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RESPIRATION IN THE LAND CRAB, *GECARCINUS LATERALIS*

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SUMMARY

The oxygen consumption, ventilation and blood gas transport were investigated in the tropical land crab *Gecarcinus lateralis* to determine the adaptations of the respiratory system for aerial respiration. The gills of *Gecarcinus* are reduced in size and specialized, in part, for salt and water uptake. The epibranchial space of the branchial chamber is very much enlarged and lined with what is probably a respiratory epithelium. There is a high ventilatory air-flow, produced by the beating of the scaphognathites, but the percentage extraction of oxygen is extremely low. This may be the result of ventilatory 'shunts', whereby a proportion of the air does not come into contact with the respiratory surfaces. The energetic cost of a high ventilation rate need not be high, because of the low inertial mass of air in comparison with water. A high oxygen tension gradient of 103 torr is maintained across the respiratory surfaces. This is interpreted as an adaptation to achieve a high oxygen diffusion rate through the reduced surface area of the gills. The blood has a relatively high oxygen capacity which is again thought to be an adaptation to compensate for the reduced gill surface area. Carbon dioxide tensions and content were high as in other terrestrial animals. Overall, the respiratory adaptations are thought to be related primarily to the reduction in the respiratory surface area which has evolved to deal with the problems of water conservation in these terrestrial animals.

INTRODUCTION

The tropical land crab *Gecarcinus lateralis* is generally considered to be one of the most terrestrial of the decapod Crustacea. The crabs live in burrows well above tide level, and their only contact with the sea is the brief period of immersion experienced by the females when the fertilized eggs are deposited at the edge of the tide (Bliss, 1979). Surprisingly little work has been carried out to determine the adaptations of the respiratory system associated with the necessity for aerial respiration. Copeland (1968) described the morphology of the gills which are reduced in size and have an accessory function in salt and water uptake, whilst Diaz & Rodriguez (1977) drew attention to the large volume of the branchial chamber and the possible respiratory function of the lining epithelium. Some of the transport characteristics of the blood were described by Redmond (1968) and more recently Smatresk, Preslar & Cameron

(1979) have described changes in the blood chemistry of crabs following enforced exercise. The ventilation of the branchial chambers by means of the beating of the scaphognathites, under normal conditions and under hypoxia and hypercapnia was described by Cameron (1975). The object of the present study was to describe the major characteristics of ventilation, circulation and blood gas transport of *Gecarcinus* in relation to its terrestrial mode of life.

MATERIALS AND METHODS

Crabs were air-freighted from the Cayman Islands and from Bermuda. The animals, which ranged in size from 20–80 g, were kept in large tanks in the laboratory and were provided with a substrate consisting of a mixture of sand, peat and leaf litter in which they were able to form their characteristic burrows. The crabs were maintained at 25 °C under a 12 h light:dark regime, were fed daily with a mixture of vegetables and had access to a dish of fresh water. The animals were kept in the laboratory for several weeks to enable them to acclimatize to laboratory conditions before experiments were commenced. All experiments on the animals were carried out at 25 °C.

Respiration measurements

Initially the rate of oxygen consumption was measured with constant pressure respirometers (Davies, 1966). These experiments showed that following the disturbance caused by handling, it normally took 4–5 h for the rate of oxygen consumption to decline to a lower and more constant rate which was representative of undisturbed, inactive animals. In all subsequent experiments, therefore, the animals were allowed to settle for at least 5 h before recordings were made or blood samples were taken.

More detailed studies of respiration rates were made using an adaptation of the method of Johansen, Lenfant & Mecklenburg (1970) and Taylor (1976) in which a rubber mask was fitted over the anterior part of the carapace. From this a large bore tube (5 mm internal diameter) passed to an inverted graduated cylinder filled with water. In order to minimize resistance to ventilation, the end of the tube was maintained 2–3 mm below the surface of the water as the exhaled air was collected in the cylinder. The ventilation volume ($\dot{V}_a$) was determined after equilibration of the pressure of the gas within the cylinder with atmospheric pressure, by adjusting the water level inside the cylinder to that in the surrounding vessel. A Radiometer oxygen electrode inserted into the exhalent tube, allowed determinations of the exhalent P_{O_2} to be made and oxygen consumption was then calculated, using the Fick principle. No significant differences were found in the rates of oxygen uptake, using the two different methods.

