J. Anat. (1990), **172**, pp. 129–148
With 12 figures
Printed in Great Britain

A morphological and morphometric study of the prosimian lung: the lesser bushbaby *Galago senegalensis*

J. N. MAINA

Department of Veterinary Anatomy, University of Nairobi, P.O. Box 30197, *Nairobi, Kenya*

(*Accepted* 29 *March* 1990)

INTRODUCTION

Among mammals, it is only in the order Primate that the extant members in fair measure present graded features approximating to the stages of the evolution from the early ancestral (prosimian) primates through to anthropoid apes and man (Huxley, 1863; Clark, 1962, 1970). The primates hence constitute a remarkably heterogeneous and variably specialised taxon exhibiting a notable range of body size and differing modes of life (Heglund, 1985). Classification of the primates attracts great attention due to its relevance to the evolution of man (Charles-Dominique, 1970). The prosimians which include the lemurs, bushbabies and tarsiers are regarded behaviourally, anatomically and physiologically to be the most primitive living primates (Szalay, 1968; Charles-Dominique, 1970, 1978; Bourliere, 1974) and exhibit many unique structural and functional features which, when viewed comparatively, illustrate the primate phylogeny (Napier & Walker, 1967). Studies of the prosimian biology, however, only received interest in the relatively recent past (Doyle & Martin, 1974; Martin, 1978; Stevens, Edgerton, Haines & Meyer, 1981). The present studies have illustrated that this group is in some respects functionally and structurally unique among the primates. The basal metabolic rate (BMR), for example, has been shown to be lower in the prosimians (Muller, 1979, 1985) than in the simian species, where the BMR is close to, or higher than, that predicted from body mass (Bruhn, 1934; Malinov & Wagner, 1966; Morrison & Middleton, 1967; Nakayama *et al.* 1971). Body temperature in the simiae is generally 1° to 2 °C above that of most prosimian species (Muller, 1985). Heat exposure was observed to cause great elevation of the respiratory frequency in the greater bushbaby (*Galago crassicaudatus*) than in the baboon (Hiley, 1976) and, in the same study, water loss through the skin in the bushbaby was found to be relatively very low. The response speed of the rhesus monkey was found to be by far greater than that of the prosimians (Ehrlich, 1968*a*, *b*). Morphologically the bushbabies have an atypically well-developed rete mirabile in the limbs for counter-current heat exchange and a thick woolly cover (Whittow *et al.* 1977).

The lesser bushbaby (*Galago senegalensis*), the subject of this study, is a small member of the family Lorisidae. It is the most populous primate in Africa (Haines, 1982) and adapts well to maintenance in captivity and to the rigours of experimental manipulation (Stevens *et al.* 1981). Despite these favourable features, the potential of the bushbaby as an experimental primate model for biomedical research has not been well exploited (Stevens *et al.* 1981; Haines, 1982). The main contributing factor may be due to the paucity of published detail on the morphology of these elusive, habitually arboreal and nocturnal animals compared to, for example, the more easily accessible New World and Old World monkeys and the anthropoid apes which are more

frequently used as animal models for human studies. In spite of the assumed closeness between man and the other simians, it is becoming evident that the fact that two groups of animals are systematically placed in the same higher category is by itself no guarantee that a particular system under investigation is an appropriate model for a human system, as is apparent from accounts by Stevens *et al.* (1981) and Haines (1982). The prosimians, for example, in general have a well-developed appendix which is absent in the monkeys and present in man. These differences have apparently arisen from the differing extents in the evolution and adaptations that the various primate groups have undergone (Clark, 1970). The objectives of the present study were as follows. Firstly, to describe the morphology of the lung of the lesser bushbaby *Galago senegalensis*, which has hitherto not been investigated. Secondly, to establish the morphometric features of the structural components of the lung in an attempt to gain an insight into its anatomical gas exchange potential. Thirdly, to compare such data with those from other primates that have been investigated to a similar extent and then to correlate them with the mode of life that this bushbaby leads. Fourthly, to evaluate whether the lung of the lesser bushbaby could be, structurally, an appropriate organ model for biomedical pulmonary studies.

MATERIALS AND METHODS

Five mature specimens of the lesser bushbaby *Galago senegalensis* were procured from a breeding stock of a colony maintained by the Institute of Primate Research, Ololua Forest, Nairobi. In the laboratory, they were killed by intraperitoneal injection with Euthatal (May & Baker) and weighed. The trachea was exposed after the resection of the ventral neck muscles and cannulated. An incision was made caudal to the last rib exposing the diaphragm which was carefully punctured on both sides of the mediastinum creating a pneumothorax. The lungs were subsequently fixed by intratracheal instillation with 2·3% glutaraldehyde buffered in sodium phosphate (total osmolarity 350 mOsm and pH 7·4) at a pressure head of 25 cm water until no more fixative was seen to flow into the pulmonary airways. A ligature was placed caudal to the cannula to retain the intrapulmonary fixative. The lungs were removed together with the heart, after transecting the sternum, and immersed in fixative. The heart and other adhering extrapulmonary tissues were trimmed off and a further ligature placed at the tracheal bifurcation. The volume of the lung was determined by the weight displacement method (Scherle, 1970).

Sampling

Each of the lobes of the lung, the left cranial, the middle left, the caudal left, the cranial right, the middle right, the caudal right and the accessory was cut transversely into eight approximately equal slices with a sharp blade. Alternately, the slices were chosen for light and electron microscopy.

Light microscopy

The selected slices were cut into smaller pieces technically adequate for processing for light microscopy by standard laboratory techniques. The first satisfactory section was taken from each piece and stained with haematoxylin and eosin. The volume densities of the parenchyma and the non-parenchyma (see below) were determined field by field by point-counting using a quadratic lattice grid etched on a graticule with 100 points, mounted in the eyepiece of a microscope, at a final magnification of $\times 100$. The parenchyma essentially comprised the alveoli and the interalveolar tissue,

including the blood capillaries. These components constituted the gas exchange region of the lung, while the non-respiratory part, the non-parenchyma, was made up of the large air conducting passages up to the terminal bronchioles and the blood vessels larger than capillaries. The volume density (V_v) of these two main components of the lung was arrived at as the ratio of the points falling onto each of the components (P_p) to that in the test system (P_t). Thus for parenchyma (p):

$$V_{vp} = P_p P_t^{-1}. \tag{1}$$

The absolute volumes of these components were calculated from the volume of the lung (VL). Thus for the parenchyma (p):

$$V_p = V_{vp} VL. \tag{2}$$

Electron microscopy

The slices, picked for electron microscopy were diced into small pieces (about 1 mm^3) which were separately processed. This entailed postfixation in 2% osmium tetroxide for 2 hours, block staining in uranyl acetate with maleic acid, followed by dehydration in graded concentrations of ethanol starting at 50% through to absolute and propylene oxide before infiltration and embedding in Epon. A block was picked randomly, from a group derived from each slice, and trimmed to remove any non-parenchymatous structures after which ultrathin sections were cut, counterstained with lead citrate and examined on a Zeiss EM 10 microscope at an accelerating voltage of 60 kV.

Five electron micrographs were taken at a primary magnification of × 1600 from a predetermined corner of a grid square, to avoid bias. Where the defined corner, the top right hand corner, fell entirely in the alveolar lumen, such blanks were recorded and substituted in the final calculation. For each specimen 140 negatives were taken. These were enlarged by a factor of 3·5 giving a final magnification of × 5600. A simple square lattice test system (A – 100) of Weibel (1979) was superimposed and printed onto the electron micrographs for analysis.

The volume densities of the components of the parenchyma, namely the alveoli, the blood capillaries and the tissue of the interalveolar septum, were determined by point-counting and their absolute values calculated from the volume of the parenchyma (eq. 2). For the alveoli (a), for example, the volume density (V_v) was the ratio of the points falling onto the alveoli (P_a) against those in the whole of the test system (P_t). Thus:

$$V_{va} = P_a P_t^{-1}. \tag{3}$$

The absolute volume of the alveoli (V_a) was calculated from its volume density V_{va} and the volume of the parenchyma (V_p). Thus:

$$V_a = V_{va} V_p. \tag{4}$$

The surface densities of the alveoli, the blood-gas (tissue) barrier, the capillary endothelium, and the red blood cells were determined by intersection counting. The surface density of the alveoli (S_{va}) was, for example, calculated from the alveolar intersections (I), and the total length of the test system in real units (Lt) i.e. after adjustment for magnification. Thus:

$$S_{va} = 2I_a Lt^{-1}. \tag{5}$$

The surface areas were calculated from the surface density and the volume of the parenchyma (V_p). Thus for the alveolus:

$$S_a = S_{va} V_p. \tag{6}$$

The harmonic mean thicknesses of the blood-gas (tissue) barrier and the plasma layer were calculated by intercept length measurement using a logarithmic scale. For the tissue barrier, for example, the harmonic mean thickness (τh_t) was computed from the total number of intercepts (n), the sum of the reciprocals of the intercepts ($\Sigma 1/L$) and the final magnification (M). Thus:

$$\tau h_t = \left(n/\Sigma\frac{1}{L}\right)M^{-1}. \tag{7}$$

The diffusing capacities of the tissue barrier (Dt_{O_2}) and the plasma layer (Dp_{O_2}) were estimated from their respective surface areas (S), harmonic mean thicknesses (τh) and the oxygen permeation constant (K). The diffusing capacity of a barrier (D) is directly proportional to the surface area and inversely proportional to the thickness of a barrier. Thus, the diffusing capacity of the blood-gas (tissue) barrier to oxygen (Dt_{O_2}) was determined as follows:

$$Dt_{O_2} = Kt_{O_2}\frac{St}{\tau h_t}. \tag{8}$$

As the plasma layer is sandwiched between the capillary endothelium and the red blood cell membrane, the surface area of the plasma is estimated as the mean of its two boundaries, i.e. that of the endothelium (Sc) and the erythrocyte (Se). Thus, the diffusing capacity of the plasma layer (Dp_{O_2}) was determined as follows:

$$Dp_{O_2} = Kp_{O_2}\frac{Sc+Se}{2\tau h_p}. \tag{9}$$

The diffusing capacity of the red blood cells (De_{O_2}) was calculated from the volume of the pulmonary capillary blood (V_c) and the oxygen uptake coefficient by the whole blood (θ_{O_2}). A mean venous haemotocrit of 49% for a male and a female specimen of *Galago senegalensis*, reported by Stevens *et al.* (1981), was adopted in the calculation. Thus:

