

## Intrapulmonary Variation of Gas Partial Pressures and Ventilation Inequalities in Chelonian Reptiles

Warren W. Burggren<sup>1\*</sup>, Mogens L. Glass<sup>2</sup>, and Kjell Johansen<sup>2</sup>

<sup>1</sup> School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR4 7TJ, England

<sup>2</sup> Department of Zoophysiology, University of Aarhus, DK-8000 Aarhus C, Denmark

Accepted April 5, 1978

**Summary.** 1) Variations of respiratory gas partial pressures, as well as ventilation inequalities in different regions of the lungs of unanaesthetized, unrestrained *Pseudemys scripta*, *Testudo graeca* and *Testudo hermanni* have been examined. Both direct cannulation of the lungs and indirect methods involving instantaneous monitoring of expired gases have been used.

2) Respiratory gas pressures vary between lateral chambers of the lungs by less than 3–4 mmHg. The data indicate that ventilation and perfusion in undisturbed animals are normally matched to a similar extent throughout a large portion of the lung. No pulmonary ventilation inequalities normally occur.

3) In contrast, distressed *Pseudemys* show marked ventilation inequalities, presumably induced by postural changes including head and limb withdrawal into the carapace.

(Burggren et al., 1978). In spite of this accumulation of data, little is currently known about regional variations in pulmonary function in reptiles: their lungs remain essentially respiratory 'black boxes'.

In mammalian lungs considerable stratification of both perfusion and ventilation may occur, and ventilation-perfusion ratios,  $P_{O_2}$ ,  $P_{CO_2}$  and R vary considerably on a regional basis (West, 1974). Whether regional differences in gas tensions predicted for reptilian lungs (Wood and Lenfant, 1976), as well as regional ventilation-perfusion inequalities, exist in chelonians remains to be established. The lungs of the carpet python show considerable stratification of perfusion (Read and Donnelly, 1972), but their elongation and striking division into saccular and alveolar components may preclude direct comparison of ophidian lungs with those of other reptiles. Chelonian lungs are generally much less alveolized than those of mammals, and the bronchial system is also considerably less developed. However, the presence or absence of ventilation inequalities cannot easily be predicted simply on a morphological basis. The situation may be further complicated in reptiles by normally occurring periods of apnoea, which could tend to mask pulmonary ventilation inequalities and regional gas partial pressure variations by allowing time for diffusion of gases between lung compartments.

The object of the present investigation was to determine the extent of variation in respiratory gas partial pressures in different regions of the lungs of unanaesthetized and unrestrained Chelonia. Standard, non-intrusive tests of pulmonary function were also employed to assess the extent of ventilation inequalities.

### Materials and Methods

Experiments were performed on 11 specimens of the turtle *Pseudemys scripta*, and the tortoises *Testudo graeca* and *Testudo hermanni*, weighing between 700 and 1100 g. All experiments were performed at 20–22 °C.

### Introduction

The morphology and mechanics of lung ventilation have been examined in both fresh water and terrestrial Chelonia (Marcus, 1937; Gans and Hughes, 1967; Gaunt and Gans, 1970), in Ophidia (Rosenberg, 1973) and in the Crocodylia (Gans and Clark, 1976). Other authors have reported on the nature of ventilatory control in reptiles which normally breath either intermittently or continuously (see review by Wood and Lenfant, 1976; Glass et al., 1978). The periodic, dynamic nature of pulmonary perfusion and the mechanisms influencing it have also been investigated (see review by White, 1976; Shelton and Burggren, 1976; Burggren, 1977; Johansen et al., 1977). Recently, the quantitative relationship between overall lung ventilation and perfusion as influenced by chemoreceptor-mediated control of both functions has been examined

\* Present address: Department of Zoology, Univ. of British Columbia, Vancouver, British Columbia, Canada V6T 1W5

### Lung Morphology

Lungs were carefully exposed and removed from freshly killed *Pseudemys* and *Testudo*. In *Testudo* the lungs adhere very closely to the vertebral column and pelvic girdle, so a portion of the plastron and skeleton was dissected out with each tortoise lung. The main bronchus of individual lungs was occlusively cannulated, and the lung inflated to an intrapulmonary pressure of approximately 5 cmH<sub>2</sub>O. The inflated lung was then 'air-fixed' for 24 h at a temperature of 50–60 °C (Tenney and Tenney, 1970). The internal structure of the air-fixed lung was then examined by dissection.