Measurements of heart rate and of the rate of beating of the scaphognathites were made using the impedance technique (Taylor, 1976), the leads for the latter being inserted ventrally into the branchial chamber through holes drilled in the branchiostegite.

Blood gas analysis

Post-branchial blood samples were withdrawn through a hole previously drilled through the carapace above the pericardium, dorsal to the heart. Care was taken that this hole did not pierce the hypodermis. The hole was covered with a small patch of rubber membrane (1 mm thick) which was sealed to the carapace with cyanoacrylate adhesive. This allowed blood samples to be taken using a syringe without loss of blood and with minimal disturbance to the animal. Pre-branchial blood samples were taken via the arthrodial membrane at the base of the pereiopods.

The blood samples were used to determine either the P_{O_2} and oxygen content, or pH, carbon dioxide content and lactate concentration. Some difficulty was experienced, however, in obtaining P_{O_2} and pH measurements, since the blood of *Gecarcinus* tends to clot very rapidly and it was often necessary to disregard results from blood samples in which clotting had begun. The P_{O_2} of the blood was measured by injecting the samples into a thermostatted chamber containing a Radiometer oxygen electrode. Oxygen content of the blood was determined by the method of Tucker (1967). Blood pH measurements were made using a Radiometer G299A capillary pH electrode and K172 reference electrode. The total CO_2 content of 30 μl samples of blood was determined by the method of Cameron (1971). The P_{CO_2} and concentration of bicarbonate and carbonate ions were then calculated from the pH and CO_2 content using the Henderson–Hasselbalch equations in the following forms:

$$\mathrm{pH} = \mathrm{pK_1'} + \log \frac{C_{CO_2} - \alpha CO_2 . P_{CO_2}}{\alpha CO_2 . P_{CO_2}}$$

and

$$\mathrm{pH} = \mathrm{pK_1'} + \log \frac{[HCO_3^-]}{\alpha CO_2 . P_{CO_2}} = \mathrm{pK_2'} + \log \frac{[CO_3^{2-}]}{[HCO_3^-]}.$$

Since values for the constants pK_1', pK_2' and αCO_2 have not been determined in *Gecarcinus*, values for these were derived from the data of Truchot (1976) for *Carcinus maenas*. The values obtained for the concentrations of bicarbonate and carbonate ions and for the P_{CO_2} may therefore be subject to slight error.

Lactate concentrations in pre-branchial blood were measured enzymatically using the method of Gutman & Wahlefeld (1974). All blood parameters were measured at the experimental temperature of 25 °C.

Oxygen dissociation curves for the blood of *Gecarcinus* were determined *in vitro* by tonometring blood samples in a Radiometer BMS II at 25 °C, with gas mixtures supplied by gas mixing pumps (Wösthoff, Bochum, W. Germany). The total oxygen content of 20 μl samples of blood was then determined using the method of Tucker (1967). To determine the extent of the Bohr effect, the pH of the blood was varied by modifying the partial pressure of CO_2 in the gas mixtures. The pH at the P_{50} was then measured using a Radiometer capillary pH electrode.

Notation and calculations

Because of the variation in the notation and units used in invertebrate respiratory physiology we have utilized a notation based upon that of McMahon, McDonald &

Wood (1979). Thus oxygen contents and uptake rates are expressed gravimetrically in μM, although volumetric units have been included in places to facilitate comparisons with the previous literature.

We have, however, deviated from the practice of previous workers in dealing with size-dependent parameters. It has been customary to express oxygen uptake, ventilatory flow, blood flow, and even the rate of beating of scaphognathites and heart on a weight-specific (usually kg) basis. However, since these weight-specific values are themselves size dependent, misleading conclusions can result from comparisons of animals of differing size. To circumvent this problem, we have made measurements from animals of a range of body sizes, plotted regression lines and have derived values for a 'standard' 30 g animal from the regression lines.

