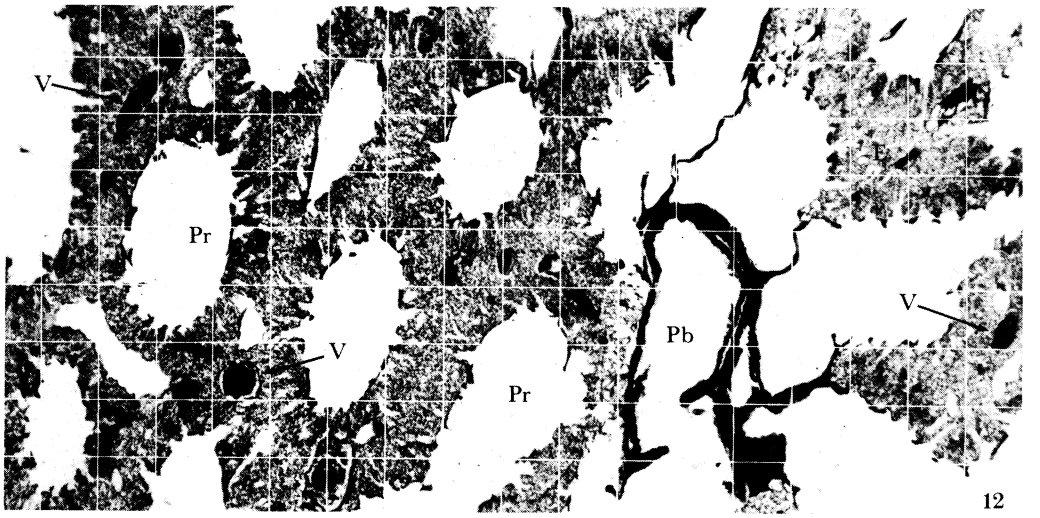

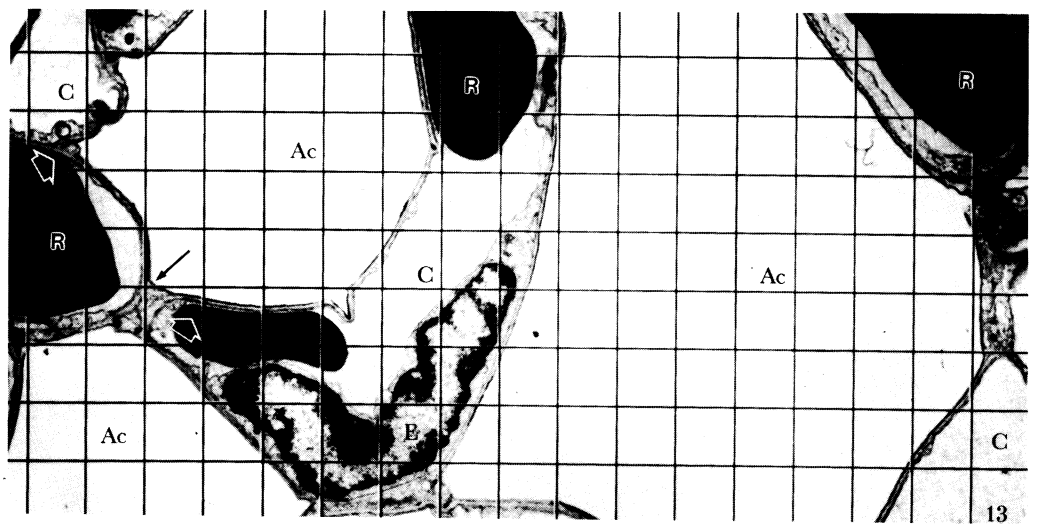

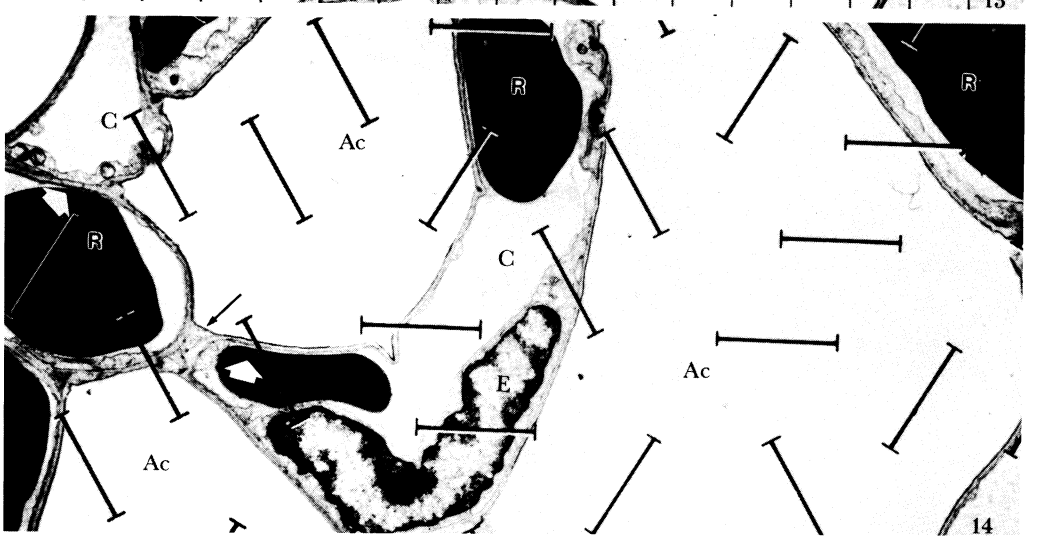

FIGURES 12–14. For description see opposite.

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corrugated than that of other air-breathing vertebrates. Corrugation has been regarded as physiologically advantangeous on the grounds that it preserves a reasonable degree of mechanical stability and at the same time offers a lower overall resistance to gaseous diffusion than a barrier of uniform thickness (Weibel 1973; Meban 1980). However, it is noteworthy that the Etruscan shrew, which is a minute and therefore metabolically demanding animal, has a ratio of only about 2:1. Weibel (1972) and Gehr *et al.* (1980) accounted for this by the opposite line of argument, i.e. that the low ratio is an extreme effort to reduce overall barrier thickness so that it approaches τ_{ht}.

(viii) *Pulmonary capillary blood volume*

The ratio of the pulmonary capillary blood volume to the alveolar surface area in mammalian lungs, $V_c S_a^{-1}$ ($cm^3\ m^{-2}$) has been termed 'capillary loading' (Gehr *et al.* 1980). A high capillary loading (13.3) was reported in the lung of the red-eared turtle, *Pseudemys scripta elegans*, by Perry (1978) and a range of 12.4–18.88 was obtained by Hughes & Weibel (1976) in the lungfish (*Lepidosiren paradoxa*). The strictly equivalent ratio for the avian lung would be the ratio of the volume of the pulmonary capillary blood to the surface area of the air capillaries, i.e. $V_c S_a^{-1}$. However, in table 5 $V_c S_t^{-1}$ is given instead of $V_c S_a^{-1}$, because $V_c S_t^{-1}$ is more meaningful, because it is based on the functional surface area of the air capillaries, i.e. the blood–gas (tissue) barrier itself. Obviously $V_c S_t^{-1}$ will always be slightly higher than $V_c S_a^{-1}$, as S_a is always higher than S_t. Perry (1978) interpreted capillary loading as indicating that 'a low ratio of pulmonary capillary volume to respiratory surface area implies favourable conditions for gas exchange: a high degree of exposure of the capillary blood'.

The lowest values of $V_c S_t^{-1}$ (table 5) were observed in the falconiform *Falco tinnunculus* (0.73 $cm^3\ m^{-2}$) and the passeriforms (*Hirundo fuligula* (0.67 $cm^3\ m^{-2}$) and *Passer domesticus* (0.94 $cm^3\ m^{-2}$). The mean value of $V_c S_t^{-1}$ in the passeriform species (1.20) was lower than that of the charadriiforms (1.40) and anseriforms (1.39), all three of these groups being reasonably well represented in this study. The highest values were observed in *Gallus gallus* (1.62) and the

Description of plate 2

Figure 12. Photomicrograph of a histological section of the lung of the passeriform *Estrilda astrild*, with a superimposed quadratic lattice grid for differential point counting to estimate the volume densities of the main components of the lung (table 2). A 'point' is formed wherever a vertical line crosses a horizontal line. The volume density of each component (i.e. the percentage volume of that component within the lung) is proportional to the number of points that fall on the component. Abbreviations: E, exchange tissue; Pr, parabronchial lumen; V, blood vessels larger than capillaries; Pb, lumen of primary bronchus. Magn. ×135.

Figure 13. Transmission electron micrograph of the lung of the charadriiform herring gull (*Larus argentatus*), with a superimposed quadratic lattice grid. The volume densities of the main components of the exchange tissue (table 3) can be estimated from the proportion of 'points' falling on each component, as in figure 12. The surface areas of the resistance barriers of the air–haemoglobin pathway (table 4) can be estimated by intersection-counting (figure 15). The harmonic mean thicknesses of the blood–gas tissue barrier (τ_{ht}) and plasma layer (τ_{hp}) (table 6) can be estimated from measurements of intercept length (figure 16). Abbreviations: Ac, air capillaries; C, blood capillaries; E, nucleus of endothelial cell; R, red blood cells. The arrow represents a region where air capillaries lie adjacent to each other; arrowheads (white) show regions where blood capillaries lie adjacent to each other. The regions indicated by arrowheads and arrows are categorized as tissues not involved in gas exchange. Magn. ×5800.