$$De_{O_2} = \theta_{O_2} V_c. \tag{10}$$

The membrane diffusing capacity (Dm_{O_2}) and the total anatomical pulmonary diffusing capacity (DL_{O_2}) were estimated from the relevant diffusing capacities of the components of the air-haemoglobin pathway, namely Dt_{O_2}, Dp_{O_2} and De_{O_2}. Thus:

$$\frac{1}{Dm_{O_2}} = \frac{1}{Dt_{O_2}} + \frac{1}{Dp_{O_2}} \tag{11}$$

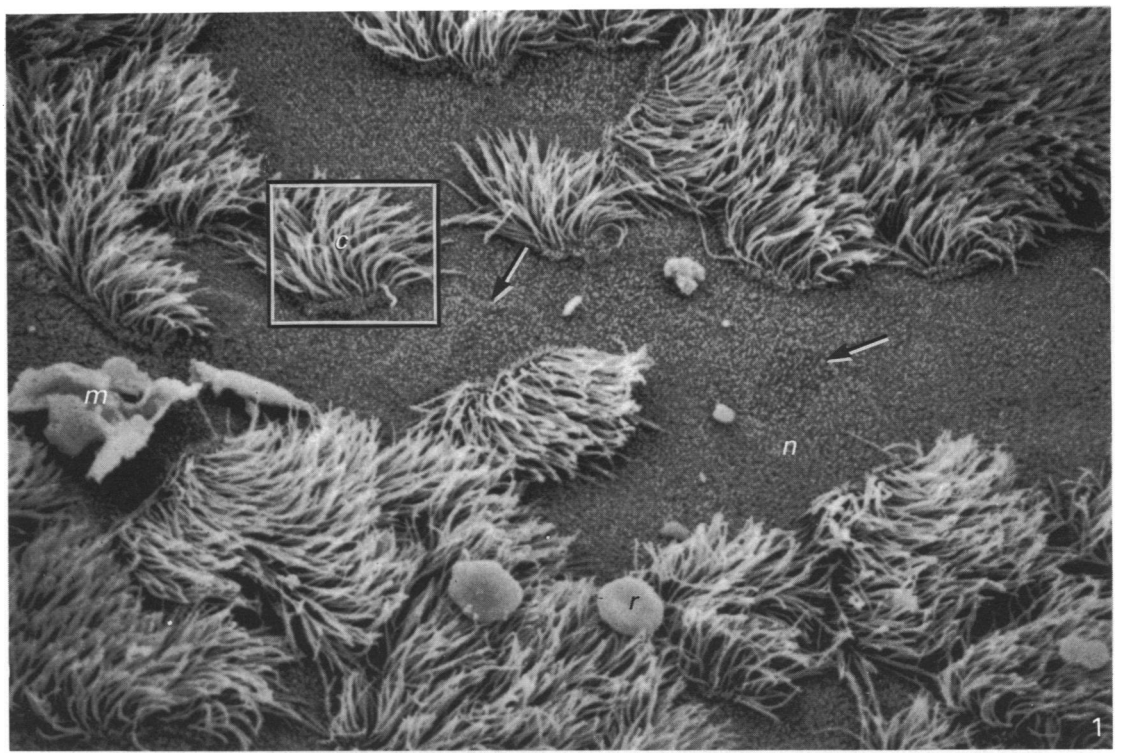
and

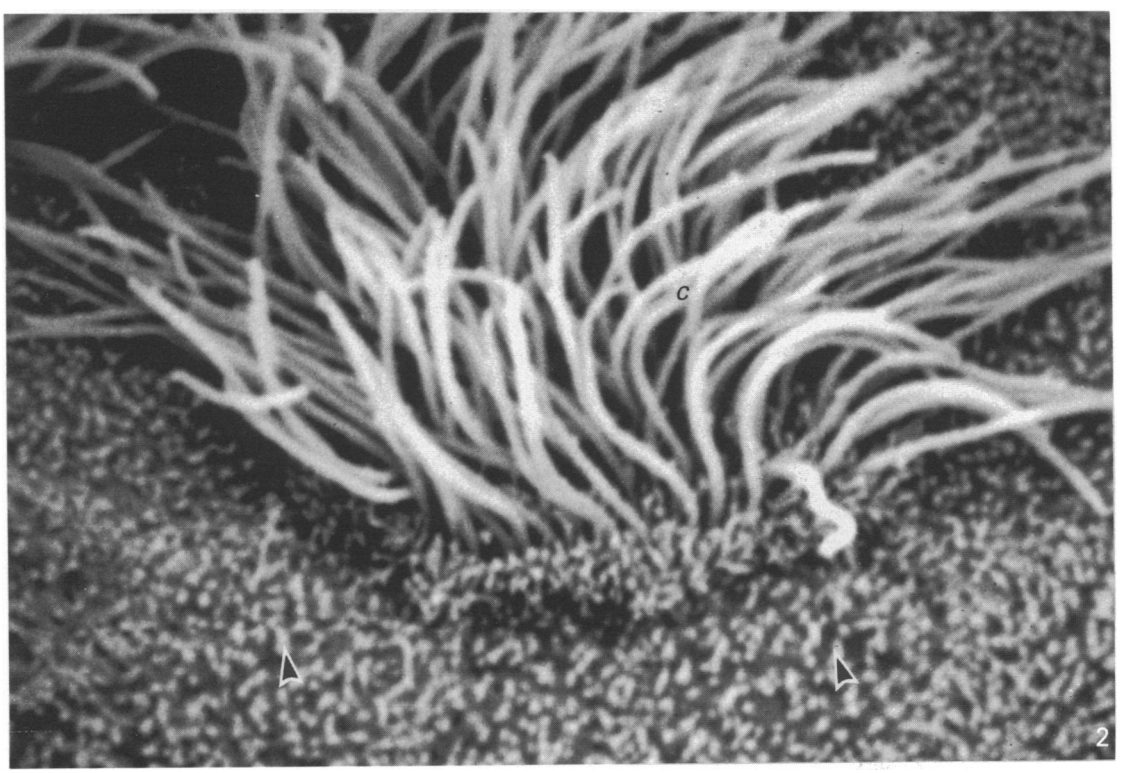
$$\frac{1}{DL_{O_2}} = \frac{1}{Dt_{O_2}} + \frac{1}{Dp_{O_2}} + \frac{1}{De_{O_2}}. \tag{12}$$

To facilitate meaningful quantitative comparisons, the model employed here is essentially that presented by Weibel (1970/71) extensively used in the structural analysis of the mammalian lung (Gehr *et al.* 1981), and earlier utilised on the baboon lung (Maina, 1987) and on the vervet monkey (Maina, 1988).

Fig. 1. Scanning electron micrograph of the surface of the trachea of the lesser bushbaby *Galago senegalensis* showing the epithelium that comprised ciliated cells (*c*) and non-ciliated cells (*n*) that form tracts on the surface. *m*, mucus plug; *r*, aberrant red blood cell; arrows, epithelial cell junctions. ×2230.

Fig. 2. A high power view of the ciliated cell (*c*) in the enclosed area shown in Figure 1. The arrowheads indicate the microvilli that cover the non-ciliated cells. ×9642.


c
m
n
r
1


c
2

Scanning electron microscopy

The pieces of the lung left after processing tissues for light and electron microscopy and parts of the trachea were dehydrated by passing them through graded concentrations of alcohol starting at 70% through to absolute where five daily changes were made. The tissues were subsequently critical point dried in liquid carbon dioxide, mounted on metal chucks, sputter-coated with gold-palladium complex and viewed on ISI-SS60 scanning electron microscope at an accelerating voltage of 11 kV.

RESULTS

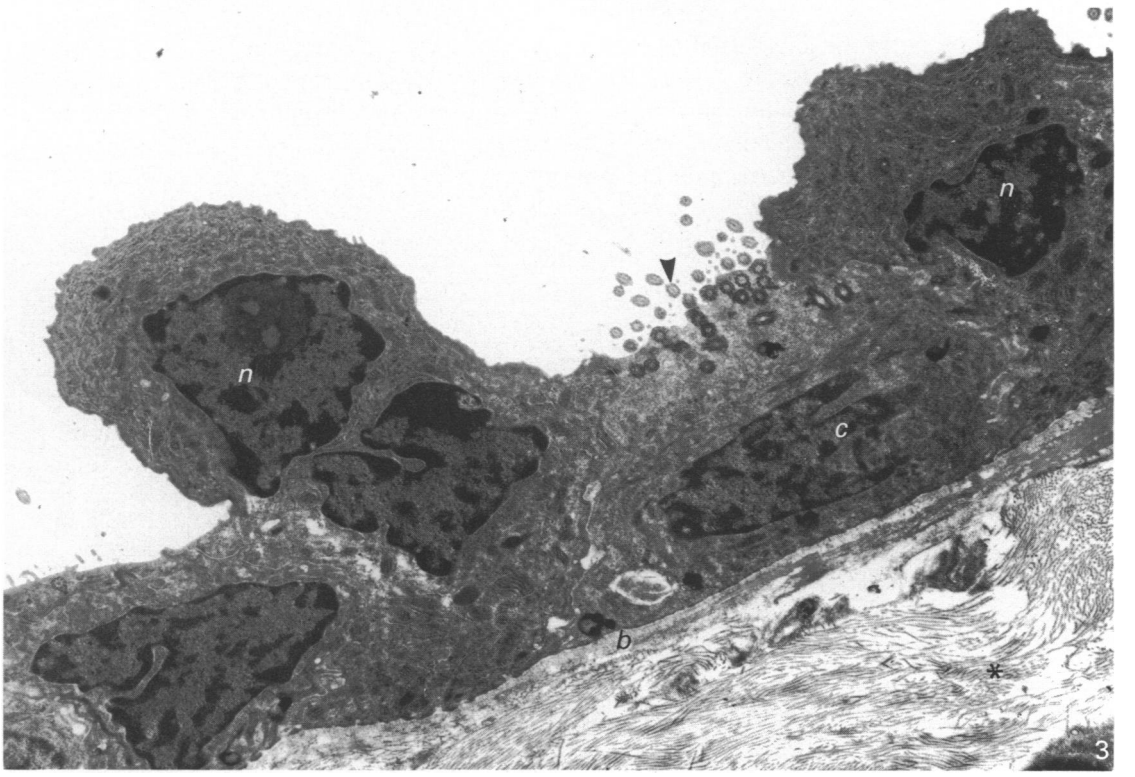
The pulmonary system of the lesser bushbaby comprised a left and right lung. The left lung was made up of three distinct lobes, a cranial, middle and caudal lobe while the right lung had four lobes namely cranial, middle, accessory and caudal lobes. The trachea bifurcated into the left and right principal bronchi that entered the lung at the hilus, giving rise to the lobar bronchi which in turn led to the various bronchiolar generations.