Respiratory coefficients, to characterize various parts of the respiratory system, were calculated as in McMahon *et al.* (1979). However, the Transfer Factor (T_{O_2}) which describe the diffusion characteristics of the gills (being equivalent to $D.A/L$ in the diffusion equation of Krogh (1919) where D is the diffusion constant, A the area and L the length of the diffusion path) was calculated by the original method of Randall, Holeton & Stevens (1967):

$$T_{O_2} = \frac{\dot{V}_{O_2}}{\Delta P_{O_2}} \quad \text{and} \quad T_{O_2} = \frac{\dot{M}_{O_2}}{\Delta P_{O_2}}$$

where $\dot{V}_{O_2}$ and $\dot{M}_{O_2}$ are the oxygen uptake rates of a 30 g animal and ΔP_{O_2} is the mean oxygen tension gradient across the gills, calculated from:

$$\Delta P_{O_2} = \tfrac{1}{2}(P_{i.O_2} + P_{e.O_2}) - \tfrac{1}{2}(P_{a.O_2} + P_{v.O_2}),$$

and is expressed as μM or μl $O_2.min^{-1}.torr^{-1}$. In this form, the Transfer Factor may be used in the analysis of oxygen diffusion across the gills of the particular size of animal (in this case 30 g).

RESULTS

The relationship between weight-specific oxygen consumption and body weight of inactive *Gecarcinus* is shown in Fig. 1. The values obtained are somewhat lower and less variable than those obtained by Cameron (1975) for active animals. The rate of heartbeat (Fig. 2) decreases with increasing body weight, showing a similar relationship to that of the rate of weight-specific oxygen consumption.

The rate of beating of the scaphognathites also shows a weight-specific relationship (Fig. 2). The rate was high (Table 1), although somewhat lower than that recorded by Cameron (1975) for similar sized animals. Periods of apnoea were occasionally observed in the resting animals and asynchrony of the beating of the two scaphognathites was commonly observed. Periods of reversed beating ('reversals') accompanied by an increase in rate were recorded from time to time. These were normally of short duration, but occasional long bursts lasting several minutes were observed. The high rate of beating by the scaphognathites produced a relatively high ventilatory flow ($\dot{V}_a$). As a result, the mean decrease in oxygen tension of the air was only 3·2 torr giving a percentage extraction ($Extr_a$) of only 2·0% (Table 1). The air convection requirement ($\dot{V}_a/\dot{M}_{O_2}$ or $\dot{V}_a/\dot{V}_{O_2}$), was 5·8 ml.μM^{-1} or 260 ml.ml^{-1} which compares closely with the mean value of 236 ml.ml^{-1} obtained by Cameron (1975).

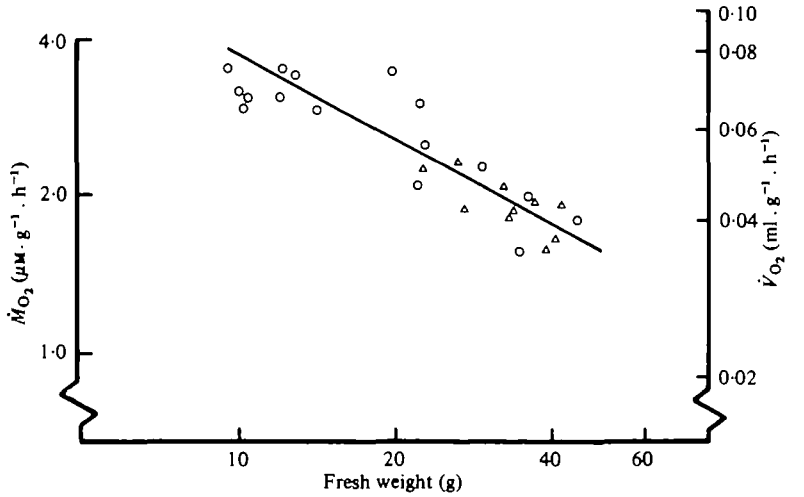

Fig. 1. The relationship between weight specific oxygen uptake rates and body weight of *Gecarcinus lateralis* at 25 °C. ○, Measured with a constant pressure respirometer. △, Determined by the Fick principle. Regression equation for $\dot{M}_{O_2}$: $\log \hat{y} = 1{\cdot}098 - 0{\cdot}53 \log X$.