Figure 14. Transmission electron micrograph as in figure 13. The micrograph is overlaid with a random short line test grid for estimating the arithmetic mean thickness of the blood–gas tissue barrier ($\bar{\tau}_t$) (table 6) by counting the point hits and intersections of the test grid (see Appendix). With this grid a 'point' is formed by each end of each short line. Magn. ×5800.

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charadriiform *Cepphus carbo* (1.66). The values of $V_c S_{a^{-1}}$ in mammalian lungs range from 0.63 cm^3 m^{-2} in the shrew *Crocidura poensis* (Gehr *et al.* 1980) to 2.16 cm^3 m^{-2} in the domestic cow (*Bos bovis*) (table 2 of Gehr & Erni (1980)).

In the 25 avian species (excluding *Gallus*) in which we estimated the total volume of pulmonary blood, it constituted 19–31 % of the lung volume (tables 2 and 3); of this volume of blood, 49–80 % was in the blood capillaries of the exchange tissue. These values are comparable to those of Duncker (1973), who found in six species of bird that the total pulmonary blood volume comprised 18–35 % of the total volume of the lung, 60–75 % of this being in the blood capillaries. In our 25 avian species, the total pulmonary capillary blood (V_c) constituted a mean value of 16.3 % (s.d. 4.0) of the total lung volume. In the 37 mammalian species examined by Gehr *et al.* (1981*a*), V_c constituted a mean value of only 8.1 % of the total lung volume. Our values are consistent with Duncker's (1973) conclusion that the pulmonary capillary blood of birds forms a relatively large proportion of the total lung volume. The greatest volume of pulmonary capillary blood in any species of bird has been found in the Humboldt penguin (*Spheniscus humboldti*). When the volume of capillary blood is standardized against body mass (i.e. $V_c W^{-1}$), a value of 8.0 cm^3 kg^{-1} is obtained for this species; the mean value of $V_c W^{-1}$ in the charadriiform, psittaciform, columbiform and passeriform species in table 3 is only 4.1 cm^3 kg^{-1}. The exceptionally large volume of pulmonary capillary blood in the Humboldt penguin compensates for its remarkably thick blood–gas (tissue) barrier (0.530 μm), and gives this species a reasonably high total specific morphometric diffusing capacity for oxygen (0.051 ml O_2 s^{-1} $mbar^{-1}$ kg^{-1}).

As would be expected, a strong correlation ($r = 0.984$) was observed between the pulmonary capillary blood volume and body mass in our birds (figure 10). Similarly, in a large population of mammalian species a strong correlation ($r = 0.994$) was observed between V_c and body mass (Gehr *et al.* 1981*a*). In figure 10 the regression line for the birds is somewhat above that for the mammals of similar body mass, suggesting that V_c may be greater in the birds than in the mammals. Statistical examination has shown ($p < 0.01$) that the regression lines for birds and mammals represent distinct populations (table 10), but may be assumed to be parallel, with a common slope of 0.956 (figure 10). If this assumption is adopted, the y-intercept corresponding to a mass of 1 g becomes 5.23 mm^3 and that for the mammals 4.30. Thus V_c in the birds in general is estimated to be about 22 % greater than in the mammals of similar body mass. This is consistent with Duncker's (1973) suggestion that a relatively greater volume of pulmonary capillary blood may be one of the main factors accounting for the comparatively great capacity of the avian lung for gas exchange.

(ix) *Pulmonary diffusing capacity*

Diffusing capacity of the blood–gas (tissue) barrier. In this study, the mass-specific D_{tO_2} (ml O_2 (s mbar kg)$^{-1}$ (1 bar = 10^5 Pa)) ranged from 0.130 in *Gallus gallus* to 4.01 in the passeriform *Hirundo fuligula* (table 7). The mean value of $D_{tO_2} W^{-1}$ for the passeriforms (1.60 ml O_2 (s mbar kg)$^{-1}$) was very much higher than that for the non-passeriform species (excluding *Gallus*), i.e. 0.79. The only other study in which estimates of the specific diffusing capacities of the blood–gas (tissue) barrier, of the plasma layer and of the membrane have been reported for the avian lung, is that by Dubach (1981). Her values ($D_{tO_2} W^{-1}$) were 2.03 ml O_2 (s^{-1} $mbar^{-1}$ kg^{-1}) for *Passer domesticus* and 1.56 for *Melopsittacus undulatus*; our values for these two species were, respectively, 2.90 and 1.45 (tables 1 and 7). Dubach's value for the hummingbird

Colibri coruscans was 3.53; this was lower than that of one of our passeriforms, *Hirundo fuligula*, perhaps surprisingly because the hummingbirds are outstandingly energetic and metabolically active birds (Epting 1980). However, the genus *Hirundo* is also an energetic group, but it is possible that our single specimen of *H. fuligula* may not have been representative of the species.

The morphometric data necessary for the calculation of D_{tO_2} in mammals are often presented in the literature, but the actual values for individual animals are seldom reported. The specific D_{tO_2} for the mouse (*Mus musculus*) was found by Geelhaar & Weibel (1971) to be 0.090 ml O_2 (s mbar kg)$^{-1}$, this value being lower than almost all of our birds (table 7). Our lowest value (0.130 ml O_2 (s mbar kg)$^{-1}$) occurred in the domestic fowl (*Gallus gallus*). However, even this is substantially higher than the data reported for fish and reptiles: for example, a value of 0.0020 ml O_2 (s mbar kg)$^{-1}$ was obtained by Hughes & Weibel (1976) for the lungfish (*Lepidosiren paradoxa*); 0.0019 was estimated for the tench (*Tinca tinca*) by Hughes (1972); a range of 0.0087–0.0163 for the red-eared turtle (*Pseudemys scripta elegans*) was noted by Perry (1978); and values of 0.0343 and 0.0291, respectively, were reported for the lungs of two species of lizard *Tupinambis nigropunctus* and *Varanus exanthematicus* by Perry (1981).

Diffusing capacity of the plasma layer. Because of the marked difference (by a factor of about 14) between our values for the harmonic mean thickness of the plasma layer and those reported by Dubach (1981), the values which we obtained for the specific D_{pO_2} (ml O_2 (s mbar kg)$^{-1}$) were remarkably different from hers. Thus our mean values for *Passer domesticus* and *Melopsittacus undulatus* (table 7) were, respectively, 1.37 and 0.879, whereas hers were 16.71 and 9.86, respectively.

Diffusing capacity of the membrane. The discrepancy between our values for τ_{hp} and those of Dubach (1981) is also reflected in the values of the specific membrane-diffusing capacity, D_{mO_2} (ml O_2 (s mbar kg)$^{-1}$), as τ_{hp} is included in the model used for calculating D_{mO_2}. Thus our mean specific D_{mO_2} values for *Passer domesticus* and *Melopsittacus undulatus* were 0.94 and 0.55, whereas Dubach's were 1.81 and 1.35, respectively.

In our study, the passeriform species gave the highest specific D_{mO_2}, with a mean of 0.64 as compared with 0.34 for the non-passeriform species (excluding *Gallus*). The lowest value for any species was found in the domestic fowl (*Gallus gallus*) (0.079), and the highest in the passeriform *Hirundo fuligula* (1.68). In the hummingbird *Colibri coruscans*, Dubach (1981) obtained a value of 3.0 ml O_2 (s mbar kg)$^{-1}$.

Total morphometric pulmonary diffusing capacity. This estimates the maximum possible gas conductance of the lung under ideal conditions of ventilation and perfusion and a positive partial pressure gradient over the entire barrier (Weibel 1970–1; Siegwart *et al.* 1971; Gehr *et al.* 1981*b*). Such conditions are seldom, if ever, realized *in vivo* even in maximum exercise (Scheid & Piiper 1970; Scheid 1979) and therefore the physiologically estimated pulmonary diffusing capacity is expected to be lower than the morphometric value.

The mean specific total morphometric diffusing capacity, D_{LO_2} (ml O_2 (s mbar kg)$^{-1}$), for the passeriform species was 0.083 (table 7), appreciably higher than in the anseriforms (0.046) and charadriiforms (0.049) and indeed than in the whole group of non-passeriform species (excluding *Gallus*) (0.054). Within the passeriform species themselves the single specimen of *Hirundo fuligula* showed the highest specific D_{LO_2} (0.190). As already noted, the hirundinids are typically highly energetic. Unfortunately, Dubach (1981) did not report the total morphometric diffusing capacity of the hummingbird (*Colibri coruscans*), but a high value can be predicted from her estimate of the specific D_{tO_2} for this species. The lowest value for specific

D_{LO_2} among the 26 species investigated in our study occurred once again in the domestic form of *Gallus gallus* (0.015 ml O_2 (s^{-1} $mbar^{-1}$ kg^{-1})); Vidyadaran (1987) reported a value of 0.017 in the domestic fowl. In the wild form of *Gallus gallus*, i.e. the wild red jungle fowl, he obtained a rather similar value (0.018), indicating that domestication alone cannot account for the very low D_{LO_2} in the domestic fowl. From a survey of their pulmonary morphometric characteristics as reported in the literature, Vidyadaran suggested that the lungs of the galliform birds in general may turn out to be relatively inefficient gas exchangers. He also made a comprehensive morphometric study of the lungs of a rail, the white-breasted water-hen (*Amaurornis phoenicurus*), and found its specific D_{LO_2} to be 0.056, i.e. slightly higher than the means of the anseriform (0.046) and charadriiform (0.049) birds in our study; because this species adopts a ground-dwelling mode of life similar to that of the wild red jungle fowl, Vidyadaran suggested that a low specific D_{LO_2} is not necessarily a concomitant of this mode of life.