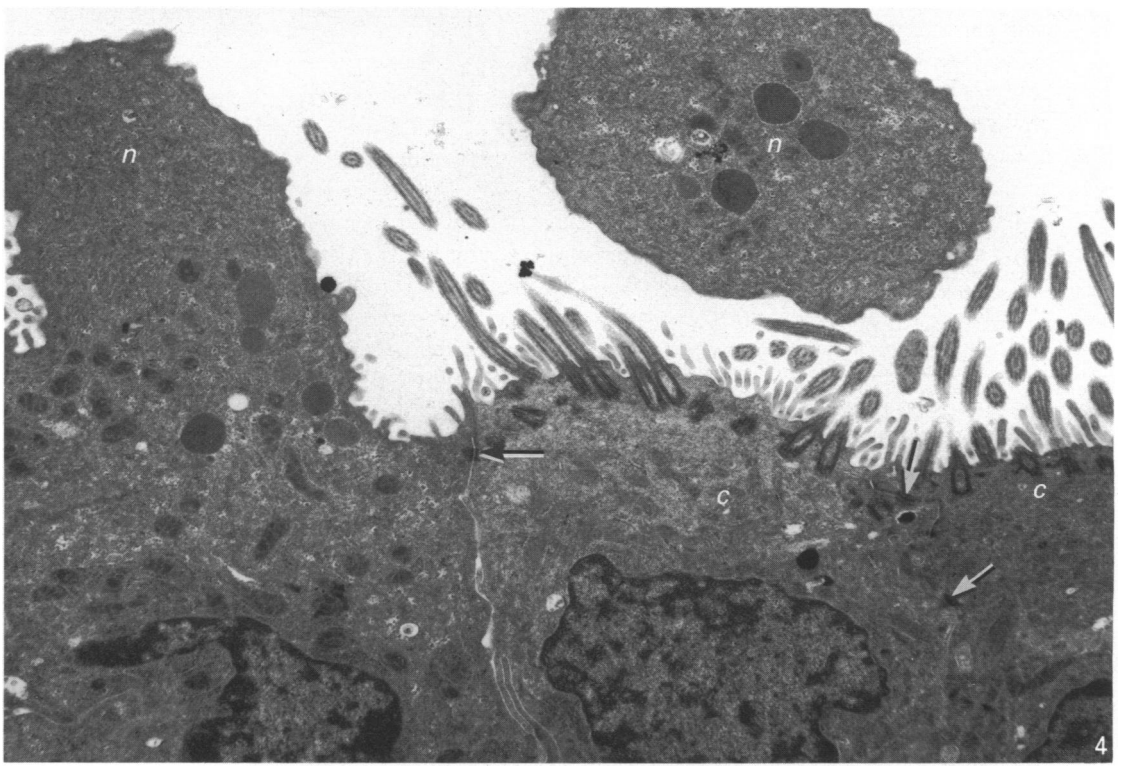
The trachea was lined by ciliated and non-ciliated cells (Figs. 1, 2) interspersed among which were columnar non-ciliated goblet cells (Figs. 3, 4). The non-ciliated cells formed characteristic tracts on the tracheal epithelium (Fig. 1). Ultrastructurally, the columnar cells had an amorphous typically indented nucleus with well-developed chromatin materials. These cells had numerous mitochondria diffusely distributed in the cytoplasm, large electron-dense secretory granules and an abundance of rough endoplasmic reticulum. At the bronchiolar level the epithelial cells formed distinct tight junctions with the adjacent ciliated cells (Figs. 3, 4). The epithelial cells lay on a well-defined basement membrane that comprised elastic tissue, smooth muscle and collagen network (Fig. 3).

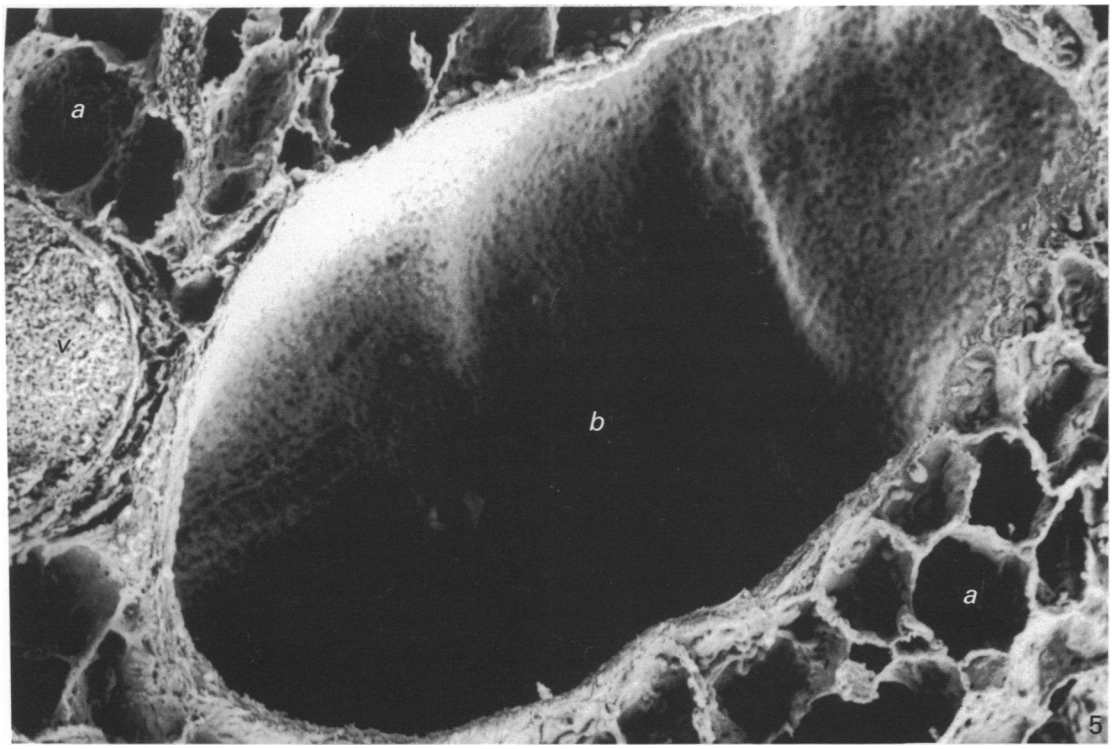
The lung essentially consisted of two regions, with the gas exchange components comprising the parenchyma. The parenchyma was made up of the alveoli, blood capillaries and the tissue of the interalveolar septum while the non-parenchyma consisted of the large air conducting passages and the large blood vessels (Figs. 5, 6). The air and blood conducting systems and the alveoli formed a cohesive system, the alveoli being closely attached to the air conducting passages and blood vessels (Figs. 5–7). Probably this structural continuum is important in the proper phasic contraction and relaxation of the lung with mechanical ventilation. The interalveolar septum was, at various points, perforated by numerous interalveolar pores, the pores of Kohn (Figs. 7, 8). A cluster of alveoli opened into each alveolar duct (Fig. 8). A single alveolus consisted of a lumen delineated by an interalveolar septum (Fig. 9). In the septum were intercalated blood capillaries which bulged into the adjacent alveolar surface (Figs. 9, 10). The alveolar surface was lined by the extensive squamous smooth epithelial cells, the Type I cells (Fig. 11). These cells were deficient in cell organelles.

Fig. 3. A transmission electron micrograph of the bronchiolar epithelium showing the pillar-like non-ciliated cells (*n*) intermixed with the ciliated cells (*c*). The non-ciliated cells have numerous mitochondria, electron-dense bodies and rough endoplasmic reticulum. The epithelial cells lie on a basement membrane (*b*). The subepithelial space (asterisk) consists of collagen and elastic fibres. ×7578.

Fig. 4. A close-up of the epithelial cells showing the non-ciliated cells (*n*) and the ciliated cells (*c*). Both cells contained abundant rough endoplasmic reticulum. Secretory granules, however, only characterised the non-ciliated cells. The ciliated and non-ciliated cells fuse at distinct tight junctions (arrows). ×9778.