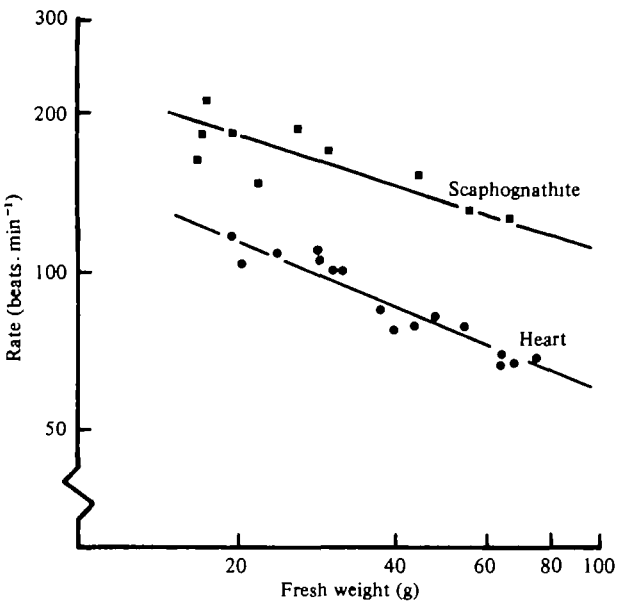

Fig. 2. The relationship between rates of beating of the scaphognathites and of the heart and body weight of *Gecarcinus lateralis* at 25 °C. Regression equations: *Heart* $\log \hat{y} = 2{\cdot}62 - 0{\cdot}43 \log X$; scaphognathite $\log \hat{y} = 2{\cdot}68 - 0{\cdot}32 \log X$.

The oxygen tension of post-branchial blood was high (80·5 torr) and this fell to a mean P_{O_2} of 25·6 torr in the mixed venous blood of the ventral sinus. Redmond (1968) obtained considerably lower values, 32 torr and 9 torr respectively, perhaps as a result of using more active crabs and not taking precautions which are now known to be necessary to minimize stress immediately prior to blood sampling. The mean oxygen carrying capacity of the blood (i.e. dissolved plus bound oxygen, see Mangum, 1977) was 0·76 μM . ml^{-1} and the mean oxygen capacity (i.e. bound oxygen) was

Table 1. *Respiratory and circulatory parameters for oxygen in* Gecarcinus lateralis *at* 25 °C

(Mean values ± standard deviations; n = 10–25.)

OXYGEN CONSUMPTION

$\dot{M}_{O_2}$ (μM.min^{-1})*	$1{\cdot}03 \pm 2{\cdot}48 \times 10^{-1}$
$\dot{V}_{O_2}$ (μl.min^{-1})*	$23{\cdot}14 \pm 3{\cdot}47$

VENTILATION

$\dot{V}_a$ (ml.min^{-1})*	$6{\cdot}02 \pm 1{\cdot}74$
f_{sc} (beats.min^{-1})*	186 ± 22
P_{i,O_2} (torr)	158·0
P_{e,O_2} (torr)	154·8

CIRCULATION

	P_{O_2} (torr)	C_{O_2} (μM.ml^{-1})	C_{O_2} (ml.100 ml^{-1})	S_{O_2} (%)	$\dot{V}_b$* (ml.min^{-1})	f^*_{heart} (beats.min^{-1})	S^*_v (ml.beat^{-1})	Blood O_2 capacity† (μM.ml^{-1})	Blood O_2 capacity† (ml.100 ml^{-1})
Post-branchial	$80{\cdot}5 \pm 7{\cdot}1$	$0{\cdot}63 \pm 0{\cdot}10$	$1{\cdot}41 \pm 0{\cdot}20$	96	4·1	$97 \pm 9{\cdot}5$	0·042	0·76	1·7
Pre-branchial	$25{\cdot}6 \pm 2{\cdot}6$	$0{\cdot}38 \pm 0{\cdot}06$	$0{\cdot}85 \pm 0{\cdot}05$	64					