### Lung Cannulation and Gas Tension Measurement

Anaesthesia for cannulae implantation was induced with cold torpor by placing the animals in a 1 °C cold room for 12–15 h before surgery. Details of the lung cannulation technique have been given elsewhere (Burggren, 1975). The animals were allowed to warm to room temperature and recover for 24 h after surgery, and were unrestrained and unanaesthetized during the course of all experiments. Chronically implanted lung cannulae remained patent for several days, and the subsequent dissection of animals sacrificed after experimentation to determine the exact cannula location revealed little or no pulmonary contusion or edema.

Pulmonary gas samples were drawn directly from unanaesthetized animals with cannulae which were chronically implanted in 4 different lateral chambers of the same lung. Invariably, the most anterior and posterior of the lateral chambers were cannulated. The other two cannulae were implanted in two of the more central lateral chambers at points equally spaced from each other and from the most anterior and posterior cannulae (see Fig. 1 for cannulae locations). 0.2 ml samples of lung gases were drawn simultaneously from each of these 4 lateral chambers immediately following the final inspiration of a breathing series (*Pseudemys*) or a single inspiration (*Testudo*). Total volume of each gas sample series was 0.8 ml, and compared to the 60–80 ml single lung volume of the animals represented an insignificant change in pulmonary volume. Gas samples were analyzed for  $P_{O_2}$  and  $P_{CO_2}$  in a Radiometer BMS 3 blood gas analyzer which was frequently calibrated. Partial pressures of expired gas were analyzed on a breath-to-breath basis with a Searle Medspect II mass spectrometer. A hollow plastic cylinder 4 mm in internal diameter and 40 mm long was glued over the nostrils of the animal. The shaft of a hypodermic needle was inserted through the wall of this plastic cylinder to within 1 mm of the nostrils. The sampling catheter of the mass spectrometer was attached to the needle and continuously sampled gas from immediately in front of the nostrils at a rate of 30 ml/min.

### Results and Discussion

Representative drawings of sagittal sections through the right lung of a *Pseudemys scripta*, *T. graeca* and *T. hermanni* are presented in Figure 1. After entering the lung, the first generation bronchus immediately divides into a short anterior and a longer posterior branch in all three species. In *T. hermanni* the second generation bronchi are well defined, heavily ringed with cartilage, and run in the medial region of the lung directly to the anterior and posterior regions of the parenchyma (Fig. 1C), but in *T. graeca* and *Pseudemys scripta* the intrapulmonary bronchi are

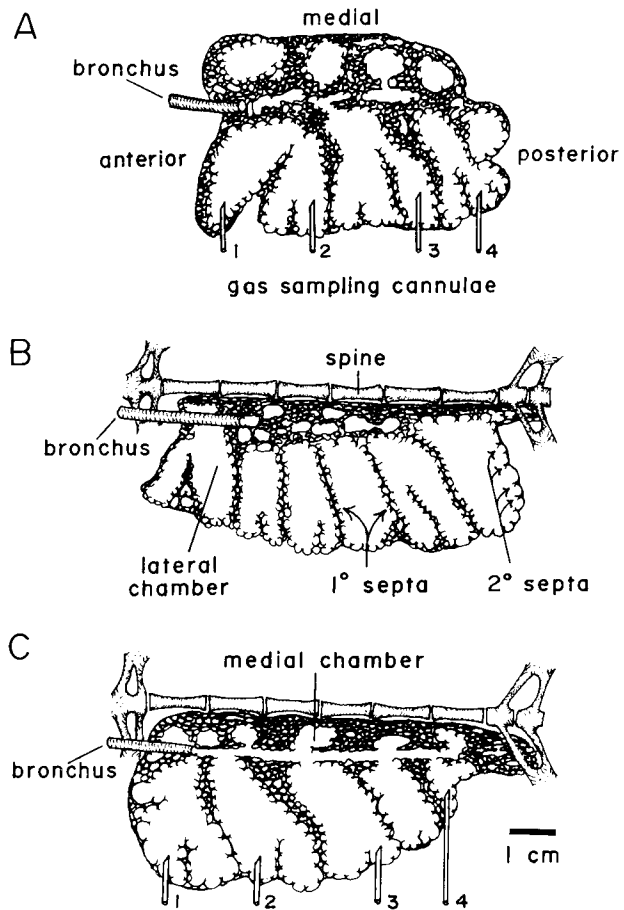


Fig. 1A–C. Diagrammatic drawings in a ventral aspect of representative sagittal sections midway through air-fixed right lung preparations from A *Pseudemys scripta*, B *Testudo graeca* and C *Testudo hermanni*