n
n
c
b
*
3


n
n
c
c
4



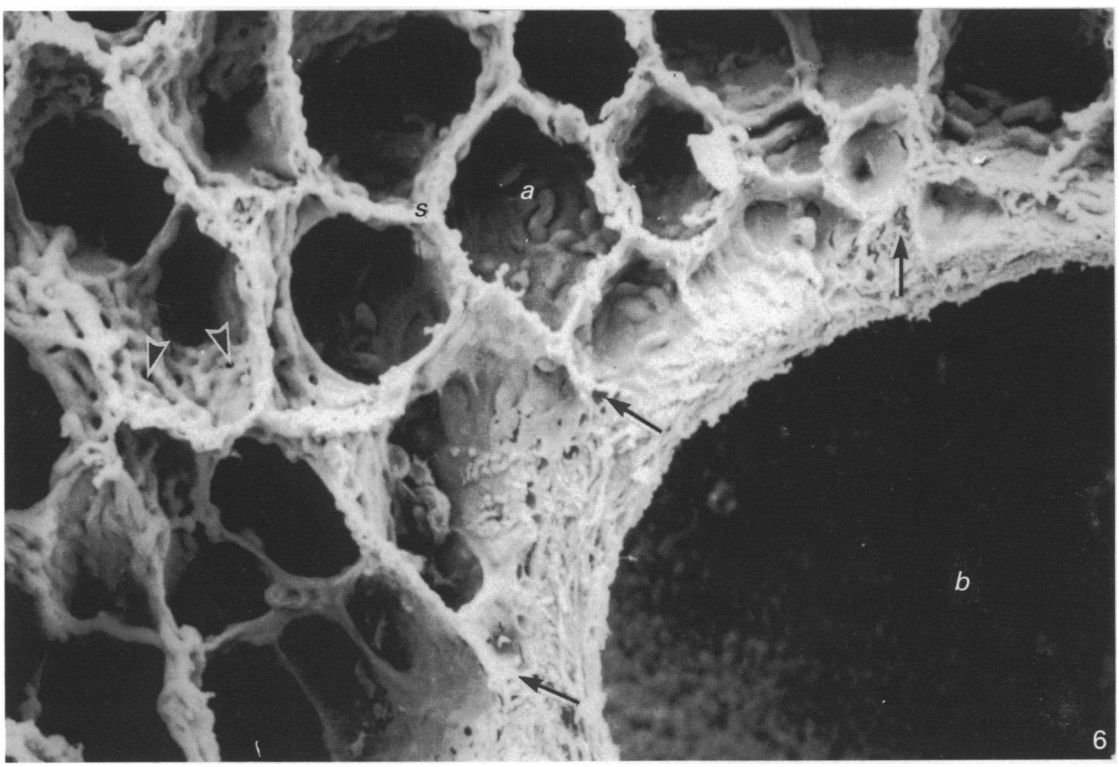
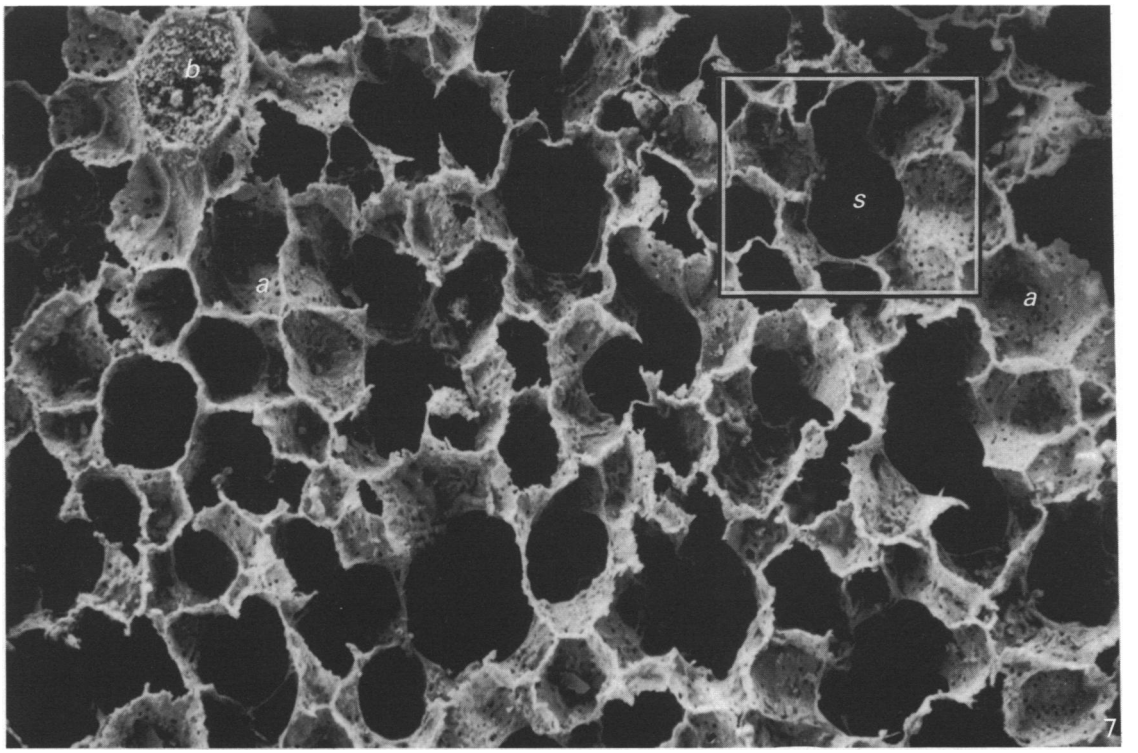


Fig. 5. Scanning electron micrograph showing a terminal bronchiole (*b*) surrounded by alveoli (*a*) and lying adjacent to a blood vessel (*v*). × 162.

Fig. 6. A close-up of the area of fusion between the alveoli (*a*) and the terminal bronchiole (*b*) shown by arrows. *s*, interalveolar septum; arrowheads, interalveolar pores. The intimate union between the alveoli and the air-conducting passages and blood vessels ensures uniform contraction of the lung with mechanical ventilation. × 366.



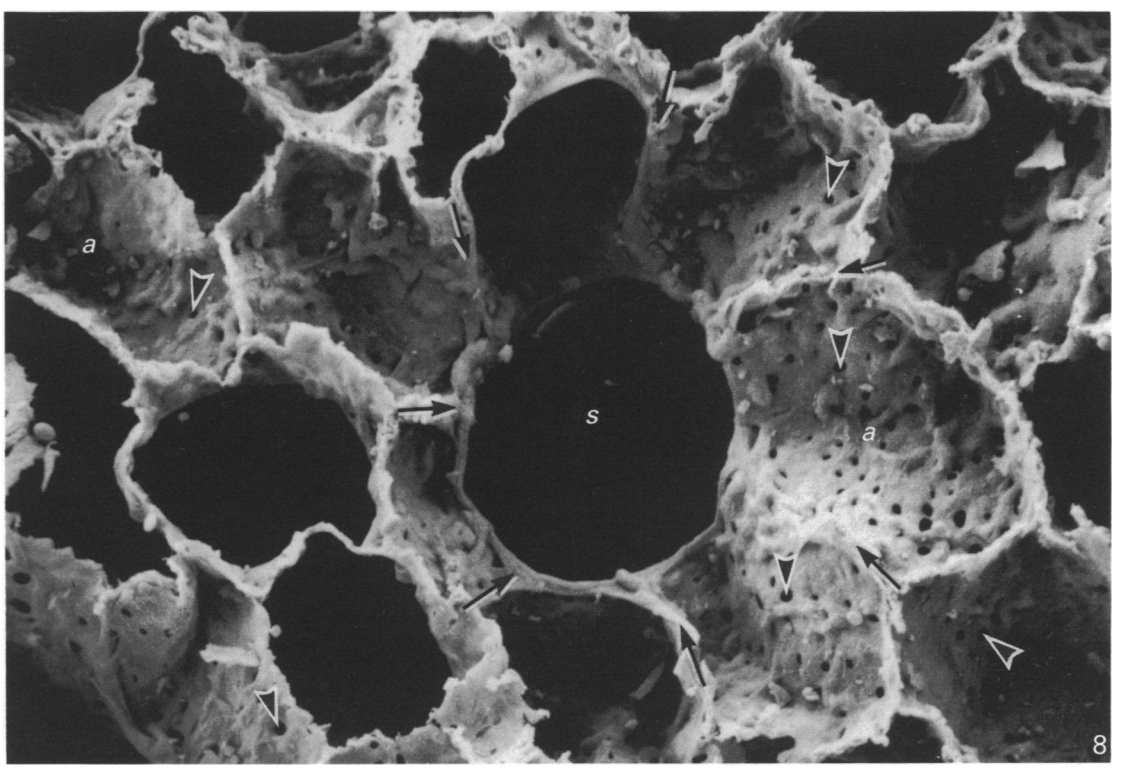


Fig. 7. A scanning electron micrograph showing the parenchyma, the respiratory region of the lung. *a*, alveoli; *b*, blood vessel; *s*, respiratory bronchiole. The interalveolar pores can be seen perforating the septum and interconnecting the alveoli. × 149.

Fig. 8. A close-up of the area enclosed in Figure 7 showing an alveolar duct (*s*) with the alveoli (*a*) opening into it. The arrows show the interalveolar septa and the arrowheads, interalveolar pores. × 370.