EXCHANGE COEFFICIENTS

$Extr_a$ (%)	ΔP_{O_2} (torr)	$Extr_b$ (%)	$T^*_{O_2}$ (μM.min^{-1}.torr^{-1})	$T^*_{O_2}$ (μl.min^{-1}.torr^{-1})	$\dot{V}_a/\dot{V}_b$*	$\dot{V}_a/\dot{M}^*_{O_2}$ (ml.μM^{-1})	$\dot{V}_a/\dot{V}^*_{O_2}$ (ml.ml^{-1})	$\dot{V}_b/\dot{M}^*_{O_2}$ (ml.μM^{-1})	$\dot{V}_b/\dot{V}^*_{O_2}$ (ml.ml^{-1})
$2{\cdot}01 \pm 1{\cdot}6$	103·4	39·7	$9{\cdot}98 \times 10^{-3}$	0·224	1·46	5·80	260·15	3·97	177·18

* Values for a standard 30 g animal.

† Oxygen carrying capacity at P_{O_2} 158 torr.

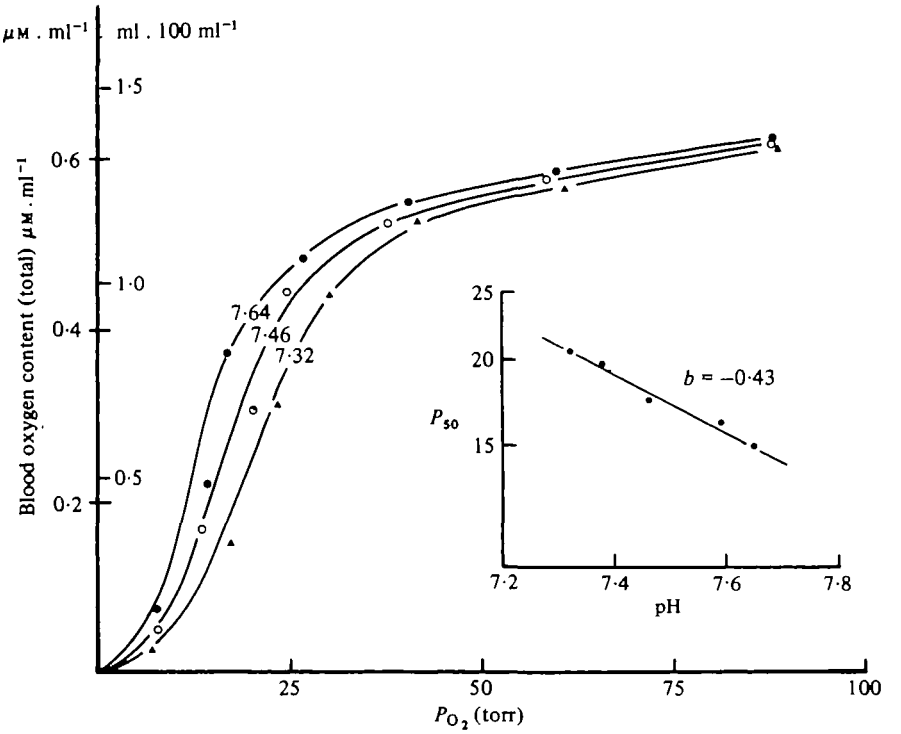

Fig. 3. Oxygen dissociation curves for whole blood of *Gecarcinus* determined at three pH values obtained by tonometering the blood at P_{CO_2} 6 torr (pH 7·32), 8 torr (pH 7·46) and 10 torr (pH 7·64). Insert: Plot of P_{50} *v* pH to show Bohr shift.