much less distinct. A third generation of very short bronchioles given off along the length of the bronchus immediately open without further branching both into small medial chambers formed by the presence of extensive tertiary septa and into 5–8 larger lateral chambers of variable size formed by primary septate divisions. Hence, with only 3–4 generations of airways, anatomical dead space is very small, amounting to less than 0.5% to 1.5% of total lung capacity in *Pseudemys* and *Testudo*, respectively (Crawford et al., 1976). The lateral chambers, whose walls develop only secondary septa, share primary septal walls and their longitudinal axis is approximately perpendicular to the longitudinal axis of the lung (Fig. 1). Rarely there are non-bronchial connections in the primary septal walls between lateral chambers. Thus, Wolf (1933) has reported a few such connections between lateral chambers, but Gans and Hughes (1967) were unable to find any evidence for them in *Testudo graeca*. There is a marked latero-medial gradation

**Table 1.** Distribution of respiratory gas partial pressures in the lateral chambers of the lungs of *Pseudemys* and *Testudo*. Mean values  $\pm$  standard deviation are presented. Location of sample sites are indicated in Figure 1

Species	Number of measurements		Anterior chamber (site 1)	Mid-anterior chamber (site 2)	Mid-posterior chamber (site 3)	Posterior chamber (site 4)	Level of significance of anterior/posterior difference (site 1/site 4)
<i>Testudo graeca</i>	17	$P_{O_2}$	144.5 $\pm$ 3.3	143.5 $\pm$ 3.6	143.0 $\pm$ 3.6	142.5 $\pm$ 3.2	0.001
		$P_{CO_2}$	12.1 $\pm$ 1.2	12.2 $\pm$ 1.1	12.5 $\pm$ 1.3	13.0 $\pm$ 1.3	0.02
<i>Testudo graeca</i>	10	$P_{O_2}$	141.9 $\pm$ 2.5	141.0 $\pm$ 2.4	140.4 $\pm$ 2.1	140.0 $\pm$ 2.2	0.01
		$P_{CO_2}$	—	—	—	—	—
<i>Testudo graeca</i>	12	$P_{O_2}$	141.0 $\pm$ 3.6	140.5 $\pm$ 3.4	137.2 $\pm$ 3.5	137.2 $\pm$ 3.5	0.001
		$P_{CO_2}$	—	—	—	—	—
<i>Testudo hermanni</i>	8	$P_{O_2}$	138.7 $\pm$ 1.5	137.3 $\pm$ 1.5	135.6 $\pm$ 1.7	133.6 $\pm$ 2.0	0.01
		$P_{CO_2}$	9.9 $\pm$ 0.9	10.7 $\pm$ 1.0	11.3 $\pm$ 1.1	11.9 $\pm$ 1.0	0.002
<i>Testudo hermanni</i>	13	$P_{O_2}$	137.1 $\pm$ 2.7	136.4 $\pm$ 2.5	135.8 $\pm$ 2.6	135.5 $\pm$ 2.6	0.001
		$P_{CO_2}$	13.3 $\pm$ 0.7	13.7 $\pm$ 0.7	13.9 $\pm$ 0.8	14.0 $\pm$ 0.9	0.02
<i>Pseudemys scripta</i>	5	$P_{O_2}$	97.0 $\pm$ 13.7	—	95.2 $\pm$ 17.4	93.0 $\pm$ 18.3	n.s.
		$P_{CO_2}$	—	—	—	—	—
<i>Pseudemys scripta</i>	7	$P_{O_2}$	123.9 $\pm$ 9.5	123.8 $\pm$ 9.1	123.0 $\pm$ 9.0	118.6 $\pm$ 9.5	0.05
		$P_{CO_2}$	18.2 $\pm$ 5.9	19.4 $\pm$ 7.7	20.7 $\pm$ 6.8	21.5 $\pm$ 5.9	0.02
<i>Pseudemys scripta</i>	13	$P_{O_2}$	122.8 $\pm$ 6.8	121.2 $\pm$ 7.3	120.3 $\pm$ 10.9	119.0 $\pm$ 9.3	0.05
		$P_{CO_2}$	—	—	—	—	—

of secondary and tertiary septa with the medial regions of the lung extensively subdivided into numerous chambers ranging from 0.5–5.0 mm in diam. (Fig. 1). In the Chelydridae and the Testudinidae the complexity of the lung often decreases posteriorly (Marcus, 1937), but this tendency is not very evident in *Pseudemys scripta* or *Testudo graeca*.