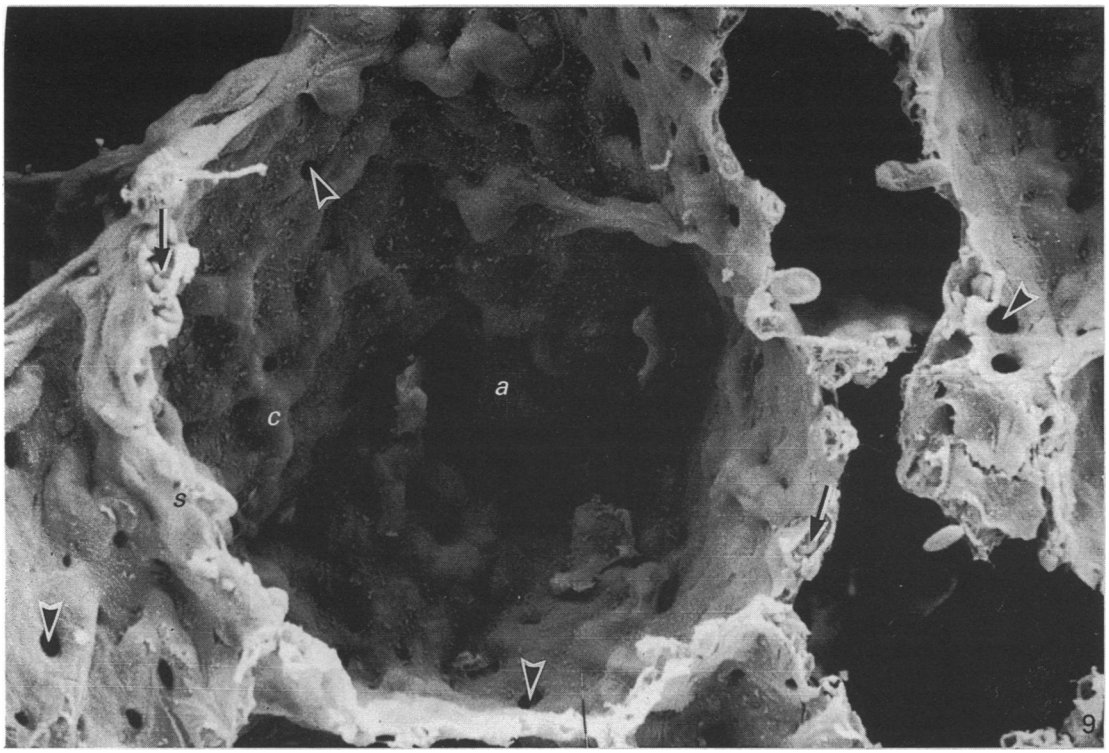
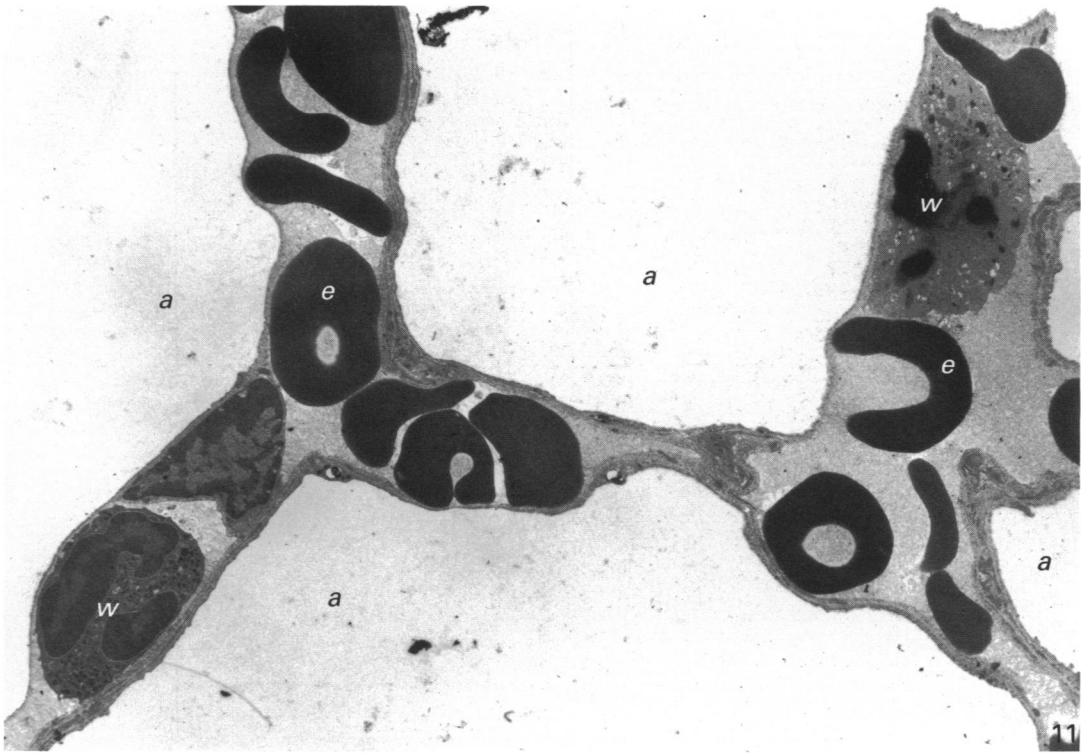


Fig. 9. A scanning electron micrograph of an alveolus (*a*) showing the blood capillaries (*c*) that bulge into its lumen and the interalveolar septum (*s*) that contains the blood capillaries (arrows). The arrowheads show the interalveolar pores. ×955.

Fig. 10. A close-up of the alveolar surface showing the bulging blood capillaries (*c*). Asterisks, interalveolar pores; *s*, interalveolar septum; arrowheads, squamous epithelial cell junctions; these cells line most of the alveolar surface. ×2565.



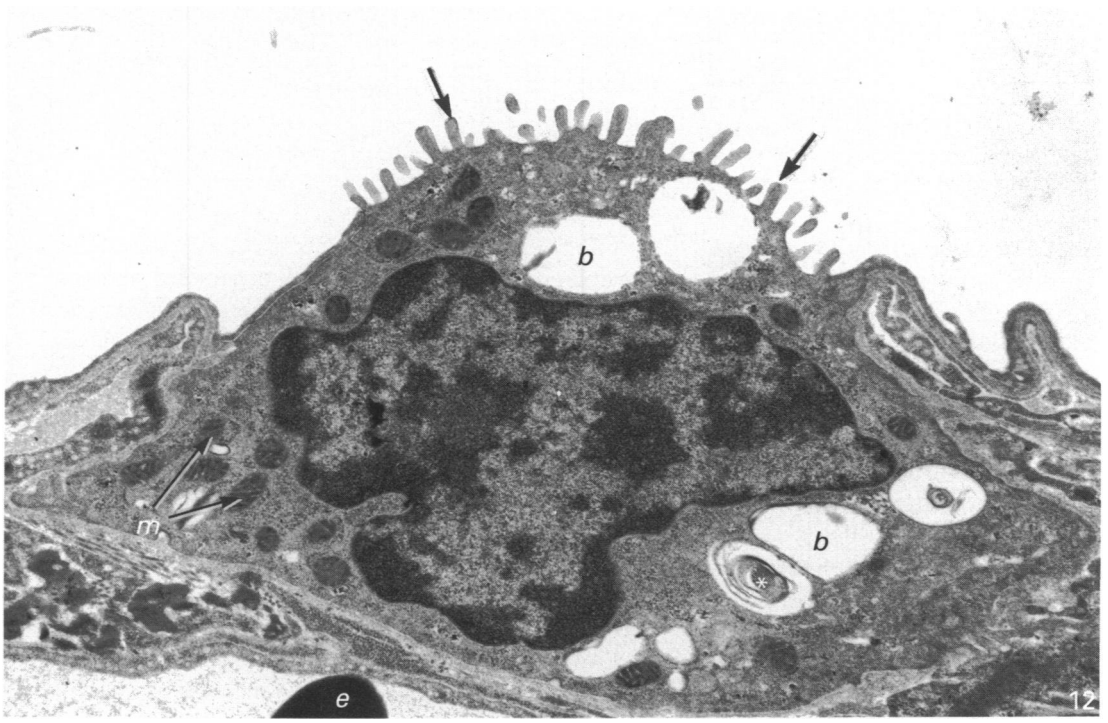


Fig. 11. A transmission electron micrograph of the lung parenchyma showing the alveoli (*a*) and the blood capillaries that contain the red blood cells (*e*). *w*, white blood cell. ×8000.

Fig. 12. A view of the alveolar surface showing a Type II (granular) pneumocyte with microvilli (arrows) on the free surface. These cells are characterised by mitochondria (*m*) and by vacuolated (due to tissue processing) osmiophilic lamellated bodies (*b*). The asterisk shows a lamellated body with the surfactant precursor material still intact. *e*, erythrocyte. ×14500.

Table 1. *Body weight (W) and lung volume (VL) of five specimens of the bushbaby Galago senegalensis with volume densities (%) and absolute volumes of the main components of the lung namely the parenchyma (p) and non-parenchyma (np)*

Specimens	Body weight (W) (g)	Volume of the lung (VL) (cm^3)	Parenchyma (p) (%)	Parenchyma (p) (cm^3)	Non-parenchyma (np) (%)	Non-parenchyma (np) (cm^3)
1	1180	62·8	94·77	59·53	5·23	3·28
2	1080	45·3	89·63	40·60	10·37	4·70
3	1060	59·95	90·54	54·28	9·46	5·67
4	1250	52·6	90·37	47·53	9·63	5·07
5	1020	48·8	91·69	44·75	8·31	4·06
Mean + S.D.	1118 84·48	53·89 6·60	91·40 1·81	49·30 6·77	8·66 1·81	4·56 0·83

Table 2. *Volume densities (%) and absolute volumes (cm^3) of the components of the parenchyma of the lungs of five specimens of the bushbaby Galago senegalensis*

Specimen	Alveoli (%)	Alveoli (cm^3)	Interalveolar tissue (%)	Interalveolar tissue (cm^3)	Blood capillary (%)	Blood capillary (cm^3)	Red cells (%)	Red cells (cm^3)
1	88·77	52·85	3·83	2·28	7·40	4·41	6·55	3·90
2	85·37	34·66	4·78	1·94	9·85	4·00	4·83	1·96
3	85·98	46·67	4·94	2·68	9·08	4·93	5·63	3·06
4	87·07	41·38	4·59	2·18	8·34	3·97	6·80	3·23
5	88·76	39·72	3·69	1·65	7·55	3·38	4·95	2·22
Mean + S.D.	87·19 1·40	43·06 6·22	4·37 0·51	2·15 0·34	8·44 0·93	4·14 0·51	5·75 0·81	2·87 0·70

Occasional granular (cuboidal) pneumocytes, the Type II cells (Fig. 12) that bore stubby microvilli on their free surface and contained numerous cell organelles, such as mitochondria and the characteristic osmiophilic lamellated bodies, were observed. The blood-gas barrier essentially comprised an extremely attenuated Type I cell, a common basal lamina and an endothelial cell.

The results of the morphometric survey are summarised in Tables 1–5. The mean volume density of the parenchyma was 91 % and that of the non-parenchyma about 9 % (Table 1). Of the main components of the parenchyma, the alveoli comprised the greatest proportion (87 %) followed by the blood capillaries (9 %) and the interalveolar tissue (4 %) (Table 2). In general, the surface area of the capillary endothelium (*Se*) exceeded that of the alveolus (*Sa*) which, in turn, was greater than that of the blood-gas (tissue) barrier (*St*) (Table 3). The mean harmonic mean thickness of the blood-gas (tissue) barrier was 0·355 μm while that of the plasma was 0·174 μm (Table 3). Table 4 shows the diffusing capacities of the resistance barriers along the air-haemoglobin pathway, namely that of the tissue barrier (Dt_{O_2}), the membrane (Dm_{O_2}) and the total anatomical diffusing capacity (DL_{O_2}), the most comprehensive estimator of the lung's structural potential for gas exchange. The mean Dt_{O_2} in the five specimens was 0·3299 ml O_2 sec^{-1} $mbar^{-1}$ while the mean of the minimum and maximum values of DL_{O_2} was 0·0734 ml O_2 sec^{-1} $mbar^{-1}$. Values of the pulmonary parameters normalised with body mass are summarised in Table 5. The mass specific volume of

Table 3. *Surface areas of the alveoli (Sa), the capillary endothelium (Se) the blood-gas (tissue) barrier (St) and the red blood cells (Sr). The harmonic mean thicknesses of the blood-gas (tissue) barrier (τh_t) and the plasma (τh_p) are also shown*