0·53 μM.ml^{-1} at a P_{O_2} of 158 torr. The total oxygen content of post-branchial blood was 0·63 μM.ml^{-1} (1·41 ml.100 ml^{-1}). By reference to oxygen dissociation curves (see later), haemocyanin is 96 % saturated at the post-branchial oxygen tension of 80·5 torr so that 0·51 μM.ml^{-1} (= 81 %) are carried by the pigment and 0·12 μM.ml^{-1} (= 19 %) are carried in physical solution. By contrast, in the pre-branchial blood at a P_{O_2} of 25·6 torr, 0·34 μM.ml^{-1} (= 89 %) are carried by the pigment and 0·037 μM.ml^{-1} (= 11 %) are carried in physical solution. By subtraction therefore, 68 % of the oxygen supplied to the tissues is carried by the pigment and 32 % is carried in solution in the plasma.

Oxygen dissociation curves for whole blood, determined at P_{CO_2} 6, 8 and 10 torr, are shown in Fig. 3. For the *in vivo* range of pH (7·479–7·414, Table 2), the *in vitro* P_{50} values were between 17–20 torr. The blood exhibited a positive Bohr shift and the slope of the line log ΔP_{50}/pH for the pH range 7·2–7·6 was −0·43 (ΔP_{50}/pH unit = 17 torr).

Because of the inherent difficulties of sampling blood from within individual gills, the assumption was made that there is no venous shunt at the gills, and that gill perfusion is therefore equal to cardiac output ($\dot{V}_b$) which could then be calculated by the Fick principle. For a 30 g crab $\dot{V}_b$ was calculated to be 4·1 ml.min^{-1}, and for a mean heartbeat of 97 min^{-1}, the stroke volume was estimated to be approximately 4·2 × 10^{-2} ml.beat^{-1}. The flow of oxygen to the tissues, or the capacity rate, was calculated from the product of C_{a,O_2} and $\dot{V}_b$ and has the value of 2·58 μM O_2.min^{-1}. Of this, 40 % diffuses from the blood as it passes through the tissues ($Extr_b$).

Table 2. *Respiratory and circulatory parameters for carbon dioxide in* Gecarcinus lateralis *at 25 °C*

(Mean values ± standard deviations; n = 10–25.)

	$^*P_{CO_2}$ (torr)	C_{CO_2} (μM.ml^{-1})	$^*[HCO_3^-]$ (μM.ml^{-1})	$^*[CO_3^{2-}]$ (μM.ml^{-1})	$[CO_2]$ (μM.ml^{-1})	pH	Lactate (μM.ml^{-1})
Post-branchial	7·6	8·7 ± 0·7	8·4	$9·9 \times 10^{-3}$	0·21	7·479 ± 0·05	
Pre-branchial	9·1	9·1 ± 0·8	8·7	$8·9 \times 10^{-3}$	0·28	7·414 ± 0·03	1·38 ± 0·03

* Values calculated from the Henderson–Hasselbalch equations.

Values for the total blood carbon dioxide content and pH, together with the derived values for P_{CO_2}, dissolved CO_2 and $[HCO_3^-]$ and $[CO_3^{2-}]$ ions are given in Table 2.

DISCUSSION

The rates of oxygen uptake by active *Gecarcinus* were comparable to those recorded in the same species by Cameron (1975). However, in the present study all measurements were made on resting animals following a period of 4 h, during which time the animals were undisturbed. The oxygen uptake rates under these conditions were approximately one-half of the rates recorded in animals shortly after handling. Comparisons of $\dot{M}_{O_2}$ with other land crabs are difficult either because of difference in body size, or because $\dot{M}_{O_2}$ and body size regression equations are not given (e.g. McMahon & Burggren, 1979). Values of $\dot{V}_{O_2}$ of approximately 0.17 ml $O_2 . g^{-1} . h^{-1}$ recorded for *Coenobita brevimanus* of 10 g weight by Burggren (1975) were approximately double the $\dot{V}_{O_2}$ which we have recorded for quiescent *Gecarcinus* of similar weight. Since the *Coenobita* appear not to have been left for 4–5 h before measurements began, it is likely that the values recorded by Burggren are for active, rather than quiescent animals. However, the $\dot{M}_{O_2}$ of a 30 g *Gecarcinus* recorded by us, compares closely with the rate recorded for similar size quiescent ghost crabs *Ocypode quadrata* (Burnett, 1979).