Apparently, the only data for the physiologically determined pulmonary diffusing capacity of the avian lung are those reported for *Gallus gallus* by Scheid & Piiper (1970) and for the domestic form of the muscovy duck (*Cairina moschata*) by Meyer *et al.* (1977), Scheid *et al.* (1977) and Burger *et al.* (1979). The value reported for *Gallus* was 0.0187 ml O_2 (s mbar)$^{-1}$ and the mean of the values obtained by these authors for *Cairina* was 0.028 ml O_2 (s mbar)$^{-1}$. The minimum morphometric D_{LO_2} for *Gallus* was also 0.019 ml O_2 (s mbar)$^{-1}$ (table 7, and Abdalla *et al.* (1982)), i.e. similar to the physiological D_{LO_2}. Vidyadaran (1987) found the minimum morphometric D_{LO_2} of *C. moschata* to be 0.054, i.e. about twice the physiological value and the mean morphometric value to be 0.091, about 3.3 times the physiological value. This degree of agreement between the morphometric and physiological estimates of D_{LO_2} in these two species of bird is within the range predicted by Weibel (1984) for mammals, according to which the morphometric value is expected to exceed the physiological by between 1.4 and 7 times.

It is possible to make broad comparisons of the specific D_{LO_2} of birds with that of some other vertebrates. Among our birds, the lowest mean mass-specific D_{LO_2} was 0.0149 ml O_2 (s mbar kg)$^{-1}$ in the domestic fowl. However, even this was much higher than the equivalent specific values, 0.003 and 0.004, respectively, of the gas exchange apparatus of the lungfish (*Lepidosiren paradoxa*) (Hughes & Weibel 1976) and of the climbing perch (*Anabas testudineus*) (Hughes *et al.* 1973). These low values in lower vertebrates are consistent with the relatively small oxygen consumption of ectothermic vertebrates (Schmidt-Nielsen 1980).

In some very small mammals the specific D_{LO_2} is relatively great. Thus the Etruscan shrew (*Suncus etruscus*), which has a mean body mass of only 2.6 g, has a specific D_{LO_2} of 0.098 ml O_2 (s mbar kg)$^{-1}$ (Gehr *et al.* 1980), and this exceeds all of the birds in table 7 except *Hirundo fuligula*. Correspondingly high values also occur in the white mouse (*Mus musculus*) and in the Japanese waltzing mouse (*Mus wagneri*) (Geelhaar & Weibel 1971). The highest specific D_{LO_2} reported in any mammal was found in a bat, *Epomophorus wahlbergi*, i.e. 0.245 ml O_2 (s mbar kg)$^{-1}$ (Maina & Nicholson 1982; Maina *et al.* 1982*c*). No bird is known to attain this level, but we do not yet have data for hummingbirds. Despite having an essentially mammalian type of lung with tidal air-flow, bats are reported to possess an exercise capacity as great as that of birds (Bartholomew *et al.* 1964; Carpenter 1975*b*). Morphometric observations on the lungs of six bat species (Maina *et al.* 1982*c*; Maina & King 1984) showed that this may be explained by an extremely large lung volume (figure 4), a very extensive surface area for gas exchange (figure 5) and an exceptionally thin blood–gas barrier (figure 8), all of which lead to a remarkably great D_{LO_2} (figure 11).

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The total morphometric $D_{L O_2}$ for the species of bird examined here (excluding the domestic fowl, *Gallus gallus*) was positively correlated ($r = 0.978$) with body mass (table 9, figure 11). This is expected, because two parameters which are directly related to $D_{L O_2}$, i.e. the surface area of the blood–gas (tissue) barrier and blood capillary volume, are also positively correlated with body mass (figures 4 and 10). A strong positive correlation between $D_{L O_2}$ and body mass has also been observed in mammals (Weibel 1972, 1973; Gehr *et al.* 1981*a*). In figure 11 the regression line for the birds is slightly above that for the mammals, indicating that $D_{L O_2}$ may be somewhat higher in birds generally than in mammals. Statistical examination has shown ($p < 0.01$) that the regression lines for the birds and the mammals represent distinct populations (table 9), but may be assumed to be parallel, with a common slope of 0.914. If this assumption is adopted, then for the birds the y-intercept corresponding to a mass of 1 g becomes 0.91×10^{-4} ml O_2 (s mbar)$^{-1}$ or 7.29×10^{-3} ml O_2 (min mmHg)$^{-1}$ and that for the mammals 0.75×10^{-4} ml O_2 (s mbar)$^{-1}$ or 5.99×10^{-3} ml O_2 (min mmHg)$^{-1}$. Thus $D_{L O_2}$ in birds generally is estimated to be about 22% greater than in mammals of similar body mass†.

(*b*) *Critique of the methodology*

(i) *Range of materials*

Our material initially consisted of 160 birds from 42 species and 10 orders, and lung volume and body mass were recorded in all of these (table 1). By using light microscopy we established the volumes of the main components of the lung in 140 of these birds from 38 species and 10 orders (table 2). Finally, on 90 of these birds, from 26 species and 9 orders, we also made a comprehensive investigation of morphometric parameters with the electron microscope (tables 3–7 inclusive). It can be seen from n in tables 1–3 that some species (and some orders) are represented by only one or two specimens. These low numbers were due to the scarcity of specimens, severe though appropriate constraints of conservation, and difficulties in fixation particularly in small species. Clearly the results obtained from such low numbers of specimens may not be representative of their taxa, but the total lack of such data in the literature warrants their inclusion.

Many orders, and several interesting groups with specialized functional characteristics, are not represented in our allometric estimates. Among the latter are the heaviest birds capable of sustained flapping flight (e.g. the swan, *Cygnus*), large flightless birds (e.g. the ostrich, *Struthio*), and the most specialized diving forms (e.g. penguins, Sphenisciformes). After the study on which this account is based had been completed, however, the volumes of the lungs of the ostrich (*Struthio camelus*), 35 cm^3 kg^{-1} (Maina, unpublished data), and emu (*Dromaius novaehollandiae*), 36.7 cm^3 kg^{-1} (unpublished data) (Maina & King 1989), have been determined and a comprehensive survey of the lungs of a penguin, the Humboldt penguin (*Spheniscus humboldti*), has been carried out (Maina & King 1987). Because of the length of this paper these data have not been fully incorporated in it. However, the mass-specific volumes of the ostrich and emu lungs were reasonably similar to that of the smaller species of bird; the ostrich has to contend with many predators and is well known as a fast runner. As already

† The new constants for Θ_{O_2} mentioned in the footnote to p. 11 await confirmation and extension to other avian species, but application of them to our data for the avian species reported in this paper would increase our values for $D_{e O_2}$ and $D_{L O_2}$ by mean factors of about 1.60 and 1.51, respectively. This indicates that these values for birds exceed those for mammals by an even greater margin than we have suggested (see Appendix and figure 17).

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stated, the Humboldt penguin had a notably thick blood–gas (tissue) barrier (τ_{ht} 0.530 μm) and a high $V_c\ W^{-1}$ (8 $cm^3\ kg^{-1}$); it had a $D_{L\,O_2}\ W^{-1}$ of 0.051 ml O_2 (s mbar kg)$^{-1}$, which lies within the range of the flying species of bird reported here though towards the lower end of their values (Maina & King 1987).

These limitations in our material enjoin caution in accepting our allometric functions as representative of the 9000 or so extant species of birds. Further morphometric research is required to consolidate our conclusions. (See also the additional note on p. 57.)

(ii) *Estimation of lung volume*

It was assumed that the avian lung, when fixed *in situ*, undergoes minimal shrinkage because it is firmly attached by pleural filaments to the horizontal septum, vertebrae, and to the ribs, which are deeply embedded in the costal sulci. When the fixed lung is being removed there are no signs that these filaments have already ruptured and allowed the lung to separate from the structures enclosing it. It was therefore concluded that the volume of the fixed lung was closely similar to that of the lung in the live animal. This assumption is supported by the mean values of the combined volume of the left and right lungs of 16 specimens of *Passer domesticus* (0.8 cm^3, s.d. 0.10) and 12 specimens of *Melopsittacus undulatus* (1.11 cm^3, s.d. 0.16) which were obtained by Dubach (1981); her technique was to inject silicone rubber into the airways and measure the volume of the cast. Her values were not significantly different ($p > 0.5$ and $0.5 > p > 0.1$, respectively) from those which we obtained for these two species (i.e. 0.76, s.d. 0.12, for *Passer domesticus*, and 1.025, s.d. 0.113, for *Melopsittacus undulatus*).

During the estimation of lung volume by water displacement some water may have entered the airways through the ostia. However, when the lung was removed from the body it was full of fixative that, because of surface tension, cannot escape readily from the ostia. This error is therefore expected to be small, and is confirmed by the close similarity to the volume estimated by the entirely different method of Dubach (1981).

(iii) *Tissue shrinkage*

Light microscopy. Shrinkage by about 14% occurred during histological processing. The structural components of the lung, of which the main components are the exchange tissue and the lumina of the parabronchi and secondary bronchi, shrink in about the same relative proportions. Because the volume of the fixed lung (which, for reasons given in the previous section, is believed to be closely similar to the volume of the fresh lung in life) forms the basis for calculating the absolute volume of its four main components, the values for the latter should also represent approximately the actual values in life. The almost constant volume of the avian lung during breathing has recently been confirmed by Jones *et al.* (1985), who observed a volume change of only 1.4%.