The distribution of respiratory gas partial pressures along the longitudinal axis of the lung of the three species is indicated in Table 1. Mean values of gas pressures occurring simultaneously in different lateral chambers of a single lung in each animal were determined. Relative to the regional variations in lung gases, there was considerable variation in the absolute levels of  $P_{O_2}$  and  $P_{CO_2}$ , both between animals and between consecutive breaths in individuals, especially in *Pseudemys*. The latter was mainly the result of varying interbreath intervals. Significance levels of differences in gas pressures between the most anterior and posterior lateral chamber in each measurement were assessed with a Student's paired or dependent *t*-test. In every animal examined  $P_{O_2}$  was significantly higher and  $P_{CO_2}$  significantly lower at the anterior end of the lung than at the posterior end, with a gradation of values between these two regions. However, the overall variation in gas partial pressures throughout the lateral chambers of the lung at any given time usually was less than 3–4 mmHg, and more often barely within resolution of the gas analysis

equipment. In two animals gas sampled simultaneously from identical positions in the left and the right lung were found to contain identical gas compositions. Although data in Table 1 were derived from gas samples taken immediately after inspiration, numerous other experiments revealed essentially the same gas tension distribution after 1 min of apnoea.

Wolf (1933) has proposed an 'avian' flow pattern in turtle lungs with inspired air first passing directly to the posterior chamber before entering the anterior chambers where most respiratory gas exchange occurs. If correct, gas tensions in posterior chambers would closely reflect inspired gas tensions, while  $P_{O_2}$  and  $P_{CO_2}$  in the anterior regions would be much closer to pulmonary capillary blood values. Gans and Hughes (1967) refuted Wolf's (1933) hypothesis of sequential ventilation by examining measurements of intrapulmonary pressure gradients in *Testudo graeca*. The present study brings more direct evidence against this hypothesis by the demonstration of a near uniform distribution of respiratory gases along the longitudinal axis of the lung.

Wood and Lenfant (1976) predicted that the heterogeneous structure of the chelonian lung would result in regional differences in pulmonary gas composition. Investigations of pulmonary gas exchange relying upon representative lung gas samples would hence have questionable value. Clearly, in *Pseudemys* and *Testudo*, however, regional gas partial pressure differ-

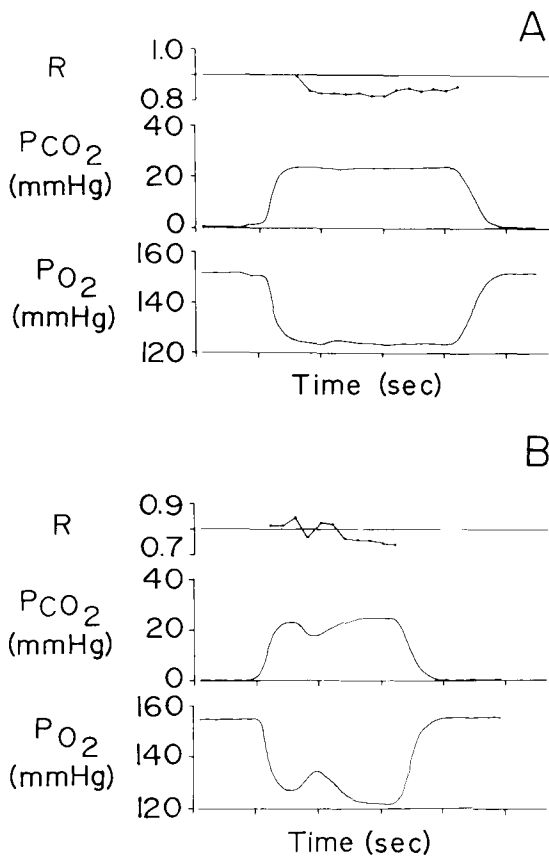


Fig. 2A and B. Expired respiratory gas tensions and calculated pulmonary exchange ratio during a single expiration (A) in an undisturbed *Pseudemys scripta* and (B) in a highly stressed turtle with its head and limbs withdrawn deeply into its shell

