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GAS EXCHANGE THROUGH THE LUNGS AND GILLS IN AIR-BREATHING CRABS

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Summary

Lung and gill performance in gas exchange have been evaluated in eight species of air-breathing crabs with two different lung circulatory designs, those with portal systems and smooth lung linings, and those without portal systems and with invaginated and evaginated lung linings. In all species, the lungs were extremely effective in oxygen uptake whilst the performance of the gills was inferior. An exception to this was *Gecarcoidea natalis*, which has gills highly modified for aerial gas exchange; its gills and lungs were equally efficient in O_2 uptake. The relative efficiencies of the lungs and gills in CO_2 excretion differed between species, with the gills being the major site of CO_2 loss in the more amphibious species and the lungs having an increasingly important role in the more terrestrial crabs. The presence or absence of lung portal systems was not found to correlate with either saturation rates or efferent oxygen concentrations, with both lung types being extremely efficient in O_2 uptake. The lungs with portal systems showed a large increase in oxygen content in the first lacunar bed and progressively smaller increases in the next two; these lungs may, therefore, have some reserve for exercise.

Introduction

Air-breathing crabs have universally retained gills but have also developed accessory breathing organs, usually lungs formed from the inner lining of the branchiostegites. A noticeable shift in the position of the viscera in terrestrial crabs is associated with this development. The digestive gland and gonads, which protrude along the dorsal margins of the branchiostegites in aquatic crabs, have become restricted to the central thoracic cavity, thus freeing the branchiostegal surfaces for gas exchange. Aquatic crabs generally have large gills with very thin closely packed lamellae, and often the anterior gills are lined by a thin ‘respiratory’ epithelium, whereas the posterior gills are lined with thick ‘osmoregulatory’ cells (Copeland and Fitzjarrell, 1968; Pequeux *et al.* 1988;

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Compère *et al.* 1989). The structural modifications of the gills and lungs of land crabs indicate the retention of a gas-exchange function in the gills and strongly suggest a major role for the lungs in gas exchange (see von Raben, 1934; Diaz and Rodriguez, 1977; Greenaway and Farrelly, 1984, 1990; Farrelly and Greenaway, 1987, 1992, 1993). Thus, the lungs are well vascularized with an extremely short blood/gas diffusion distance and often have adaptations to increase surface area (Greenaway and Farrelly, 1990), all of which greatly increase the diffusing capacity of the respiratory system. In contrast, the gills are reduced in size and area and the epithelium is usually modified for ion transport (long apical leaflets, deep basal infoldings and densely packed mitochondria), with relatively long blood/gas diffusion distances (Farrelly and Greenaway, 1992). These features alone would suggest an osmoregulatory rather than a gas-exchange function, but the development of lamellar stiffening and spacing devices by many species suggests a need for convection and hence the retention of gas exchange.

The relative contributions of these organs and their efficiency in the excretion of carbon dioxide and uptake of oxygen are poorly known and may well differ between species, especially if the amphibious habit is retained. To measure the efficiency of these organs in gas exchange, it is necessary to sample pre- and post-pulmonary and afferent/efferent branchial blood. This has been achieved only for the large terrestrial anomuran *Birgus latro* (Greenaway *et al.* 1988), in which the efferent branchial vessel is accessible *via* a flexible branchiostegal flap. In contrast, the efferent branchial veins in brachyurans, which have a rigid branchiostegite, cannot be sampled without damaging the lung and the branchiopericardial veins, which carry post-branchial blood to the heart, run deep within the thorax and are inaccessible to sampling. Recent advances in our knowledge of the vasculature of the lungs, however, enables sampling of pre- and post-pulmonary blood. Pericardial blood in terrestrial crabs represents the mixed returns from the branchial and pulmonary systems, and comparison of the gas contents of this mixed blood with that of post-pulmonary blood allows indirect assessment of the relative efficiencies of the gills and lungs in gas exchange (Greenaway and Farrelly, 1990). However, measurements of the relative blood flows to the gills and lungs are necessary to apportion gas exchange unequivocally to the two respiratory organs.

Several circulatory patterns have been identified in the lungs of land crabs, using corrosion casting techniques (Farrelly and Greenaway, 1993). The simplest of these patterns consisted of an afferent system which interdigitates with an efferent system. The blood passes from one to the other through a single lacunar network located close to the respiratory surface; for example, in the Ocypodidae and Mictyridae (Fig. 1A). In the second pattern, the afferent system is separated from the efferent one by two interdigitating portal systems (branching networks, arising and terminating in a lacunar bed), and blood passes through three lacunar systems during transit of the lung; for example, in the Gecarcinidae, Grapsidae and Sundathelphusidae (Fig. 1B). The lung circulation in both types runs in parallel with that of the branchial circulation, with each lung returning haemolymph to the pericardium *via* a large pulmonary vein which flows around the perimeter of the branchiostegite.

The above morphological studies unveiled the possibility of sampling directly from the pulmonary vein and from individual portal systems within the lung circulation. In this paper we assess both the efficiency of the lungs (compared with the gills) and the efficiency of different lung circulatory designs, i.e. portal *versus* non-portal lungs or single *versus* multiple capillary pass lungs.