Electron microscopy. The osmolarity of the solutions used in processing is undoubtedly critical in morphometry, but what constitutes the effective osmolarity and how much the different constituents (mainly the fixative and buffer) contribute to the effective osmolarity is far from settled (Barnard 1976; Mathieu *et al.* 1978; Weibel 1979a; Lee *et al.* 1982). Also, the effects of fixatives on different tissues have not been comprehensively investigated. These uncertainties are illustrated by the success of Lee *et al.* (1982) in obtaining minimal shrinkage and good fixation of smooth muscle cells with a hyperosmotic buffered solution of glutaraldehyde (400 mOsm). Shrinkage during processing for electron microscopy is known to be very small when glutaraldehyde-based fixatives of physiological osmolarity are employed; values of 5%

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or less have been estimated by Weibel & Knight (1964), Mathieu *et al.* (1978) and Meban (1980). Such small shrinkage has been ignored in pulmonary morphometry. Because of this and because of varying evidence about what constitutes the effective osmolarity of the solutions used in processing, we have not attempted to adjust our values.

In most of our birds the lungs were fixed with a buffered glutaraldehyde solution of 350 mOsm, which is close to the value of 340 mOsm given by Sykes (1971) for the plasma of the domestic fowl. Some were fixed with a solution of 460 mOsm (for details see §2). Fixatives and processing techniques similar to those which we employed have been shown to cause minimal shrinkage (Karnovsky 1965; Hopwood 1967; Hayat 1970; Weibel 1970–1; Meban 1980). Also, it seems reassuring that the values for the harmonic mean thickness of the blood–gas (tissue) barrier (a parameter which would be especially vulnerable to shrinkage or swelling) are closely similar in Dubach's (1981) and our observations on *Anas platyrhynchos*, *Gallus gallus*, *Columba livia*, *Melopsittacus undulatus* and *Passer domesticus* (see §4*a*(v)).

(iv) *Morphometric techniques*

(1) *Harmonic mean thickness of the plasma layer*. As already noted, there is a major discrepancy between our estimate of the harmonic mean thickness of the plasma layer (τ_{hp}) and that reported by Dubach (1981). There also seem to be rather large differences between the estimates of τ_{hp} in birds by us and Dubach on the one hand, and in mammals by Weibel and his co-workers on the other. Factors that may have contributed to these discrepancies are the use of different magnifications or different measurement scales, and the spatial relationships of the blood plasma in electron micrographs, as follows.

(1.1) *Magnification of electron micrographs*. Dubach's (1981) measurements of τ_{ht} and τ_{hp} were made at magn. ×14000, and ours at about ×7500. The higher magnification would undoubtedly give a better resolution and hence may be expected to yield more accurate measurements. But a greater number of electron micrographs have to be analysed, because the number of representative intercept lengths per micrograph is smaller; unfortunately Dubach did not state the number that she measured, or whether she had established that her sample size was sufficient. Anyway, there were no serious discrepancies between Dubach's estimates of τ_{ht} and ours, although hers were made at magn. ×14000 and ours at ×7500; it therefore seems unlikely that differences in magnification made an important contribution to the discrepancy in τ_{hp}. Perry (1981) was able to estimate τ_{ht} in reptiles at magnifications of only ×5000.

(1.2) *Scale used to measure intercept length*. We measured the intercept lengths with a linear millimetre scale. Unfortunately it is not clear whether the measurements reported by Dubach (1981) were obtained by a linear or a nonlinear scale.

The relative suitability of various alternative scales for measuring intercept lengths has been quite extensively discussed (Weibel 1970–1, 1979*a*; Gundersen *et al.* 1978; Perry 1981). Weibel (1963*a*, *b*) used a linear scale in his experiments. His important paper of 1970–1 then suggested the use of a nonlinear scale and this evidently formed the basis for thickness measurements in mammalian pulmonary morphometry by Weibel and his co-workers during later years. The use of a nonlinear scale may entail some loss of accuracy in measuring large intercepts, but because the values are converted into reciprocals, the large measurements have less effect than the small ones.

We conclude that the use of different scales may have contributed to the discrepancies, but is unlikely to be a major factor.

(1.3) *Spatial relations of blood plasma*. Perry (1978) has expressed reservations on the

significance of parameters requiring intracapillary measurements. His doubts are based on the proposition that 'the distance between the erythrocyte surface and the capillary wall in flowing blood is ten times greater than that observed on electron micrographs, and convection within the plasma and erythrocytes is ignored in morphometric estimates of D_{LO_2}'. As a result of physiological variations in the microcirculation of the lung, τ_{hp} must inevitably be a much more variable parameter than τ_{ht}. Weibel (1970–1) proposed that the spatial relationships observed on the electron micrographs be taken to represent the situation *in vivo*, until proved otherwise. As this assumption has not yet been challenged we have accepted it, albeit with misgivings.

Unfortunately, the thickness of the plasma layer has to be known if the total morphometric diffusing capacity of the lung (D_{LO_2}) is to be estimated. However, because the diffusing capacity of the tissue barrier and that of the red cell are also included in the model, the effect of any error in τ_{hp} is diminished during the calculation of D_{LO_2}. It could perhaps be argued that the diffusion capacity of the tissue barrier, D_{tO_2}, should receive the main emphasis, not D_{LO_2} (and certainly not D_{pO_2} and D_{mO_2}, which are especially affected by τ_{hp}). It will be recalled that Dubach's values for D_{tO_2} agree reasonably well with ours. A further drawback about D_{pO_2} and D_{eO_2} is the wide ranges of the constants required for their calculation; the constant needed for D_{tO_2} is much more precise. Nevertheless, despite these problems with D_{pO_2} and D_{eO_2} the ultimate aim must surely be to establish a reliable estimate of D_{LO_2}, as the latter alone expresses the total capacity of the lung for the diffusion of oxygen and is the only value that can be compared with the physiological diffusing capacity of the lung.

(2) *Arithmetic mean thickness of the blood–gas (tissue) barrier.* A difference was observed in the values of the arithmetic mean thickness ($\bar{\tau}_t$) in our and Dubach's (1981) studies. Thus Dubach reported $\bar{\tau}_t$ for *Passer domesticus* and *Melopsittacus undulatus* to be, respectively, 0.218 and 0.210 μm; these values are much lower than ours, which were 1.03 and 0.98 μm, respectively. Our values give a ratio of $\bar{\tau}_t$ to τ_{ht} for *Passer domesticus* and *Melopsittacus undulatus* of 10.8 and 8.3, respectively. These are far higher than the corresponding ratios of 1.9 and 1.8 reported by Dubach for these two species. A ratio of $\bar{\tau}_t$ to τ_{ht} as low as that reported by Dubach would imply, according to the argument of Weibel (1973) and Meban (1980), that the blood–gas (tissue) barrier of the avian lung is not highly corrugated; the avian barrier would thus be similar to that of the Etruscan shrew *Suncus etruscus* (Weibel 1972; Gehr *et al.* 1980), where this ratio is only 2.0. The last-mentioned authors and Dubach (1981) explained the low ratio in the shrew and in the birds, respectively, as a result of the lack of connective tissue elements in the blood–gas (tissue) barrier, a structural feature confirmed in our study. However, this ratio ranged from 1.1 to 2.3 in Amphibia and Reptilia, even though connective tissue elements were numerous in their blood–gas (tissue) barriers (Meban 1980).

We cannot explain the discrepancy between Dubach's value and ours for $\bar{\tau}_t$.

(v) *Assumptions made in calculating pulmonary diffusing capacity*

The physical coefficients utilized in this study, i.e. K_{tO_2}, K_{pO_2}, and the oxygen uptake coefficient for whole blood Θ_{O_2}, have been obtained from mammalian tissues, as strictly equivalent coefficients for birds have not been established†. Weibel (1979*b*) and Weibel *et al.* (1981*a*) have questioned the validity of applying the same physical coefficients, particularly

† See the footnote to p. 11.

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that of Θ_{O_2}, to the different taxa of animals and precise values for the morphometric D_{LO_2} of birds will require coefficients for the avian tissues. Nevertheless, comparisons of the specific diffusing capacities at least between different species of birds are valid, even when mammalian coefficients have been used.

The values for the venous haematocrit incorporated in the model were mostly taken from the literature (table 7), except those for the columbiform *Streptopelia decaocto*, which we measured ourselves. Because of the unavailability of data for some of the rarer species, the haematocrit of a closely related species was used wherever possible. It is acknowledged that when several specimens of a species can be obtained, it would be better to measure the haematocrit rather than rely on data from the literature.

The great majority of the work on the morphometry of the mammalian lung has been based on fixation of the lung by infusing the airways at a constant pressure head of 20–25 cm of water above the highest point of the sternum. It was suggested by Weibel *et al.* (1981*b*) that under these conditions the final total volume of the fixed lungs would be about 70–90 % of the total lung capacity. Our avian lungs were fixed by infusing the fixative into the airways at the same head of pressure. As the avian lung is virtually inexpansible, we concluded that the volume of the fixed lung was similar to the volume of the lung in the living bird (see §4*b* (ii)). Although comparisons of the morphometric parameters of the lungs of different classes of vertebrate should ideally be done at identical levels of expansion, under the prevailing conditions it would seem reasonable to compare the morphometric characteristics of the mammalian lung with those of the avian lung.

(vi) *Assumptions underlying the statistical analysis*

The regression analysis described (§2*c* (i)), incorporates a number of assumptions.