The branchial chambers of most land crabs have undergone some modification in the course of their evolution. In most cases the gills have become reduced in number and in size (Gray, 1957) and in some crabs the epithelial lining of the branchial chambers has become convoluted to serve as an accessory lung (Diaz & Rodriguez, 1977). In *Gecarcinus* the volume of the branchial chamber is enormously increased, giving a large epibranchial space which is lined above with a simple, vascularized epithelium which probably also participates in oxygen uptake (Diaz & Rodriguez, 1977). The gills are reduced in size, and the last two pairs appear to be modified for salt and water uptake and probably play a very small part in the uptake of oxygen (Copeland, 1968). Ventilation of the branchial chamber is by means of the beating of the scaphognathites. Air is drawn in only through the Milne-Edwards opening at the base of the chelipeds, the remainder of the branchiostegite making a tight fit against the abdominal plates. The air then flows through the anterior gills, whose individual lamellae are kept apart by knob-like protuberances, and into the large volume of the epibranchial space before passing through the scaphognathite chamber to the exterior.

The rate of beating of the scaphognathites is high, producing a high rate of convective air-flow. Associated with this, the percentage extraction is extremely low, at only 2·0%. This value is similar to those recorded in other terrestrial crabs, e.g. 2·3% for *Gecarcinus* (Cameron, 1975), 2·9% for *Cardisoma* (Herreid, Lee & Shah, 1979) and 5·2% for *Birgus* (Cameron & Mecklenburg, 1973). An index of the requirement for ventilation to meet respiratory demands can be obtained from the ratio of $\dot{V}_a/\dot{V}_{O_2}$, termed the air convection requirement. In water breathers, values of 300 to more than 1000 ml.ml^{-1} have been observed, whereas air breathers typically exhibit values of less than 50 (Dejours, Garey & Rahn, 1970; Mangum, 1977). In *Gecarcinus* the air convection requirement is 260 ml.ml^{-1} (236 ml.ml^{-1}, Cameron, 1975). The high rate of ventilation can probably be explained in terms of air 'shunts' at the respiratory surfaces, with only a proportion of the air which is drawn in actually coming into contact with the gill and (in view of the large epibranchial air volume), the branchial chamber epithelium. The potential disadvantage of a high rate of ventilation, is probably not in the energetic costs involved (since as Cameron (1975) pointed out air has a relatively low inertial mass) but in the potential evaporative loss of water. The functional significance of the enlarged epibranchial space, which may be largely responsible for the requirement for a high rate of ventilation, is still not apparent.

Reversal of ventilatory flow has not been described in other land crabs. In aquatic crabs it has been suggested that reversals may increase the ventilatory flow over the posterior gills (Arudpragasam & Naylor, 1964), increase blood flow to the gills (Blatchford, 1971) or may be analogous to coughing in vertebrates, serving to dislodge particles trapped on the gill lamellae (Hughes, Knights & Scammell, 1969; Wilkens & McMahon, 1972). Recent experimental findings (Schembri, 1979) now favour the latter hypothesis and this would appear to be the only satisfactory explanation for the phenomenon in *Gecarcinus*.

The post-branchial oxygen tension of 80·5 torr in *Gecarcinus* is high, and compares with the value of 78 torr in *Birgus* (Cameron & Mecklenburg, 1973), although two other land crabs *Coenobita* and *Ocypode* have post-branchial oxygen tensions of only 13·7 and approximately 21 torr respectively (McMahon & Burggren, 1979; Burnett, 1979). The high P_{a,O_2} of *Gecarcinus* is achieved despite the reduction in gill area available for diffusion. The rate of diffusion per unit surface area is probably increased in comparison with other crabs. In the absence of actual surface area measurements, it is only possible to speculate, but it appears likely that this is achieved, in part, by the maintenance of a high P_{O_2} gradient across the gills. The ΔP_{O_2} of 103 torr compares with values in aquatic crabs of 58 torr in *Cancer* (Johansen *et al.* 1970) and 80 torr in *Carcinus* (Taylor, 1976). The high gradient, in turn is produced by a low oxygen tension in the venous return (P_{v,O_2} = 26 torr) and a high mean P_{O_2} in the external medium, which results from the high rate of ventilation referred to above.