ences are very small, at least between the large lateral chambers which constitute by far the greatest volume of the lungs. Samples drawn from the lateral chambers should hence be considered representative of gases throughout a large portion of the lungs. A considerably greater degree of 'alveolation' medially than laterally could result in medio-lateral variations in pulmonary gas composition. The extent of such heterogeneity in gas pressures remains unknown.

Since direct non-bronchial connections between lateral chambers rarely occur, the uniformity of respiratory gas partial pressures along the longitudinal axis of the lung could result from an even ventilation of the various regions of the lungs. The observed uniformity of pulmonary gas pressures could alternatively arise if variable blood perfusion matched an uneven ventilation thus 'correcting' or masking the latter. Uneven ventilation-perfusion matching in the lungs can be revealed by the continuous monitoring of respiratory gas pressures during single expirations (West et al., 1957) if, as for mammals, regions of the lungs with quite different ventilation-perfusion

ratios empty at different times during expiration. The value of the pulmonary gas exchange ratio  $R$ , which depends on the relationship between ventilation and perfusion, will change during the course of a single expiration if regional ventilation-perfusion mismatching occurs.  $P_{O_2}$  and  $P_{CO_2}$  measured during continuous sampling at the nostrils normally revealed no alteration of the gas exchange ratio during the expiratory phase (Fig. 2A). This finding indicates that ventilation and perfusion are matched to yield a uniform gas exchange throughout the lungs, corroborating our hypothesis first based on direct measurements of gas partial pressures from different lateral chambers. If, however, a turtle was disturbed, resulting in head and limb withdrawal into the carapace, the gas exchange ratio showed fluctuations indicative of ventilation-perfusion inequalities (Fig. 2B). These likely resulted from an altered pattern of intrapulmonary ventilation and/or perfusion.

Few studies have addressed regional differences in the relationship between pulmonary ventilation and perfusion in other reptiles under any conditions. An altogether different situation might be expected in Ophidia, most of which have non-respiratory air sacs as elongate caudal extensions of the alveolarized lung sections. Donnelly and Woolcock (1972) reported that gas ventilation and alveolar  $P_{O_2}$  (and hence perfusion) were stratified along the alveolar region of the lungs of resting carpet pythons. During exercise, however,  $P_{A_{O_2}}$  increased disproportionately so that identical values were recorded throughout the alveolar lung, indicating that ventilation and perfusion became more evenly matched under these conditions. Read and Donnelly (1972) showed that postural changes from a horizontal to a vertical position in the carpet python resulted in a much more even perfusion of the alveolar regions of the lungs, but data on ventilation stratification were not presented.

It must be emphasized that a close matching of rates of gas ventilation and blood perfusion in various regions of the lungs does not a priori indicate that all lateral chambers are equally ventilated (here defined as each having the same fraction of their volume renewed with inspired air during a single respiratory cycle). A pulmonary compartment which has a low 'turnover rate' of gas with each breath but which is also perfused at a low rate can contain gas with identical partial pressures to that of a highly perfused, highly ventilated compartment. The presence of regional ventilation inequalities in the lungs of the Chelonia was assessed using two methods. The first technique involved indirect determination of gross regional ventilation inequalities by recording the wash-out of residual nitrogen from the lungs following a single inspiration of 100%  $O_2$ . At the start of expira-

tion, the  $P_{N_2}$  of the expired gas will rise sharply as the pulmonary dead space containing 100%  $O_2$  is progressively washed out with alveolar gas containing  $N_2$ . As expiration continues, the rate of increase in  $P_{N_2}$  will fall as 'pure' alveolar gas begins to be expired past the nostrils. If in all sections of the lungs the same fraction of gas is renewed with each respiratory cycle, the  $P_{N_2}$  of expired gas will level off and stabilize, forming an 'alveolar plateau'. Smaller inequalities in regional ventilation will not be disclosed by this technique, but if there are gross ventilation inequalities in the lung, perhaps caused by variations in airway resistance or sequential inflation and deflation of compartments, such that these various compartments fill and empty at different rates, then the  $P_{N_2}$  of the expired gas will continue to change throughout expiration and an alveolar plateau will not be formed.