First, the fitting of a single line to all the bird data for a particular parameter implies that the various species need not be distinguished from one another, and similarly for the mammals. Because it is obvious from plots of the data that the differences between species are swamped by the differences between birds and mammals and since the main purpose of fitting the regression lines was to compare birds with mammals, it seemed unnecessary to employ more complicated models allowing for differences between species; furthermore, the use of more complex models might disguise the strong relation with body mass that exists for almost all the parameters investigated.

Secondly, log–log models have been utilized throughout the regression analysis and this is justified by the fact that logarithmic transformation stabilizes the variance of the data. Such models also have the advantage that they permit convenient plotting by reducing the spread of the data.

Thirdly, the tests carried out on individual regression lines and on pairs of lines assume that the residuals after fitting the models are normally distributed. No evidence to the contrary was seen in the data plots, and the tests are in any case robust against non-normality.

Fourthly, the fitting methods assume that the variance σ^2 of Z_i is independent of i, that is to say that parameters vary no more at large body masses than at small ones. The transformation to logarithms makes this more plausible, since logs show less variation than untransformed values, and again, no evidence against this assumption can be seen in the plots of the data.

Finally, an assumption peculiar to the mammalian data was touched on in §2*c* (i). Regression

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analysis, namely that where a data point $(\bar{w}_i, \bar{y}_i)$ is used, the unknown $w_{i_1}, \ldots, w_{i_k}$ do not vary much by comparison with the full range of body masses. This assumption is necessitated by the log transform, because the weighted least-squares method would be exactly correct (provided the basic model holds, of course), if the values of

$$\frac{1}{k}(\log w_{i_1} + \log w_{i_2} + \ldots + \log w_{i_k}) \quad \text{and} \quad \frac{1}{k}(\log y_{i_1} + \log y_{i_2} + \ldots + \log y_{i_k})$$

were available; in effect, $\log \bar{w}_i$ and $\log \bar{y}_i$ are being used as approximations to these values and the approximations will be good provided the unknown $w_{i_1}, \ldots, w_{i_k}$ (and hence the unknown $y_{i_1}, \ldots, y_{i_k}$) do not vary much.

(c) *The structural basis for the efficiency of the avian respiratory system*

Lasiewski & Calder (1971) and Schmidt-Nielsen (1975*a*) have pointed out that the resting ventilation rate of birds is lower than that of mammals; on the other hand the resting metabolic rates of non-passerine birds are similar to those of mammals (Lasiewski & Dawson 1967). They also noted that, if the resting oxygen consumption is similar in non-passerine birds and mammals and yet the ventilation rate is lower in the birds, then the birds must be extracting a greater proportion of the oxygen in the respired air than the mammals. This is confirmed by the levels of oxygen in the end-expired air, which fall to about 15% in birds and only about 17% in mammals (Schmidt-Nielsen 1975*a*). On the basis of such observations the avian lung has been characterized as the outstandingly efficient gas-exchange system among the air-breathing vertebrates (Duncker 1971*b*; Lasiewski & Calder 1971; Weibel 1973). This greater efficiency of the avian pulmonary system as compared with that of mammals becomes obvious at high altitudes.

Can this apparent superiority of the avian over the mammalian lung be attributed to the morphometric parameters of the avian lung? It will be seen that only one parameter, τ_{hp}, very strongly favours the mammals. Another parameter, τ_{ht}, very strongly favours the birds; S_t and V_c also favour the birds. It is evident that on balance these morphometric parameters are substantially advantageous to the birds. Predictably, therefore, the total morphometric D_{LO_2} is better in birds than in mammals of similar body mass. However, as discussed in §4*b* there are problems in the morphometric estimation of τ_{hp}. In two species, the measurements reported by Dubach (1981) were very much lower than ours. It is not yet possible to say whether Dubach's values for τ_{hp} are underestimates or ours are overestimates. However, if the latter should prove to be the case, the balance of morphometric parameters will shift dramatically in favour of birds, leading to an even higher morphometric D_{LO_2} in birds than in mammals. Further work is needed to clarify the estimation of τ_{hp} in birds and hence the comparison of D_{LO_2} in birds and mammals.

Although the morphometric parameters of the lung do contribute, it is necessary to consider what other structural factors might further increase the respiratory superiority of birds over mammals. At least the following four other factors appear to be involved.

(i) *The small diameter of the terminal airways*

As shown in §4*a* (iii), direct measurements of the diameters of the air capillaries agree with estimates of surface density ($S_t V_x^{-1}$) in showing that the air capillaries of birds are very much smaller in diameter (a range of 3–10 μm) than the alveoli of even the smallest mammals (about

35 μm in the shrew). This should give birds a much more favourable driving force for oxygen than mammals.

(ii) *The cross-current relation of parabronchial gas and blood*

Pulmonary arterial blood approaches the parabronchus essentially at right angles to the bulk gas which is moving along the parabronchial lumen in a continuous unidirectional flow. This cross-current relationship was established experimentally by Scheid & Piiper (1972) and confirmed anatomically by Abdalla & King (1975). This arrangement enables the p_{CO_2} in end-expired air to be higher than the p_{CO_2} in arterial blood (Scheid & Piiper 1970; Piiper & Scheid 1977); such relations of p_{CO_2} are impossible in the 'uniform pool' of the mammalian lung. Thus the avian lung has a higher efficiency of gas exchange, as less ventilation is needed to achieve a certain arterialization, and with equal ventilation a higher degree of arterialization is obtained (Scheid & Piiper 1970). This cross-current relationship may be one of the most important structural factors in the respiratory superiority of birds over mammals.

(iii) *The counter-current relation of air capillary gas and blood*

In the avian exchange tissue, gas diffuses centrifugally from the parabronchial lumen, whereas the incoming blood passes centripetally from the periphery of the exchange tissue towards the parabronchial lumen (Abdalla & King 1975). Scheid & Piiper (1972) regarded this as an auxiliary counter-current relationship between the blood in the blood capillaries and the gas diffusing in the air capillaries. Later, Scheid (1979) pointed out that there is convective flow in the blood capillary only, so that this is not a true counter-current system. Presumably, however, it enhances the efficiency of the avian respiratory system.

(iv) *The air sacs*

The air sacs function as bellows, to provide the tidal air-flow. They make possible the continuous unidirectional suffusion of air through the parabronchi of the paleopulmo, as opposed to the in-and-out tidal flow through the blind-ending bronchial tree of mammals. The air-sac system minimizes the effect of dead space, by limiting it to the tracheal dead space alone (Lasiewski & Calder 1971). The air sacs therefore promote the respiratory efficiency of birds.

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Appendix

(a) *Pulmonary morphometric analysis*

(i) *Volume density*

The volume densities of the main components of the lung and those of the exchange tissue were estimated by point-counting using a graticule for the former (figure 12) and an overlay grid for the latter (figure 13). The principle is essentially that the points falling on each component relative to the total number of points in the test system gives the volume density (volume proportion, V_V) of the component. Thus for a component (a)

$$\rho_{Pa} = V_{Va},$$

where ρ_P is the point density. The absolute volumes can be calculated from the volume of the reference space (V), in this case the lung or the exchange tissue. Thus for component (a):

$$V_a = V_{Va} \times V.$$

(ii) *Surface density and surface area*

The surface density (S_V) of the components of the lung was estimated by intersection counting on electron micrographs (figures 13 and 15). Thus

$$S_V = 2I/L,$$

where I is the number of intersections with the test system and L is the total length of the test system. The surface area (S) was calculated from the reference volume, i.e. the exchange tissue (V_x). Thus for a component (a):

$$S_a = S_{Va} \times V_x.$$

(iii) *Harmonic mean thickness*

The harmonic mean thicknesses of the tissue barrier (τ_{ht}) and plasma layer (τ_{hp}) were estimated by intercept length measurement along the test system (figures 13 and 16). Thus

$$\tau_{ht} = \tfrac{2}{3}[n/\Sigma(1/L)]\,M,$$

where n is the number of intercepts measured, $\Sigma(1/L)$ the sum of the reciprocals of the intercept lengths and M is the final magnification. The minimum harmonic mean thickness was calculated from about 50 of the shortest random intercepts.

(iv) *Arithmetic mean thickness*

The arithmetic mean thickness of the tissue barrier was estimated by counting the point-hits and intersections on the test grid (figure 14). Thus

$$\bar{\tau}_t = z \cdot P/2(N_{en} + N_{ep}),$$

where z is the length of one of the test lines in real units, P is the number of points falling on the tissue barrier, N_{en} is the number of intersections of the test lines with the endothelium of the tissue barrier and N_{ep} is the number of intersections with the epithelium of the tissue barrier.