The oxygen affinity of *Gecarcinus* blood is lower than that of some aquatic decapods and this is in agreement with the correlations which Young (1972) found between the lowering of blood affinity and increasing terrestrialness in crabs. However, since this work was published, there have been a number of studies on crab respiratory physiology which have shown wide variations in P_{50} values in both the aquatic and terrestrial groups (Mangum & Weiland, 1975; McMahon *et al.* 1979; McMahon & Burggren, 1979). Whilst there appears to be little correlation between blood oxygen affinity and

terrestrialness, there does appear to be a strong association between affinity and the post-branchial oxygen tensions, as in other animals. Thus *Coenobita* has a post-branchial P_{O_2} of 13·7 torr and a blood P_{50} of only 5·5 torr, whilst in *Gecarcinus* the P_{a,O_2} is 80·5 torr and the P_{50} is 17–20 torr.

Young (1972) also drew attention to an apparent reduction of the magnitude of the Bohr shift in terrestrial crabs when compared with aquatic species and noted that a similar effect was observable in air-breathing fish. Although the values of $\Delta \log P_{50}/\mathrm{pH}$ obtained from *Gecarcinus* (−0·43, this study; −0·33, Redmond, 1968) conform to this and are lower than those recorded for any other crab, it should be pointed out that the values of −0·84 for *Coenobita* (McMahon & Burggren, 1979) and −0·76 for *Ocypode* (Burnett, 1979) tend towards the high value of −0·92 for the aquatic *Libinia emarginata* (Burnett, 1979) and contrast again with the extremely low value of −0·27 in the aquatic *Cancer magister* (Johansen *et al.* 1970). The general conclusion at present therefore is that the oxygen affinity and the magnitude of the Bohr shift are both somewhat variable features in crabs and do not correlate with the degree of terrestrialness.

The oxygen capacity of *Gecarcinus* haemocyanin at 0·53 μM.ml^{-1} (0·77 μM.ml^{-1}, Redmond, 1968) is high in comparison with aquatic crabs, although not as high as that of *Coenobita* which carries 1·24 μM.ml^{-1} at saturation (McMahon & Burggren, 1979). This is undoubtedly an adaptation which is associated with the reduction of the gill area in these crabs, and obviates the necessity to increase perfusion in order to achieve the capacity rate required for delivery of sufficient oxygen to the tissues. The blood convection requirement ($\dot{V}_b/\dot{V}_{O_2}$) is 177 ml.ml^{-1} and fits the inverse relationship with post-branchial oxygen content of the blood (C_{a,O_2}) described for a number of other animals by Dejours *et al.* (1970) and Mangum (1977).

The values for the carbon dioxide content and P_{CO_2} of the blood of *Gecarcinus* are very similar to those recorded by Howell *et al.* (1973) and by Smatresk *et al.* (1979) in the same species. The blood of aquatic animals is generally characterized by low carbon dioxide tensions, since the higher solubility of a given volume of the gas in water causes a lower partial pressure than it would in air, thus creating a larger diffusion gradient (Rahn, 1966; Howell *et al.* 1973). The post-branchial P_{CO_2} of 7·56 torr and the post-branchial carbon dioxide content of 8·71 μM.ml^{-1} are both very much higher than in aquatic crabs (Howell *et al.* 1973). In this respect therefore *Gecarcinus* conforms to the pattern of elevated carbon dioxide levels which have been found in the other terrestrial crabs *Birgus* (Cameron & Mecklenburg, 1973) and *Coenobita* (McMahon & Burggren, 1979).

The major changes observed in *Gecarcinus* associated with its terrestrial mode of life appear to be a consequence of morphological changes to the branchial chamber which are related in part to the use of some of the gills as salt and water absorption organs. The high rate of ventilation may be required to compensate for an inefficient air-flow over the respiratory surfaces, but it also maintains a high oxygen tension in the branchial chambers which aids in the diffusion of oxygen through the reduced surface area of the gills. Efficient delivery of oxygen by blood convection is aided by an increase in the oxygen carrying capacity of the blood which obviates the need for an energetically expensive increase in cardiac output.

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