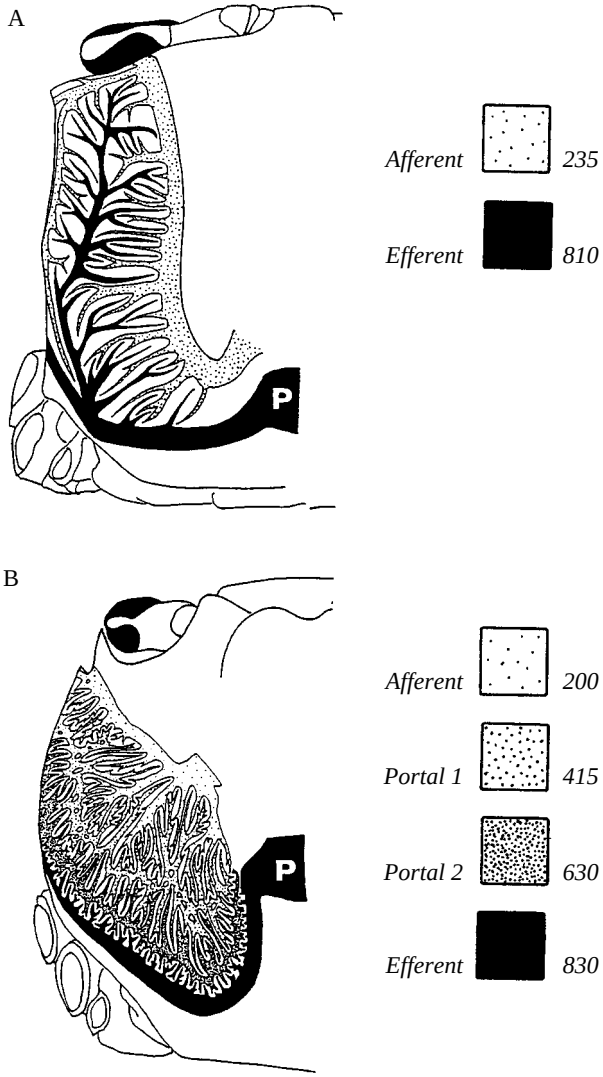

Fig. 1. Schematic drawing of the two major patterns of lung vasculature present in air-breathing brachyurans, as represented by (A) *Ocypode* and (B) *Geograpsus*. The stippled regions represent the different vessel systems in the lung, while the space between the vessels is occupied by lacunae. The oxygen content (μmol l^{-1}) achieved in each system is also indicated. P, pericardial sinus. (Adapted from von Raben, 1934.)

Materials and methods

Eight species of air-breathing brachyurans were used in the study and after collection were housed in terraria in a constant-temperature room at 25 °C and 80 % relative humidity (RH) on a 12 h:12 h light:dark cycle. *Gecarcoidea natalis* (Pocock, 1888), *Cardisoma hirtipes* (Dana, 1852), *Geograpsus grayi* (Milne Edwards, 1853) and *Geograpsus crinipes* (Dana, 1851) were collected on Christmas Island (an Australian Territory in the Indian Ocean), while *Ocypode cordimanus* (Desmarest, 1852), *Ocypode ceratophthalma* (Pallas, 1772) and *Mictyris longicarpus* (Latreille, 1806) were collected from the east coast of Australia and *Holthuisana transversa* (Von Martens, 1869) from western New South Wales. Animals were maintained on a diet of mixed vegetables and cat biscuits and were given access to fresh water and occasionally sea water.

Experimental protocols

Two experimental series were conducted. In series A, the objective was to establish the relative efficiency of the gills and lungs in gas exchange of resting crabs. This involved determination of pH and oxygen and carbon dioxide partial pressures and concentrations in pre- and post-pulmonary and pericardial blood. Comparison of respiratory gases in post-pulmonary and arterial (pericardial) blood indicated whether branchial gas exchange was greater than, less than, or similar to pulmonary gas exchange. Series B examined the profiles of gas exchange across the lung by sampling from afferent, efferent and portal systems of the lung.

Series A

Small holes were drilled through the cuticle (without penetrating the hypodermis) above the pericardium and the posterior portion of the pulmonary vein of each animal. After a minimum period of 24 h recovery, 15 μl samples of haemolymph were taken from the infrabranchial sinus, the pulmonary vein and the pericardial sinus in a 25 μl Hamilton syringe (total sampling time less than 1 min). The first 10 μl of these samples was used to determine gas concentrations and the last 5 μl was discarded to avoid contamination with dead-space air in the syringe.

After several weeks of recovery, sampling was repeated on the other side of the animals by taking 1 ml haemolymph samples with a glass syringe and determining gas partial pressures (P_{O_2} and P_{CO_2}). The last 200 μl of the samples was discarded. Syringes were stored on ice for a maximum of 15 min before analysis. Differences between pulmonary and arterial, arterial and venous, and pulmonary and venous blood gas variables were tested using the *t*-test for paired samples.