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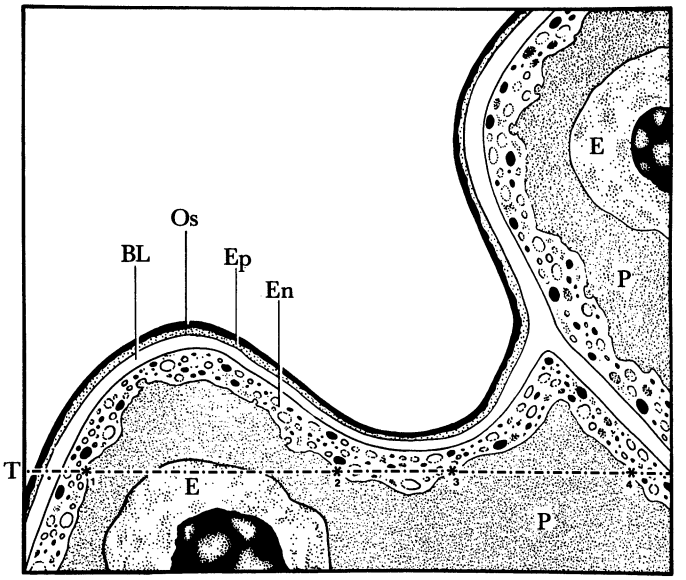

FIGURE 15. Diagram showing the principles of defining and counting intersections to estimate the surface area of the blood–gas (tissue) barrier. Intersection number 1 was counted, as it falls along a test line which is running from air to blood. Intersections 2 and 3 were counted because the surfaces there, at right angles to the test line T, are in contact with air and therefore gas exchange could take place at these sites. Intersection 4 was not counted, since the surface at right angles to the test line is blood and therefore gas exchange cannot occur here. The intersections were counted horizontally. Tests showed that counting vertically gave the same results as counting horizontally, thus demonstrating the isotropy of the components of the exchange tissue. Abbreviations: Os, osmiophilic surface layer; Ep, epithelium; Bl, basal lamina; En, endothelium; P, blood plasma; E, red blood cell.

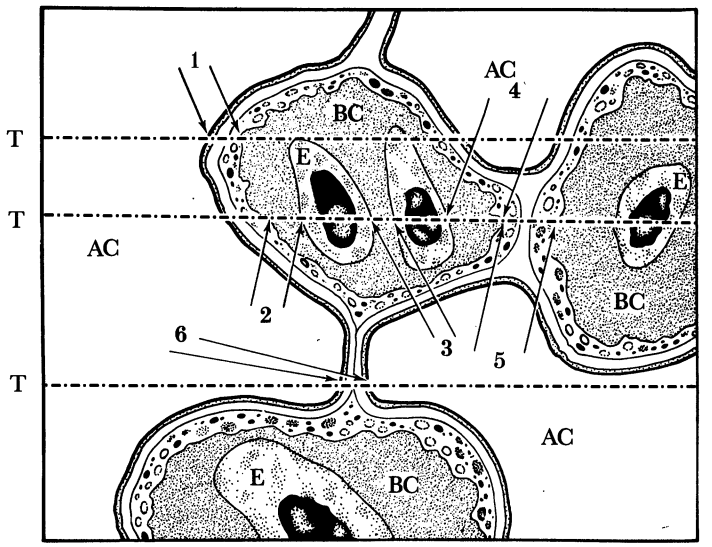

FIGURE 16. Diagram showing the criteria used to define the intercept lengths that were measured in order to estimate the harmonic mean thicknesses of the blood–gas (tissue) barrier (τ_{ht}) and plasma layer (τ_{hp}). The measurements were made horizontally along the lines of the test system, T. Estimation of τ_{ht} required intercepts such as number 1, that was measured along its length from air to blood (the path through which oxygen flows). Intercepts such as 5, which runs from blood to blood, and 6, which runs from air to air, were excluded. Estimation of τ_{hp} required measurement of intercepts such as 2, which runs from the endothelial surface of the blood–gas (tissue) barrier to the surface of a red blood cell. Intercept 4 was excluded as it does not lead to air. Test measurements were made of intercept 3, the gap between red blood cells, but they were found to have no significant effect on the values obtained from intercept 2 and were therefore discontinued. Abbreviations: AC, air capillary; BC, blood capillary; E, red blood cell.

(b) Estimation of the diffusing capacity for oxygen

The model used is that described in detail by Weibel (1970–1). It envisages the air–haemoglobin pathway as essentially comprising the tissue barrier, plasma layer and the erythrocyte. These resistance barriers (to oxygen diffusion) are arranged in series. The diffusing capacity of the tissue barrier and the plasma layer is directly proportional to their surface area and inversely proportional to their thickness. That of the erythrocyte is directly proportional to the pulmonary capillary volume.

(i) *The diffusing capacity of the tissue barrier* (D_{tO_2})

D_{tO_2} is calculated from the surface area of the tissue barrier (S_t), the harmonic mean thickness of the tissue barrier (τ_{ht}) and the oxygen permeation constant through the tissue barrier (K_{tO_2}). Thus

$$D_{tO_2} = S_t K_t / \tau_{ht}.$$

(ii) *The diffusing capacity of the plasma layer* (D_{pO_2})

D_{pO_2} is calculated from the surface area of the plasma layer (S_p), which is estimated as the mean of the surface area of the endothelium (S_c) and that of the erythrocytes (S_e), the harmonic mean thickness of the plasma layer (τ_{hp}) and the oxygen permeation constant through the plasma (K_{pO_2}). Thus

$$D_{pO_2} = S_p K_p / \tau_{hp}.$$

(iii) *The diffusing capacity of the erythrocyte* (D_{eO_2})

D_{eO_2} is calculated from the pulmonary capillary blood volume (V_c) and the rate of oxygen uptake by whole blood(Θ_{O_2}). Thus

$$D_{eO_2} = V_c \Theta_{O_2}.$$

(iv) *The membrane diffusing capacity* (D_{mO_2})

D_{mO_2} was calculated from D_{tO_2} and D_{pO_2}. Thus

$$\frac{1}{D_{mO_2}} = \frac{1}{D_{tO_2}} + \frac{1}{D_{pO_2}}.$$

(v) *The total morphometric pulmonary diffusing capacity* (D_{LO_2})

D_{LO_2} was calculated from the three resistances. Thus

$$\frac{1}{D_{LO_2}} = \frac{1}{D_{tO_2}} + \frac{1}{D_{pO_2}} + \frac{1}{D_{eO_2}}.$$

The diffusing capacity of the plasma layer and the erythrocyte, and hence the diffusing capacity of the membrane and the total diffusing capacity, were calculated as minimum and maximum values from the relevant physical constants, which are themselves the products of the solubility (α) and diffusion (D') coefficients.

(vi) *Units of the physical constants in SI units*

K_{tO_2}: 4.1×10^{-10} cm^2 (s mbar)$^{-1}$; K_{pO_2} min: 4.0×10^{-10} cm^2 (s mbar)$^{-1}$; max: 5.4×10^{-10} cm^2 (s mbar)$^{-1}$; Θ_{O_2} min: 1.13×10^{-2} ml O_2 (ml s mbar)$^{-1}$; max: 3.13×10^{-2} ml O_2 (ml s mbar)$^{-1}$.

The conversion of D_{LO_2} expressed in ml O_2 (min mmHg)$^{-1}$ to ml O_2 (s mbar)$^{-1}$ can be done by multiplying with a constant (1.2501×10^{-2}).

TABLE 10. A COMPARISON OF THE ANATOMICAL DIFFUSING CAPACITY OF THE RED BLOOD CELL (D_{eO_2}) AND THE TOTAL PULMONARY ANATOMICAL DIFFUSING CAPACITY (D_{LO_2}) CALCULATED BY THE ERYTHROCYTE NUCLEATION ADJUSTMENT METHOD OF THE MAMMALIAN OXYGEN UPTAKE COEFFICIENT (Θ_{O_2})[a] WITH THAT OBTAINED BY USING THE AVIAN VALUE FOR Θ_{O_2}[b]

(The units are in ml O_2 s^{-1} $mbar^{-1}$.)

taxon	D_{eO_2}[a]	D_{eO_2}[b]	D_{LO_2}[a]	D_{LO_2}[b]
Anseriformes				
Anas platyrhynchos	0.062	0.1101	0.050	0.1101
Anser anser	0.211	0.3386	0.172	0.2540
Falconiformes				
Falco tinnunculus	0.006	0.0112	0.0048	0.0092
Galliformes				
Gallus gallus	0.041	0.095	0.0318	0.0615
Charadriiformes				
Alca torda	0.038	0.0590	0.0290	0.0417
Cephus carbo	0.058	0.0871	0.0432	0.0620
Larus argentatus	0.033	0.0566	0.0245	0.0412
L. canus	0.012	0.0190	0.0113	0.0157
L. ridibundus	0.011	0.0228	0.0113	0.0161
Columbiformes				
Columba livia	0.025	0.0308	0.0201	0.0244
Streptopelia decaocto	0.014	0.0199	0.0117	0.0166
S. senegalensis	0.006	0.0086	0.0051	0.0069
Psittaciformes				
Melopsittacus undulatus	0.003	0.0043	0.0024	0.0035
Cuculiformes				
Chrysococcyx klaas	0.002	0.0030	0.0016	0.0030
Coliiformes				
Colius striatus	0.003	0.0038	0.0021	0.0030
Piciformes				
Pogoniulus bilineatus	0.0008	0.0013	0.0007	0.0010
Passeriformes				
Amblyospiza albifrons	0.003	0.0055	0.0029	0.0045
Cisticola cantans	0.001	0.0016	0.0009	0.0013
Hirundo fuligula	0.003	0.0040	0.0026	0.0034
Lanius collaris	0.003	0.0040	0.0022	0.0032
Passer domesticus	0.003	0.0045	0.0025	0.0037
Ploceus baglafecht	0.002	0.0038	0.0021	0.0031
Prinia subflava	0.0007	0.0011	0.0006	0.0009
Sturnus vulgaris	0.006	0.0092	0.0051	0.0077
Turdus vulgaris	0.004	0.0058	0.0031	0.0043
T. olivaceus	0.006	0.0086	0.0051	0.0068

[a] The values for D_{eO_2} and D_{LO_2} are the same as those given in table 7, but are included here for ease of comparison with the new values.