Specimen	St (m^2)	Se (m^2)	Sa (m^2)	Sr (m^2)	τh_t (μm)	τh_p (μm)
1	4·017	4·766	4·159	7·100	0·3181	0·1353
2	2·280	2·520	2·468	3·621	0·3568	0·1483
3	3·106	3·861	3·333	5·692	0·3765	0·1730
4	2·530	2·926	2·796	4·480	0·4204	0·2327
5	2·122	2·638	2·335	4·178	0·3053	0·1807
Mean +	2·81	3·334	3·02	5·01	0·3554	0·1740
S.D.	0·69	0·85	0·67	1·24	0·04	0·03

Table 4. *Anatomical pulmonary diffusing capacities for oxygen through the tissue barrier (Dt_{O_2}), the plasma layer (Dp_{O_2}), the red blood cells (De_{O_2}), the membrane (Dm_{O_2}) and the overall capacity (DL_{O_2}): units ml O_2 sec^{-1} $mbar^{-1}$ min., minimum and max., maximum*

		Dp_{O_2}		De_{O_2}		Dm_{O_2}		DL_{O_2}	
Specimen	Dt_{O_2}	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1	0·5208	1·319	1·7741	0·0498	0·1379	0·3734	0·4026	0·0439	0·1027
2	0·2536	0·821	1·1042	0·0452	0·1253	0·1938	0·2062	0·0969	0·1031
3	0·3403	1·0434	1·4034	0·0557	0·1543	0·2566	0·2739	0·0479	0·0988
4	0·2482	0·6257	0·8416	0·0449	0·2360	0·1777	0·1917	0·0358	0·1010
5	0·2867	0·7209	0·9696	0·0382	0·1058	0·2051	0·2213	0·0322	0·0716
Mean +	0·3299	0·9060	1·2186	0·0468	0·1519	0·2413	0·2591	0·0513	0·0954
S.D.	0·10	0·25	0·34	0·01	0·05	0·07	0·08	0·02	0·01

Table 5. *Some pulmonary morphometric ratios of the lung of the bushbaby, with most values normalised with body mass and in one case with the volume of the parenchyma (Vp). Symbols defined in the text or earlier Tables*

Specimen	VLW^{-1} (cm^3 g^{-1})	StW^{-1} (cm^2 g^{-1})	$VcSt^{-1}$ (cm^3 m^2)	$StVp^{-1}$ (mm^2 mm^3)	$Dt_{O_2}W^{-1}$ (ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1})	$DL_{O_2}W^{-1}$ (ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1})
1	0·0532	34·00	1·0604	69·86	0·4414	0·0621
2	0·0419	21·11	1·6207	60·79	0·2348	0·0926
3	0·0566	29·30	1·4791	61·40	0·1095	0·0692
4	0·0421	20·24	1·4199	58·83	0·1986	0·0547
5	0·0478	20·80	1·4475	52·18	0·2811	0·0509
Mean +	0·0483	25·09	1·4055	60·61	0·2531	0·0659
S.D.	0·01	5·57	0·19	5·66	0·11	0·02

the lung (VLW^{-1}) 0·0483 cm^3 g^{-1}, that of the surface area of the blood-gas (tissue) barrier (StW^{-1}) 25 cm^2 g^{-1}, the diffusing capacity of the tissue barrier ($Dt_{O_2}W^{-1}$) was 0·2531 ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1} and the total anatomical pulmonary diffusing capacity ($DL_{O_2}W^{-1}$) 0·0659 ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1}.

DISCUSSION

The advantages of using the non-human primates as research material over the common laboratory animals has been widely discussed (Napier & Walker, 1967; Lapin, 1971; Bourne, 1973; Goldsmith, 1977). In general this group has been found to be morphologically more appropriate particularly with respect to the respiratory system, the subject of this study. Thus, Crapo *et al.* (1982) observed that the lung cell numbers and sizes in man approximated to those of the baboon rather than to those of the rat. Harkema *et al.* (1987) found no appreciable differences in the composition of cell populations in the nasal epithelium of the bonnet monkey and man. The extrapulmonary airway epithelium in the bonnet monkey (*Macaca radiata*) was observed to differ from that of the frequently studied laboratory rodents in cell types, abundance and organisational complexity but resembled that of man in these respects (Wilson, Plopper & Hyde, 1984). Lenfant & Aucutt (1969) noted that the respiratory properties of the blood in five species of monkeys were within the range obtained for human blood while Patra, Gooya & Menache (1986) have reported the morphology of the nasal passages in the baboon to be very similar to that of man. Retinal topography in the bushbaby, monkey and man showed considerable similarities (Johnston & Stone, 1979). Structural evaluation of the gas exchange potential of the primate lung, however, has only been made in man (Gehr, Bachofen & Weibel, 1978), in the macaque (Kapanci, Weibel, Kaplan & Robinson, 1969; Conradi *et al.* 1971), in the olive baboon (Maina, 1987) and the vervet monkey (Maina, 1988). In view of the remarkable size, behavioural and ecological heterogeneity of the primates, at least subtle pulmonary structural differences commensurate with their disparate energetic demands might plausibly be expected.

The gross and microscopic morphology of the lung of the lesser bushbaby (*Galago senegalensis*) was essentially similar to that of the other primates and mammals in general. Ciliated and mucous goblet cells constituted the classical pseudostratified columnar epithelium that lines the trachea and the principal bronchi of the mammalian respiratory system. The epithelium decreased in complexity towards the dependent parts of the lung becoming, with the various bronchiolar generations, simple columnar, cuboidal and, at the alveolar level, the air was separated from the capillary blood by an extremely attenuated tissue barrier that consisted of a thin squamous epithelial cell, a basal lamina and an endothelial cell. The alveolar surface was made up mainly of the Type I, the squamous pneumocytes, and the Type II, the granular pneumocytes.

Morphometrically, the lung of the lesser bushbaby was found to be generally less sophisticated than that of the other primates on which comparable data are available, except that of man. The surface area of the blood-gas barrier per unit body weight in *Galago senegalensis* was 25 $cm^2 g^{-1}$, a value slightly higher than that of man (18 $cm^2 g^{-1}$) reported by Gehr *et al.* (1978) but far lower than for the vervet monkey (50 $cm^2 g^{-1}$) (Maina, 1988), the baboon (33 $cm^2 g^{-1}$) (Maina, 1987) and the macaque (33 $cm^2 g^{-1}$) (Conradi *et al.* 1971). The thickness of the blood-gas (tissue) barrier in *Galago* (0·355 μm) was within the range of that of the non-human primates (0·311–0·500 μm) (Table 6) but thinner than that for man (0·620 μm) (Gehr *et al.* 1978). The weight specific total anatomical pulmonary diffusing capacity (DL_{O_2}), the most comprehensive estimator of the lung's structural adaptations for gas exchange (Table 6) in *Galago* (0·073 ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1}) was comparable to that of the baboon (0·068) (Maina, 1987) but lower than that for *Macaca irus* (0·080) (Conradi *et al.* 1971) and the vervet monkey (0·110) (Maina, 1988). In man, the weight specific

Table 6. *Comparison of some morphometric data of the primate lung. Symbols are defined in the text or earlier Tables**

Species	VL/W (cm^3/kg)	St/W (cm^2/g)	St/Vp (mm^2/mm^3)	Vc/St (cm^3/cm^2)	Vc/VL (cm^3/cm^3)	Vc/W (cm^3/kg)	τh_t (μm)	Dt_{O_2} (ml O_2/sec/mbar/kg)	DL_{O_2}
Macaca irus	50	33	76	1·20	0·08	4·04	0·500	0·275	0·080
M. mullata	—	—	—	—	0·067	—	—	—	—
Papio anubis	46	37	92	0·84	0·068	3·08	0·478	0·400	0·06
Homo sapiens	59	18	35	1·58	0·057	2·88	0·620	0·125	0·045
C. aethiopicus	50	50	117	1·36	0·123	6·38	0·311	0·690	0·110
G. senegalensis	48·3	25	60·6	1·41	0·077	3·70	0·355	0·295	0·073

* Sources of data: *Papio*, Maina (1987); *M. irus*, Conradi *et al.* (1971) – values taken from Weibel (1973); *M. mullata*, Kapanci *et al.* (1969); *H. sapiens*, Gehr *et al.* (1978); *C. aethiopicus*, Maina (1988); *G. senegalensis*, this study.

total anatomical pulmonary diffusing capacity was only 0·045 ml O_2 sec^{-1} $mbar^{-1}$ kg^{-1}. The relatively poorly adapted human lungs may mirror the evidently less energetic lifestyle that man leads in a controlled environment where virtually all the potential predators have been subjugated if not exterminated.

The primates are a remarkably allometrically, developmentally and ethologically diverse and variably adapted group. The body size in the primates ranges in mass from the mouse-size lemur *Microcebus* (about 60 g in weight) to the notably large gorilla (about 200 kg) (Heglund, 1985). With respect to the energy cost of transport, the primates exhibit differing modes of locomotion, ranging over brachiation, quadrupedalism, bipedalism and hopping (Parsons & Taylor, 1977; Taylor, 1980; Rollinson & Martin, 1981; Heglund, 1985). Among this heterogeneous primate group, the prosimians stand out morphologically and physiologically as a unique group. Galagos are nocturnal tree dwellers whose natural habitat is Africa (Doyle, 1974). The response speed of the rhesus monkey has been found to be faster than that for galago (*Galago crassicaudatus*) and the slow loris (*Nycticebus caucang*) (Ehrlich, 1968*a*, *b*). The thermoregulatory characteristics of *G. crassicaudatus* are remarkably different from those of the baboon (*Papio cynocephalus*) and the chimpanzee (*Pan satyrus*) (Hiley, 1976). *Galago senegalensis* is unique among the galaginae. It is one of the smallest of the bushbabies being six times smaller than the greater bushbaby (*G. crassicaudatus*), feeds largely on arthropods, habitually forages near the ground, and is generally known to be more active (Crompton, 1984). The basic type of locomotion in galagos which has been described as vertical clinging and leaping may be the primary arboreal locomotor adaptation in primate phylogeny (Napier & Walker, 1967). Galagos jump to a height of more than 7 feet and nearly 14 times their body length (Hall-Craggs, 1965, 1974; Jouffroy & Gasc, 1974). Among all species, *Galago alleni* is the most specialised for jumping locomotion (Charles-Dominique, 1971). The standing vertical jump of *G. senegalensis* with a displacement of centre of gravity of at least 7 feet remarkably exceeds those quoted for most other animals of similar size (Gray, 1953). The muscles triceps surae and quadriceps femoris form 8–12% of the body weight and the quadriceps has a high proportion of fast fibres (Hall-Craggs, 1974).