Four unrestrained, unanesthetized *Pseudemys scripta* were subjected to single breath pulmonary function tests. Figure 3A shows a representative record of  $P_{N_2}$  measured in a turtle during expiration following inspiration of pure  $O_2$  towards the end of a long breathing series. An almost completely level 'alveolar plateau' in the expired  $P_{N_2}$  profile was consistently obtained in undisturbed turtles with the single breath technique. However, an expired  $P_{N_2}$  profile characteristic of pulmonary ventilation inequalities could be experimentally induced in turtles which had been provoked to deeply withdraw their head and limbs into their carapace (Fig. 3B). When these turtles were left undisturbed and assumed a more relaxed posture, alveolar plateaus in the  $P_{N_2}$  profile returned during expiration.

A second, more informative method used to assess ventilation inequalities is the multiple breath method, based on the rate of  $N_2$  washout from the lungs during many successive breaths of pure  $O_2$  (see West, 1974). In evenly ventilated lungs nitrogen in different pulmonary regions is reduced by the same fraction with each inspiration of  $O_2$ , and there is an exponential decrease in expired  $N_2$  with each breath. When multiple pulmonary compartments exist,  $N_2$  in compartments with a high rate of gas transfer falls rapidly with each breath, while  $N_2$  in poorly ventilated, slowly emptying compartments falls less rapidly. If ventilation inequalities exist, then a plot of log end-tidal  $N_2$  against the number of  $O_2$  breaths will not be linear (monoexponential), but will instead consist of an initial rapid fall in log  $N_2$  as the well ventilated compartment exchanges  $O_2$  for  $N_2$ , followed by a long period of a more gradual  $N_2$  washout of the poorly ventilated compartment(s). Thus, unlike the single breath method, ventilation inequalities will be revealed even in the unlikely event that all regions of the lung fill and empty at exactly the same time,

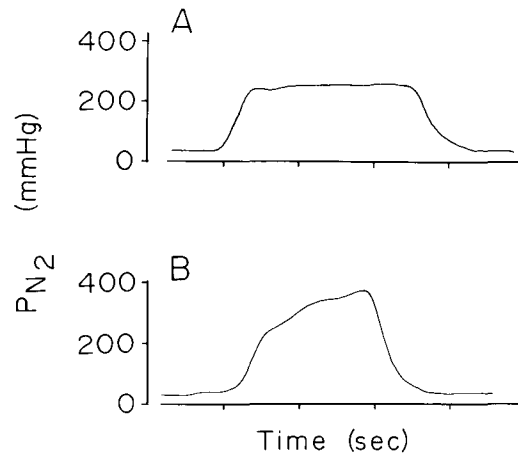


Fig. 3A and B.  $P_{N_2}$  profiles measured during a single expiration of lung gas after inspiration of 100% oxygen in (A) an undisturbed *Pseudemys scripta* and (B) a highly stressed *Pseudemys scripta* with head and limbs withdrawn deeply into its shell

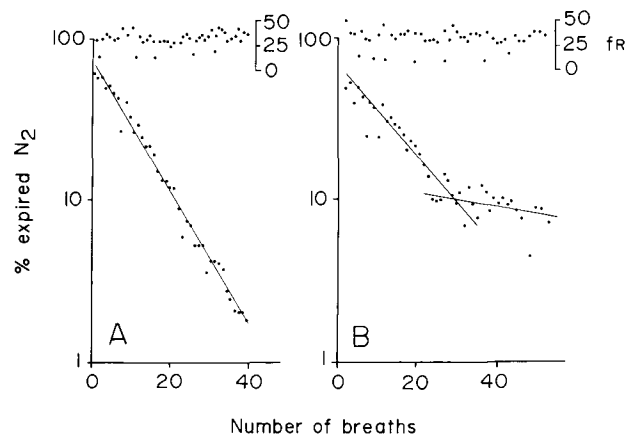


Fig. 4A–B. Nitrogen washout from the lungs of a voluntarily breathing *Pseudemys scripta* during many successive breaths of 100%  $O_2$ . In (A) are presented the results of a typical experiment on a comparatively undisturbed turtle. In (B) the turtle was highly stressed and had its head and limbs deeply withdrawn into its shell. Respiratory frequency (fr) during the course of each experiment is also indicated