[b] The mean of the oxygen uptake coefficients (Θ_{O_2}) of 2.75×10^{-2} ml O_2 s^{-1} $mbar^{-1}$ for the domestic fowl and 2.79 ml O_2 s^{-1} $mbar^{-1}$ for the muscovy duck, as reported by Nguyen Phu *et al.* (1986), was used to recalculate the avian values. The number of specimens examined in each of the species is the same as in table 3.

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(c) Effects on D_{eO_2} and D_{LO_2} of a more recent physical constant

New constants for the rate of oxygen uptake by avian whole blood (Θ_{O_2}) have recently become available (see footnote on p. 11). These values are greater than the adjusted mammalian constants that we used (see §2*b*) to calculate D_{eO_2} and D_{LO_2}. These new constants increase our values for avian D_{eO_2} and D_{LO_2} by mean factors of about 1.60 and 1.51, respectively. Statistical examination has shown ($p < 0.01$) that the regression lines for the birds and the mammals represent distinct populations, but may be assumed to be parallel with a common slope of 0.920. If this assumption is adopted, then for the birds the *y*-intercept corresponding to a body mass of 1 g becomes 1.319×10^{-4} ml O_2 (s mbar)$^{-1}$ or 10.56×10^{-3} (min mmHg)$^{-1}$, and that for the mammals is 0.726×10^{-4} ml O_2 (s mbar)$^{-1}$ or 5.81×10^{-3} (min mmHg)$^{-1}$. Thus D_{LO_2} in birds generally would be about 82% greater than in mammals of similar body mass. Table 10 shows the recalculated values (using the new constants) for avian D_{eO_2} and D_{LO_2}. The recalculated values for avian D_{LO_2} are replotted against mammalian D_{LO_2} in figure 17.

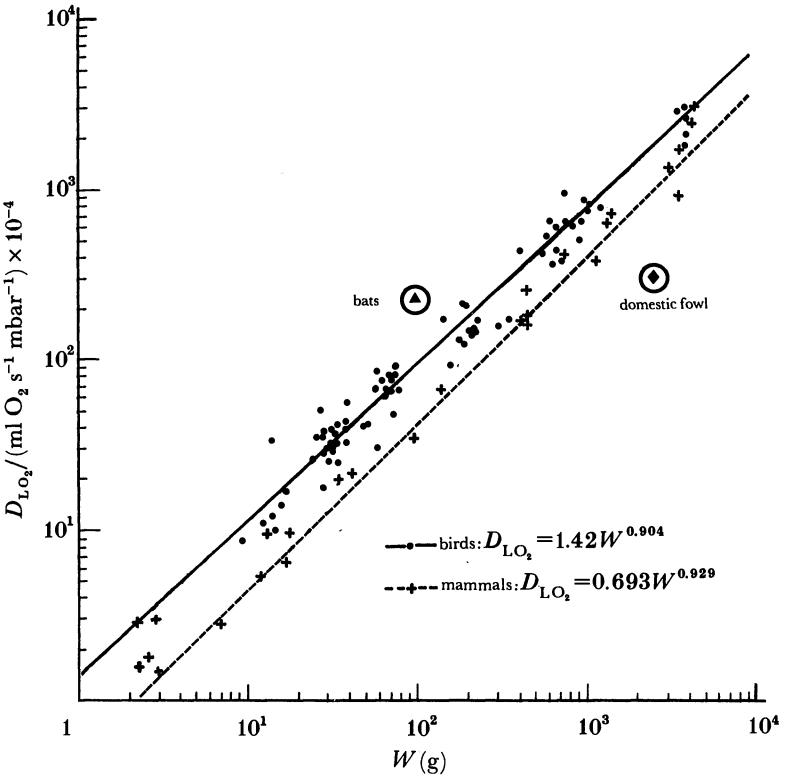

FIGURE 17. Double logarithmic plot of the mean total morphometric pulmonary diffusing capacity (D_{LO_2}) against body mass (W). The values for D_{LO_2} appertain to the combined left and right lungs together. The regression lines are based on the same data points as explained in figure 11. The data points in the avian line have been recalculated using the recently reported constant for oxygen uptake by avian red blood cells (Θ_{O_2}) (see footnote to p. 11). Owing to the higher value for avian Θ_{O_2}, the difference between the two populations is greater than in figure 11. ▲, mean value for the five bats shown in figure 11. ◆, mean value for the three domestic fowls shown in figure 11.

List of abbreviations used

D_{eO_2}	diffusing capacity (conductance) of the erythrocyte for oxygen
D_{LO_2}	total morphometric pulmonary diffusing capacity for oxygen
D_{mO_2}	diffusing capacity of the membrane for oxygen
D_{pO_2}	diffusing capacity of the plasma layer for oxygen
D_{tO_2}	diffusing capacity of the blood–gas (tissue) barrier for oxygen
H_c	pulmonary capillary haematocrit
K_{pO_2}	permeation coefficient of oxygen through blood plasma
K_{tO_2}	permeation coefficient of oxygen through the tissue barrier
S_a	surface area of the epithelium of the air capillaries
S_c	surface area of the endothelium of the blood capillaries
S_e	surface area of the capillary erythrocytes
S_p	surface area of the plasma layer
S_t	surface area of the blood–gas (tissue) barrier
V_a	volume of the air capillaries, or alveoli in the bat lung
V_c	volume of the blood capillaries
V_e	volume of the pulmonary capillary erythrocytes
V_{ec}	volume of the cytoplasm (haemoglobin) in the pulmonary capillary erythrocytes
V_L	volume of the fixed lung
V_t	volume of the blood–gas (tissue) barrier
V_{tn}	volume of the tissue not involved in gas exchange
V_x	volume of the gas exchange tissue of the lung
W	body mass
Θ_{O_2}	rate of oxygen uptake by whole blood
τ_{hp}	harmonic mean thickness of the plasma layer
τ_{ht}	harmonic mean thickness of the blood–gas (tissue) barrier
τ_{ht} (min)	minimum harmonic mean thickness of the blood–gas (tissue) barrier
$\bar{\tau}t$	arithmetic mean thickness of the blood–gas (tissue) barrier

Note added in proof (18 *September* 1989). After this paper was accepted for publication we became aware that, subsequent to our preliminary reports (Maina & Settle (1982) and Maina & King (1984)), a morphometric comparison of the lungs of mammals, reptiles and birds had been published in 1985 Duncker & Güntert. This study was based on a series of avian species somewhat different from ours. The values for avian lung volume, exchange surface area, harmonic mean thickness of the (tissue) barrier and pulmonary capillary blood volume agreed well with ours. However, Duncker & Güntert did not include the morphometric diffusing capacity of the avian lung or blood–gas (tissue) barrier and determined instead the 'anatomical diffusing factor'. This parameter involves the blood–gas tissue barrier but takes no account of the plasma layer or capillary blood volume, although the latter is acknowledged to be a major factor in the functional capacity of the avian lung. Despite the uncertainties of estimating the total morphometric diffusing capacity of the lung, it nevertheless remains the most comprehensive indicator of the anatomical potential of the lung for gas exchange. If required, the anatomical diffusing factor can be calculated from the data in our tables.

Reference

Duncker, H. R. & Güntert, M. 1985 In *BIONA–Report* 3 (ed. W. Nachtigall) (*Publ. Acad. Wiss. Lit. Mainz*). Stuttgart: Fischer Verlag.