The basal metabolic rate (BMR) has been shown to be small in prosimians (Muller, 1979, 1985), the BMR being 20–40% lower than the mammalian mass-specific standard. The simian species have a BMR close to, or higher than, that predicted by body mass (Bruhn, 1934; Malinov & Wagner, 1966; Morrison & Middleton, 1967; Nakayama *et al.* 1971; Muller, 1985). Only the night monkey (*Aotus trivirgatus*), a

nocturnally active species, shows a reduced BMR (Le Maho *et al.* 1981). Recent studies on thermoregulation and oxygen consumption in prosimians (Nelson & Asling, 1962; Yousef, Chaffee & Johnson, 1971; Hildwein & Goffart, 1975; Dobler, 1976; Whittow & Gould, 1976; Muller, 1985; McNab & Wright, 1987) have shown that the prosimians generally have lower body temperatures (33–34 °C) than most mammals of similar size, exhibit circadian changes and the basal heat production is notably below the mammalian standard. The primates, besides exhibiting differing modes of locomotion, are characterised by diverse home ranges as expressed in daily movement distance (DMD) covered (Garland, 1983); the gorilla was reported to have a DMD of only 0·5 km, the chimpanzee 3·9 km, the baboon 6·3 km, macaques 0·75 km, cercopithecines 1·13 km and man (Kalahari bushmen) 10 km. The prosimians were generally observed to have a low DMD, the lemur, for example, having a value of 0·57 km (Mitani & Rodman, 1979). Though factors such as daily energy expenditure (DEE) and ecological cost of transport (ECT) which are difficult to establish, are more informative with respect to unearthing the structural and functional adaptations required to meet the energetic rigours for survival, the foraging behaviour in the primates, from the data available, appears in fair measure to correlate with the pulmonary structural features where more agile species have better adapted lungs.

Most prosimians exhibit heterothermy to varying degrees, a low level of basal heat production, and lethargic states (Bradley & Hudson, 1974; McNab & Wright, 1987). Three possible explanations were offered to explain the unique physiological features of the prosimians such as the low BMR and body temperature by Muller (1985). These are (i) a possible primitive anatomical organisation of the prosimians, (ii) inherent features acquired during ecological evolution of this taxon and (iii) interplay of (i) and (ii). The relatively poorly adapted lungs for gas exchange of the lesser bushbaby noted in this study reflect the low energy demands that typify its life style. The poor physiological features that are a feature of the prosimians may not necessarily represent evolutionary primitive properties but may relate more to ecology than phylogeny. Homeothermy is, from an energy consumption point of view, very expensive (Bradley & Hudson, 1974). It is estimated that about 90% of the BMR of homeotherms is needed for this purpose alone (Muller, 1985). It has been estimated that a lowering of temperature at night leads to a 12% saving on energy (Bradley & Hudson, 1974). It is astounding that these adaptational features have largely been construed as characterising the earliest primates and are hence considered to be primitive in nature. The undistinguished morphometric features observed here in *Galago senegalensis* should not, in our view, be interpreted as exhibiting a degree of pulmonary primitivity or under-specialisation. Their developmental status satisfies the life style that the galago leads. That, in fact, there were no evident gross or microscopic differences between the prosimian lung and that of the other primates may support this conjecture. As mentioned by Weibel *et al.* (1980), respiration may be too important a function for survival for conservative traits to be passed on in the structural organisation of the respiratory system.

In comparison with the greater bushbaby (*G. crassicaudatus*), the lesser bushbaby (*G. senegalensis*) is said to have more predators and is more agile (Bearder & Doyle, 1974; Crompton, 1984). Similar differences were also observed by Vincent (1978) in two sympatric galaginae, *G. alleni* and *G. elegantulus* which were found to have different thermoregulatory capacities, *G. alleni* living in the lower strata of the forest where the temperature is stable and *G. elegantulus* living in the upper strata where there are wider thermal variations. This explains why *G. alleni* has a much more stable

body temperature than *G. elegantulus*. The diet of arthropods which characterises *G. senegalensis* may provide twice as much energy per gram as the plant diet on which *G. crassicaudatus* exists. This may explain the fact that the largest primate insectivores weigh approximately 200 g and the smallest folivores 800 g (Crompton, 1984). McNab (1978) and Muller, Kamau & Maloiy (1983) pointed out that arboreal mammals which feed on leaves should have a low BMR. It is probable that the lungs of the greater bushbaby (*G. crassicaudatus*), as result of its less energetic and folivorous feeding life style, are less well specialised than those of the more agile and smaller bushbabies like *G. senegalensis* but this remains to be established. The morphological heterogeneity that generally characterises the primates appears to be a common feature in the prosimians, and the galaginae in particular. There is thus a need for thorough studies on the organ systems of the primates irrespective of their presumed closeness to or distance from man before any particular species is adopted as an appropriate research animal model in man-related biomedical studies.

SUMMARY

The lung of the lesser bushbaby (*Galago senegalensis*) has been investigated morphologically and morphometrically using the transmission and scanning electron microscopes.

Grossly and microscopically, the bushbaby lung was found to be essentially similar to that of the other primates and the mammals in general. Subtle morphometric differences were, however, observed, with the bushbaby lung being generally structurally less sophisticated than that of the other primates on which comparable data are available, except for man.

The weight-specific surface area of the blood-gas (tissue) barrier in *G. senegalensis* was 25 $cm^2\ g^{-1}$. The thickness of the blood-gas barrier was 0·355 μm and the weight specific total anatomical pulmonary diffusing capacity 0·045 $mlO_2\ sec^{-1}\ mbar^1\ kg^{-1}$. The morphological similarity of the galago lung to that of man gives sufficient grounds to justify its possible use in human pulmonary studies but caution has been called for in the general utilisation of primate tissues without first establishing their morphological characteristics, just because the primates are taken to be evolutionally close to man.

The dearth of morphological studies on the various organ systems of the prosimians is pointed out.

I wish to thank the Director of the Institute of Primate Research, Nairobi for kindly making the specimens used in this study available to me. This work was generously funded by the Leverhulme Trust of London. Their financial assistance in this and other earlier studies is greatly appreciated.

REFERENCES

BEARDER, S. K. & DOYLE, G. A. (1974). Ecology of bushbabies *Galago senegalensis* and *Galago crassicaudatus* with some notes on their behaviour in the field. In *Prosimian Biology* (ed. R. D. Martin, G. A. Doyle & A. C. Walker), pp. 107–130. Pittsburgh: University of Pittsburgh Press.

BOURLIERE, F. (1974). The antecedents of man: How to remain a prosimian in a simian world. In *Prosimian Biology* (ed. R. D. Martin, G. A. Doyle & A. C. Walker), pp. 17–22. Pittsburgh: University of Pittsburgh Press.

BOURNE, G. H. (1973). The primate research center program of the National Institutes of Health. In *Non-Human Primates and Medical Research* (ed. G. H. Bourne), pp. 487–513. New York: Academic Press.

BRADLEY, S. R. & HUDSON, J. W. (1974). Temperature regulation in the tree shrew *Tupia glis*. *Comparative Biochemistry and Physiology* **48A**, 5–60.

BRUHN, J. M. (1934). The respiratory metabolism of infra-human primates. *American Journal of Physiology* **110**, 477–484.

CHARLES-DOMINIQUE, P. (1970). Evolution of lorises and lemurs. *Nature* **227**, 257–260.

CHARLES-DOMINIQUE, P. (1971). Eco-ethologie des prosimiens du Gabon. *Biology Gabon* **7**, 121–228.

CHARLES-DOMINIQUE, P. (1978). Ecological position of the family lorisidae compared with the other mammalian families. *Bulletin of the Carnegie Museum of Natural History* **6**, 26–30.

CLARK, W. E. LE GROS (1962). *The Antecedents of Man*, 2nd ed. Edinburgh: Edinburgh University Press.

CLARK, W. E. LE GROS (1970). *History of the Primates: An Introduction to the Study of Fossil Man*. London: British Museum of Natural History.

CONRADI, C., BURRI, P. H., KAPANCI, Y., ROBINSON, F. R. & WEIBEL, E. R. (1971). Lung changes after beryllium inhalation. *Archives of Environmental Health* **23**, 346–358.

CRAPO, J. D., BARRY, B. E., GEHR, P., BACHOFEN, M. & WEIBEL, E. R. (1982). Cell numbers and cell characteristics of the normal human lung. *American Review of Respiratory Diseases* **125**, 332–337.

CROMPTON, R. H. (1984). Foraging, habitat structure and locomotion in two species of *Galago*. In *Adaptations for Foraging in Non-Human Primates. Contributions to an Organismal Biology of Prosimians, Monkeys and Apes* (ed. P. S. Rodman & J. G. H. Cant), pp. 73–103. New York: Columbia University Press.

DOBLER, H. J. (1976). Development of thermoregulation in the newborn bushbaby (*Galago senegalensis Moholi*, Smith 1839). *Experientia* **32**, 194.

DOYLE, G. A. (1974). The behaviour of the lesser bushbaby. In *Prosimian Biology* (ed. R. D. Martin, G. A. Doyle & A. C. Walker), pp. 213–231. Pittsburgh: University of Pittsburgh Press.

DOYLE, G. A. & MARTIN, R. D. (1974). The study of prosimian biology. In *Prosimian Biology* (ed. R. D. Martin, G. A. Doyle & A. C. Walker), pp. 1–14. Pittsburgh: University of Pittsburgh Press.

EHRLICH, A. (1968*a*). Behaviour characteristics of the slow loris galago and rhesus monkey. In *Proceedings of the 2nd International Congress of Primatology (Atlanta–Georgia)*, Vol. 1 (ed. C. R. Carpenter), pp. 119–127. Basel: S. Karger.

EHRLICH, A. (1968*b*). Food motivated behaviour in prosimians. *Folia primatologia* **8**, 66–71.