provided that tidal volume and breathing frequency don't undergo a sustained change to new levels during the course of each experiment. Figure 4A shows a typical plot of log end-tidal  $N_2$  concentration against number of breaths in 100%  $O_2$  during a long breathing series in an unrestrained, unanaesthetized *Pseudemys*. The relationship for this turtle and the others is clearly monoexponential, indicating that the major pulmonary chambers of the turtle normally experience very similar turnover rates. The results of an experiment performed on a highly stressed turtle with head and limbs tightly withdrawn under the carapace are shown in Figure 4B. An abnormally elongated  $N_2$  washout suggestive of a second, poorly ven-

tilated lung compartment was now evident although 1) no consistent change to a new level of breathing frequency was evident during the experiment and 2) the breathing frequency range was the same in both Figure 4A and 4B. Ventilation inequalities in this turtle disappeared when a more relaxed posture was assumed once again.

Assessment of pulmonary ventilation distribution by both single and multiple breath analysis of expired nitrogen during oxygen breathing have thus revealed that in undisturbed *Pseudemys* the lungs are evenly ventilated in terms of 'alveolar' gas turnover rate. This is perhaps surprising, for not only is there a gross medio-lateral gradation of complexity in the lung structure, but the simple bronchial system affords ill-defined airways to the more distal regions of the lungs (Fig. 1). Airways in mammalian lungs are supported by cartilage and endowed with smooth muscle down to a diameter of approximately 1 mm, so ventilation inequalities resulting from collapse of the larger airways during expiration are minimized (Krahl, 1964). Also diameter changes in compensation for variable lengths of airway may occur. In chelonian lungs usually only the main bronchus and the largest of the few bronchioles contain cartilage, but no more than 3 or possibly 4 generations of the air conduction system are present. Thus, terminal airway diameters remain large relative to lung size in chelonians (Tenney et al., 1974; Fig. 1) and so there is probably little if any airway collapse during expiration. An even ventilation of chelonian lungs also occurs in spite of a tidal volume which is usually less than 10% of total lung volume (Jackson, 1973; Crawford et al., 1976). Hence the relatively large physiological dead space in undisturbed animals is evenly distributed about the lungs.

Deep withdrawals of the neck, head and limbs into the carapace in distressed chelonians will interfere with the normal respiratory movements and can result in immediate and gross regional differences in ventilation (Fig. 3B). These postural changes produce considerable rearrangement of the viscera, and the accompanying ventilation inequalities probably reflect marked changes in the shape and volume of certain pulmonary chambers with the possible restriction of their associated airways. Crawford et al. (1976) reported a homogenous ventilation distribution in the lungs of *Pseudemys* and *Testudo* based on a monoexponential washout of argon from their lungs. However, their animals were restrained with the neck fully extended and were artificially ventilated with a positive pressure pump. This highly unnatural situation may have masked or eliminated the ventilation inequalities due to postural changes which we have found can occur in distressed turtles breathing volun-

tarily but assuming unusual postures. Postural changes (from standing to supine, for example) in humans also cause a redistribution of ventilation through the lung, though in this instance the effect may be to reduce rather than increase ventilation inequalities (West, 1974).

The data presented have revealed that  $P_{O_2}$  and  $P_{CO_2}$  vary by only a few mmHg between the 5–8 major chambers of the chelonian lung during normal breathing. This situation could result from perfusion being effectively matched to regional variations in ventilation, or if ventilation and perfusion are uniform and matched throughout the lung. In spite of the anatomically simple lung structure in chelonians with a limited bronchial system and lack of extensive alveolation, gas exchange apparently is not limited by ineffective or uneven ventilation. Regional variations in size and hence in the total amount of ventilation and perfusion between lateral chambers of the lungs of course will result in dissimilar contributions to the total pulmonary gas exchange. Postural changes in distressed turtles can lead to uneven ventilation, and gas sampling for pulmonary function analysis under such circumstances could lead to erroneous interpretations.