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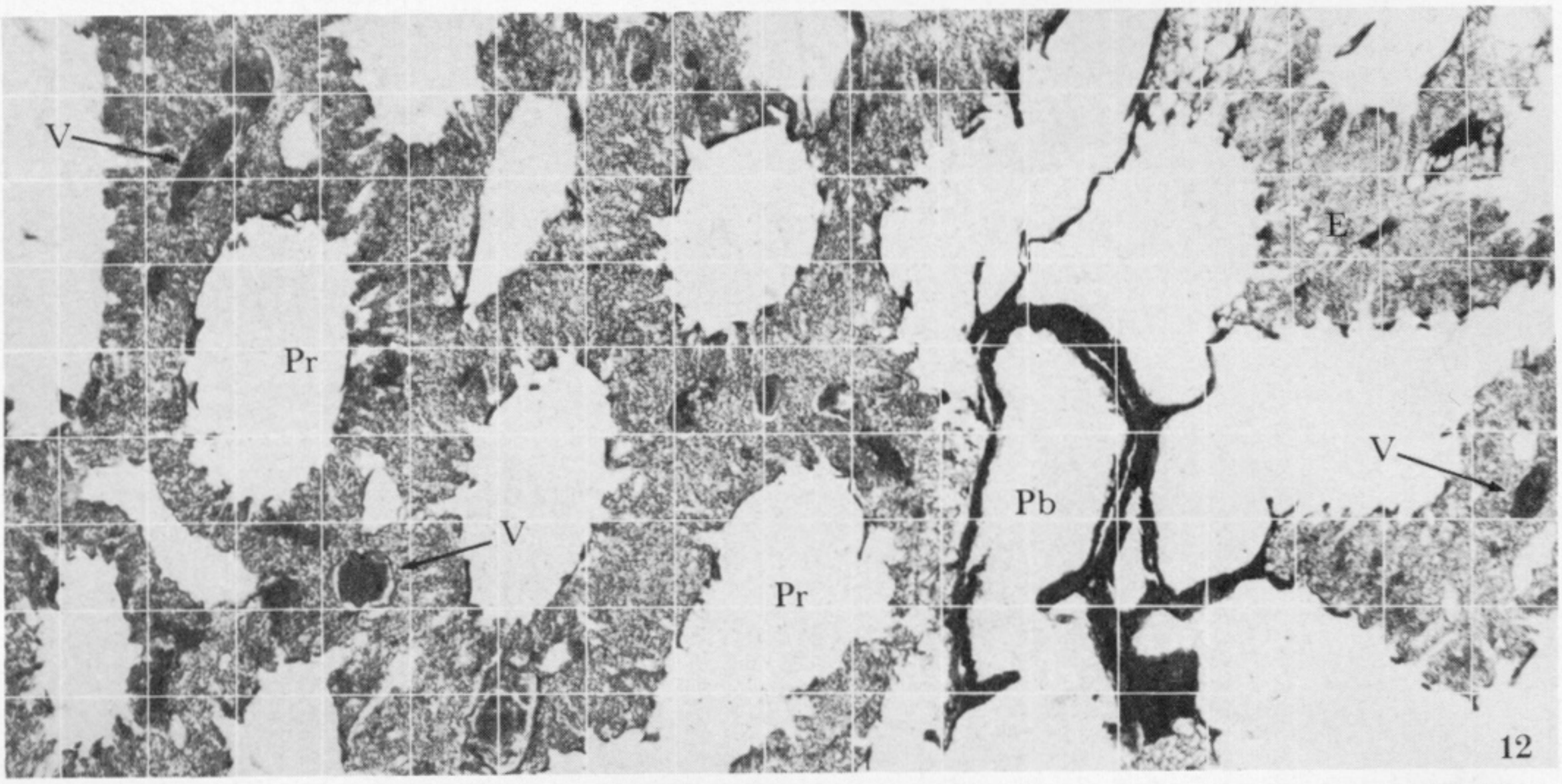
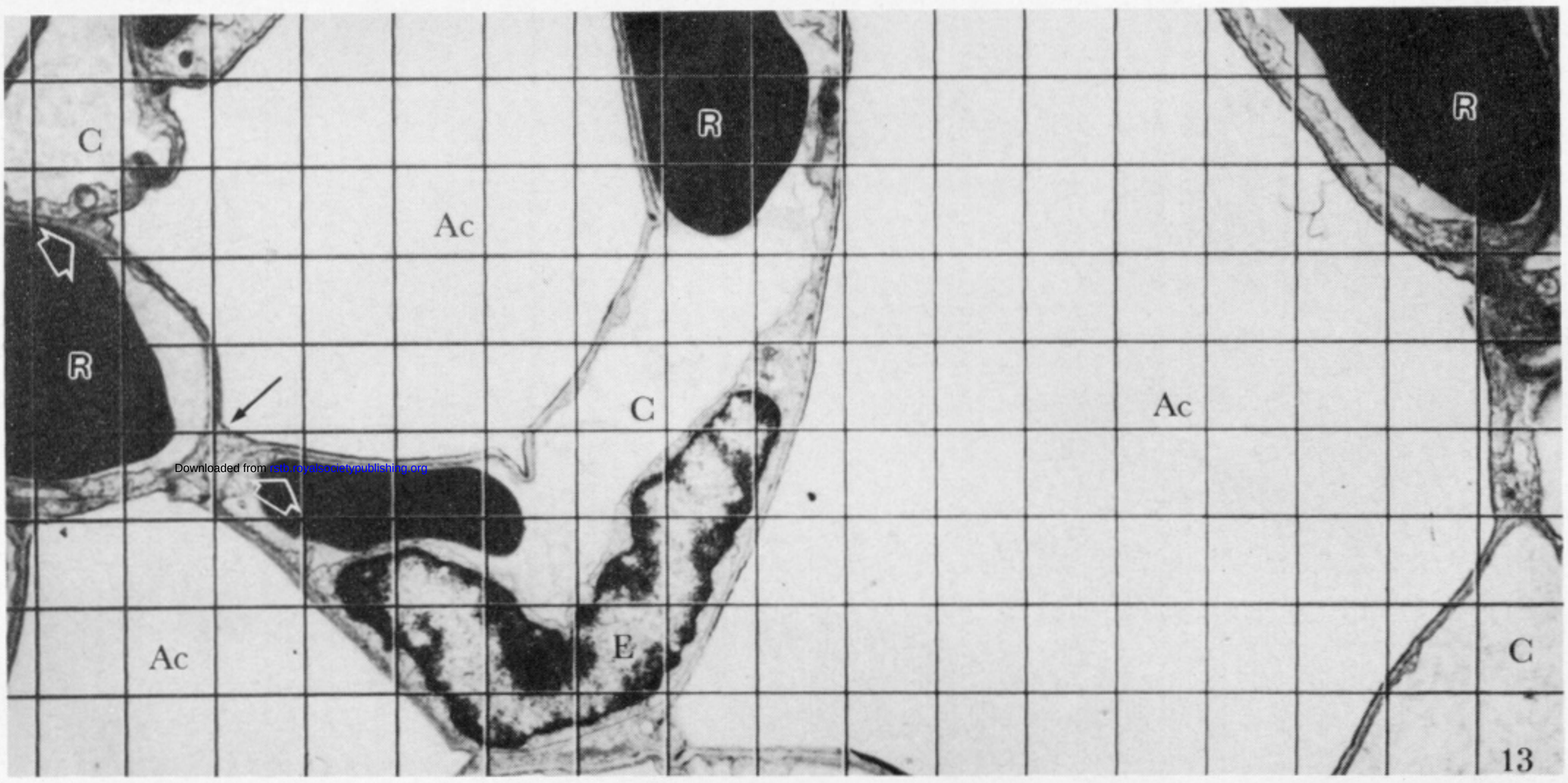
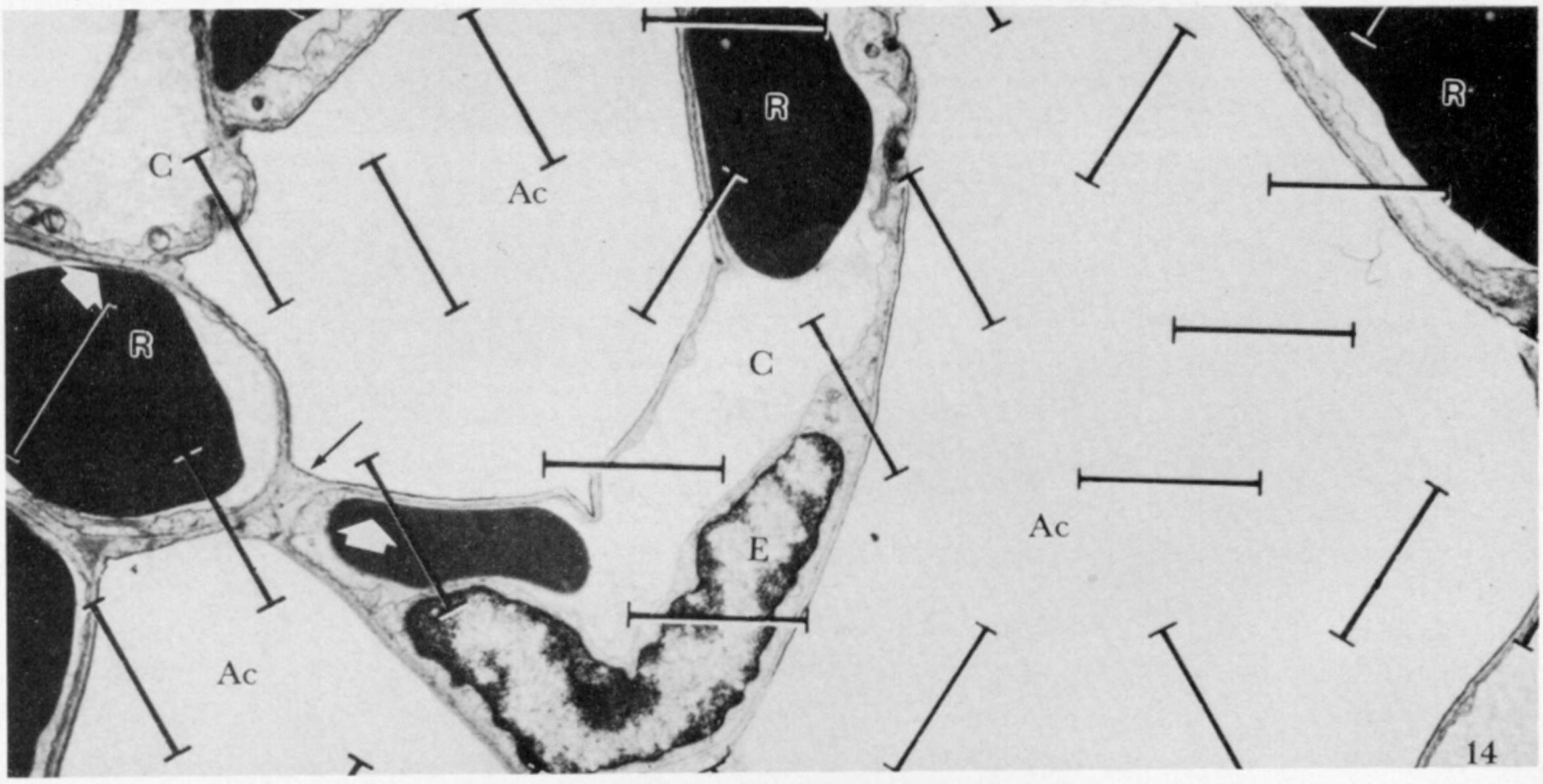
FIGURES 1–3. For description see opposite.







FIGURES 12–14. For description see opposite.