GARLAND, T. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *American Naturalist* **121**, 571–587.

GEHR, P., BACHOFEN, M. & WEIBEL, E. R. (1978). The normal human lung: Ultrastructure and morphometric estimation of diffusion capacity. *Respiration Physiology* **32**, 121–140.

GEHR, P., MWANGI, D. K., AMANN, A., MALOIY, G. M. O., TAYLOR, C. R. & WEIBEL, E. R. (1981). Design of the mammalian respiratory system. V. Scaling morphometric pulmonary diffusing capacity to body mass: Wild and domestic mammals. *Respiration Physiology* **44**, 1–64.

GOLDSMITH, E. I. (1977). Some contributions of non-human primates to human health problems through surgical research. In *Use of Non-Human Primates in Biomedical Research* (ed. M. R. N. Prasdad & T. C. A. Kumar), pp. 357–368. New Delhi: Indian Academy of Sciences.

GRAY, J. (1953). *How Animals Move*. Cambridge: Cambridge University Press.

HAINES, D. E. (1982). *Lesser Bushbaby (Galago) as an Animal Model*. Boca Raton, Florida: CRC Press Inc.

HALL-CRAGGS, E. C. B. (1965). An analysis of the jump of the lesser galago (*Galago senegalensis*). *Journal of Zoology* **147**, 20–29.

HALL-CRAGGS, E. C. B. (1974). Physiological and histochemical parameters in comparative locomotor studies. In *Prosimian Biology* (ed. R. D. Martin, G. A. Doyle & A. C. Walker), pp. 829–845. Pittsburgh: University of Pittsburgh Press.

HARKEMA, J. R., PLOPPER, C. G., HYDE, D. M., WILSON, D W., ST. GEORGE, J. A. & WONG, V. J. (1987). Nonolfactory surface epithelium of the nasal cavity of the bonnet monkey. A morphologic and morphometric study of the transitional and respiratory epithelium. *American Journal of Anatomy* **180**, 266–279.

HEGLUND, N. C., (1985). Comparative energetics and mechanics of locomotion. How do primates fit in? In *Size and Scaling in Primate Biology* (ed. W. L. Jungers), pp. 319–335. New York: Plenum Press.

HILDWEIN, G. & GOFFART, M. (1975). Standard metabolism and thermoregulation in a prosimian *Perodicticus potto*. *Comparative Biochemistry and Physiology* **50A**, 201–213.

HILEY, P. G. (1976). The thermoregulatory responses of the galago (*Galago crassicaudatus*), the baboon (*Papio cynocephalus*) and chimpanzee (*Pan satyrus*) to heat stress. *Journal of Physiology* **254**, 657–671.

HUXLEY, T. H. (1863). *Evidence as to Man's Place in Nature*. London: Pelican.

JOHNSTON, E. M. & STONE, J. (1979). The topography of the retina in three primates: the bushbaby, monkey and human. *Journal of Anatomy* **128**, 642*P*.

JOUFFROY, F. K. & GASC, J. P. (1974). A cineradiographical analysis of leaping in African prosimian (*Galago alleni*). In *Primate Locomotion* (ed. F. A. Jenkins), pp. 117–142. New York: Academic Press.

KAPANCI, Y., WEIBEL, E. R., KAPLAN, H. P. & ROBINSON, F. R. (1969). Pathogenesis and reversibility of the pulmonary lesions of oxygen toxicity in monkeys. III. Ultrastructural and morphometric studies. *Laboratory Investigation* **20**, 101–118.

LAPIN, B. A. (1971). Use of primates in biomedical research. In *Use of Non-Human Primates in Research on Human Reproduction* (ed. E. Diszfalusy & C. C. Standley), pp. 15–17. Stockholm: Kavoninska Sjukhuset.

LENFANT, C. & AUCUTT, C. (1969). Respiratory properties of the blood of five species of monkeys. *Respiration Physiology* **6**, 284–291.

LE MAHO, Y., GOFFART, M., ROCHAS, A., FELBALBEL, H. & CHATONNET, J. (1981). Thermoregulation in the only nocturnal simian: The night monkey *Aotus trivirgatus*. *American Journal of Physiology* **240**, R156–R165.

MAINA, J. N. (1987). The morphology and morphometry of the adult normal baboon lung (*Papio anubus*). *Journal of Anatomy* **150**, 229–245.

MAINA, J. N. (1988). Morphology and morphometry of the normal lung of the adult vervet monkey (*Cercopithecus aethiops*). *American Journal of Anatomy* **183**, 258–267.

MALINOW, M. R. & WAGNER, R. (1966). Oxygen uptake in the squirrel monkeys. *Laboratory Animal Care* **16**, 105–108.

MARTIN, R. D. (1978). Major features in prosimian evolution. A discussion in the light of chromosomal evidence. In *Recent Advances in Primatology*, Vol. 3 (ed. D. J. Chivers & K. A. Joysey), pp. 3–36, London: Academic Press.

MCNAB, B. (1978). Energetics of arboreal folivores: Physiological problems, ecological consequences on feeding on an ubiquitous food supply. In *Ecology of Arboreal Folivores* (ed. G. G. Montgomery), pp. 153–162. Washington, D.C.: Smithsonian Institute Press.

MCNAB, B. & WRIGHT, P. C. (1987). Temperature regulation and oxygen consumption in the Philippine tarsier, *Tarsius syrichta*. *Physiological Zoology* **60**, 596–600.

MITANI, J. C. & RODMAN, P. S. (1979). Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioural Ecology and Sociobiology* **5**, 241–251.

MORRISON, P. R. & MIDDLETON, E. H. (1967). Body temperature and metabolism in the pigmy marmoset. *Folia primatologica* **6**, 70–82.

MULLER, E. F. (1979). Temperature regulation in the slow loris. *Naturwissenchaften* **62**, 140–141.

MULLER, E. F. (1985). Basal metabolic rates in primates – the possible role of phylogenetic and ecological factors. *Comparative Biochemistry and Physiology* **81A**, 707–711.

MULLER, E. F., KAMAU, J. M. Z. & MALOIY, G. M. O. (1983). A comparative study of basal metabolism and thermoregulation in a folivorous (*Colobus gueraza*) and an omnivorous (*Cercopithecus mitis*) primate species. *Comparative Biochemistry and Physiology* **74A**, 319–322.

NAPIER, J. R. & WALKER, A. C. (1967). Vertical clinging and leaping in living and fossil primates. In *Progress in Primatology* (ed. D Starck, R. Schnieder & H. J. Kuhn), pp. 66–69. Stuttgart Gustav Fischer-Verlag.

NAKAYAMA, T., HORI, T., NAGASAKA, T., TOKURA, T. & TADAKI, E. (1971). Thermal and metabolic responses in the Japanese monkey at temperatures of 5–38 °C. *Journal of Applied Physiology* **31**, 332–337.

NELSON, L. E. & ASLING, C. W. (1962). Metabolic rate of tree-shrews (*Urogale everatti*). *Proceedings of the Society of Experimental Biology and Medicine* **109**, 602–604.

PARSONS, P. E. & TAYLOR, C. R. (1977). Energetics of brachiation versus walking: a comparison of a suspended and an inverted pendulum mechanism: *Physiological Zoology* **50**, 183–188.

PATRA, A. L., GOOYA, A. & MENACHE, M. G. (1986). A morphometric comparison of the nasopharyngeal airway of laboratory animals and humans. *Anatomical Record* **215**, 42–50.

ROLLINSON, P. & MARTIN, R. D. (1981). Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symposium of the Zoological Society of London* **48**, 377–427.

SCHERLE, W. F. (1970). A simple method for volumetry of organs in quantitative stereology. *Microscope* **26**, 57–60.

STEVENS, J. L., EDGERTON, V. R., HAINES, D. E. & MEYER, D. M. (1981). *An Atlas and Source Book of the Lesser Bushbaby Galago senegalensis*. Boca Raton, Florida: CRC Press Inc.

SZALAY, F. (1968). The beginning of primates. *Evolution* **22**, 19–36.

TAYLOR, C. R. (1980). Energetics of locomotion: Primitive and advanced mammals. In *Comparative Physiology of Primitive Mammals* (ed. K. Schmidt-Nielsen, L. Bolis & C. R. Taylor), pp. 192–199. Cambridge: Cambridge University Press.

VINCENT, F. (1978). Thermoregulation and behaviour in two sympatric galagos: An evolutionary factor. In *Recent Advances in Primatology*, Vol. 3 (ed. D. J. Chivers & K. A. Joysey), pp. 181–187. London: Academic Press.

WEIBEL, E. R. (1970/71). Morphometric estimation of pulmonary diffusion capacity. I. Model and method. *Respiration Physiology* **11**, 54–75.

WEIBEL, E. R. (1973). Morphological basis of alveolar–capillary gas exchange. *Physiological Reviews* **53**, 419–495.

WEIBEL, E. R. (1979). *Stereological Methods: Practical Methods for Biological Morphometry*. London: Academic Press.

WEIBEL, E. R., CLAASSEN, H., GEHR, P., SEHOVIC, S. & BURRI, P. (1980). The respiratory system of the smallest mammal. In *Comparative Physiology of Primitive Mammals* (ed. K. Schmidt-Nielsen, L. Bolis & C. R. Taylor), pp. 181–191. Cambridge: Cambridge University Press.

WHITTOW, G. C. & GOULD, E. (1976). Body temperature and oxygen consumption in the pentail tree shrew (*Ptilocerus lowii*). *Journal of Mammalogy* **57**, 754–756.

WHITTOW, G. C., SCAMMELL, J., MANUEL, K., RAND, D. & LEONG, M. (1977). Temperature regulation in a

hypometabolic primate, the slow loris (*Nycticebus coucang*). *Archives of International Physiology and Biochemistry* **85**, 139–151.

WILSON, D W., PLOPPER, C. G. & HYDE, D. M. (1984). The tracheobronchial epithelium of the bonnet monkey (*Macaca radiata*): A quantitative ultrastructural study. *American Journal of Anatomy* **171**, 25–40.

YOUSEF, M. K., CHAFFEE, R. R. J. & JOHNSON, H. D. (1971). Oxygen consumption of tree shrews: effects of ambient temperatures. *Comparative Biochemistry and Physiology* **38A**, 709–712.