## References

- Burggren, W.W.: A quantitative analysis of ventilation tachycardia and its control in two chelonians *Pseudemys scripta* and *Testudo graeca*. *J. exp. Biol.* **63**, 367–380 (1975)
- Burggren, W.W.: The pulmonary circulation of the chelonian reptile: Morphology, haemodynamics and pharmacology. *J. comp. Physiol.* **116**, 303–323 (1977)
- Burggren, W.W., Glass, M.L., Johansen, K.: Pulmonary ventilation: perfusion relationships in terrestrial and aquatic chelonian reptiles. *Canad. J. Zool.* **55**, 2024–2034 (1978)
- Crawford, E.C., Gatz, R.N., Magnussen, H., Perry, S.F., Piiper, J.: Lung volumes, pulmonary blood flow and carbon monoxide diffusing capacity of turtles. *J. comp. Physiol.* **107**, 169–178 (1976)
- Donnelly, P.M., Woolcock, A.J.: Ventilation and gas exchange in snake lungs. *Proc. Aust. Physiol. Pharm. Soc.* **2**, 77–78 (1972)
- Gans, C., Clark, B.: Studies on ventilation of *Caiman crocodilus* (Crocodylia: Reptilia). *Respir. Physiol.* **26**, 285–301 (1976)
- Gans, C., Hughes, G.M.: The mechanism of lung ventilation in the tortoise *Testudo graeca* Linné. *J. exp. Biol.* **47**, 1–20 (1967)
- Gaunt, A.S., Gans, C.: Mechanics of respiration in the snapping turtle *Chelydra serpentina* (Linné). *J. Morph.* **128**, 195–227 (1970)
- Glass, M., Burggren, W., Johansen, K.: Ventilation and its control in an aquatic and a terrestrial Chelonian reptile. *J. exp. Biol.* **72**, 165–180 (1978)
- Jackson, D.C.: Ventilatory response to hypoxia in turtles at various temperatures. *Respir. Physiol.* **18**, 178–187 (1973)
- Johansen, K., Burggren, W., Glass, M.: Pulmonary stretch receptors influence pulmonary blood flow and heart rate in the turtle, *Pseudemys scripta*. *Comp. Biochem. Physiol.* **58A**, 185–191 (1977)
- Krahl, V.E.: Anatomy of the mammalian lung. In: Handbook

- of physiology. Vol. 1. Respiration (eds. W.O. Fenn, H. Rahn), pp. 213-284. Washington: American Physiological Society 1964
- Marcus, H.: Lungen. Handbuch der vergleichenden Anatomie der Wirbeltiere, 3. Bd. (eds. L. Bolk, E. Göppert, E. Kallis, W. Lubsch), pp. 909-988. Berlin-Wien: Urban u. Schwarzenberg 1937
- Read, J., Donnelly, P.M.: Stratification of blood flow in the elongated lungs of the carpet python. *J. appl. Physiol.* **32**, 842-846 (1972)
- Rosenberg, H.J.: Functional anatomy of pulmonary ventilation in the garter snake. *J. Morph.* **140**, 171-184 (1973)
- Shelton, G., Burggren, W.: Cardiovascular dynamic of the Chelonia during apnoea and lung ventilation. *J. exp. Biol.* **64**, 323-343 (1976)
- Tenney, S.M., Bartlett, D., Jr., Farber, J.P., Remmers, J.E.: Mechanics of the respiratory cycle in the green turtle (*Chelonia mydas*). *Respir. Physiol.* **22**, 361-368 (1974)
- Tenney, S.M., Tenney, J.B.: Quantitative morphology of coldblooded lungs: Amphibia and Reptilia. *Respir. Physiol.* **9**, 197-215 (1970)
- West, J.B.: Respiratory physiology. Baltimore: Williams and Wilkins 1974
- West, J.B., Fowler, K.T., Hugh-Hones, P., O'Donnell, T.V.: The measurement of the inequality of ventilation and perfusion in the lung by the analysis of single expirates. *Clin. Sci.* **16**, 549-565 (1957)
- White, F.N.: Circulation. In: Biology of the reptilia. Vol. 5 (ed. C. Gans). New York: Academic Press 1976
- Wolf, S.: Zur Kenntnis von Bau und Funktion der Reptilienlunge. *Zool. Jb. Abt. Anat. Ont.* **57**, 138-190 (1933)
- Wood, S.C., Lenfant, C.: Respiration: Mechanics, control and gas exchange. In: Biology of the reptilia. Vol. 5 (ed. C. Gans). New York: Academic Press 1976