Series B

In the second series of measurements, oxygen concentrations were measured in haemolymph sampled from each vessel system within the lung [afferent, portals 1 and 2 (not present in the ocypodids) and efferent]. At each sampling, only two of the sites were

used and, after several days of recovery, the animals were sampled from a second different pair of sampling sites, so as finally to obtain a measure for each vessel system within the lung for each animal.

The animals were prepared for sampling as for series A, but with holes drilled over an afferent lung vessel (the dorsal branchiostegal vein), an efferent lung vessel (the pulmonary vein) and, in species with portal systems, over a large vessel within each lung portal system. Large blood vessels were visible through the carapace either because of density differences in the carapace tissue or because of contrasting pigmentation of the carapace over the vessels (e.g. *Gecarcoidea natalis*). *Mictyris* and *Holthuisana* were not used in this series for reasons of size and availability. The sampling protocol for these measurements was the same as for those in series A. After several days of recovery, the pH of 100 μl samples of afferent and efferent lung haemolymph was measured, and the concentrations of copper were determined in 1 ml venous samples taken from the infrabranchial sinus. Copper concentrations were used to calculate the concentrations of haemocyanin in the haemolymph, thereby estimating the maximum oxygen-carrying capacity of the blood (Hc-O_2max). Differences between the different vessel systems within the lung were tested using a *t*-test.

Haemolymph analyses

The partial pressure of oxygen and carbon dioxide (P_{O_2} and P_{CO_2}) in haemolymph samples were measured in a BMS3 blood microsystem (Radiometer, Copenhagen, Denmark) thermostatted at 25 °C. Electrodes were calibrated with humidified gas mixtures delivered by Wösthoff gas-mixing pumps (type SA 18, Wösthoff, Bochum, Germany). P_{O_2} and P_{CO_2} were displayed on the expanded scale of a PHM73 meter (Radiometer). Haemolymph pH was measured using the G299a capillary electrode of a BMS3 and displayed on a PHM72 (Radiometer).

Oxygen content (C_{O_2}) of haemolymph samples was measured by the method of Tucker (1967) according to Bridges *et al.* (1979). Carbon dioxide content (C_{CO_2}) was determined by the method of Cameron (1971) employing 15 mmol l^{-1} $NaHCO_3$ standards. Concentrations of copper in haemolymph samples were determined with a Varian AA175 atomic absorption spectrophotometer as described previously (Sparkes and Greenaway, 1984).

Results

Series A – gas exchange by lungs and gills

Oxygen uptake

Values are presented for oxygen content in arterial (pericardial), venous and post-pulmonary haemolymph in eight species of air-breathing crabs and for P_{O_2} in four of these species (Table 1). Significant differences were found in the P_{O_2} and C_{O_2} between arterial and venous haemolymph in all species examined (Table 2). Pulmonary haemolymph contained significantly more oxygen, and had a higher

Table 1. *Oxygen content and partial pressure of pulmonary (P), arterial (A) and venous (V) haemolymph in rested crabs*

	Oxygen content (μmol l^{-1})				P_{O_2} (kPa)			
Species	*N*	P	A	V	*N*	P	A	V
Gecarcoidea natalis	10	764±215	698±263	233±72	9	3.71±1.63	2.80±0.63	1.35±0.32
Cardisoma hirtipes	26	992±249*	826±195	217±104	13	3.80±1.75*	1.65±0.68	0.85±0.15
Geograpsus grayi	14	1100±243*	860±203	120±67	6	5.97±2.13*	3.44±0.64	1.41±0.39
Geograpsus crinipes	26	949±293*	733±233	269±159	8	8.40±2.56*	3.87±1.44	1.88±0.25
Mictyris longicarpus	50	828±273*	717±258	200±107	–	–	–	–
Ocypode cordimanus	40	826±241*	714±212	182±61	–	–	–	–
Ocypode ceratophthalma	8	908±202*	756±200	274±71	–	–	–	–
Holthuisana transversa	16	369±101*	272±81	132±44	–	–	–	–

*Indicates a significant difference between pulmonary and arterial values (P<0.05).
All values are means ± S.D.

Table 2. *Mean values (± S.D.) for pulmonary–arterial, pulmonary–venous and arterial–venous differences in haemolymph oxygen content and partial pressure for rested crabs*

	C_{O_2} differences (μmol l^{-1})				P_{O_2} differences (kPa)			
Species	*N*	P–A	P–V	A–V	*N*	P–A	P–V	A–V
Gecarcoidea natalis	10	67±163	531±186*	465±224*	9	0.91±1.24	2.36±1.61*	1.45±0.57*
Cardisoma hirtipes	26	166±316*	609±221*	615±226*	13	2.15±2.08*	2.95±1.73*	0.80±0.71*
Geograpsus grayi	14	240±317*	980±252*	740±214*	6	2.53±1.91*	4.56±1.73*	2.03±0.44*
Geograpsus crinipes	26	216±374*	680±334*	464±282*	8	4.53±3.07*	6.52±2.53*	1.99±1.41*
Mictyris longicarpus	50	112±375*	628±293*	517±279*	–	–	–	–
Ocypode cordimanus	40	113±321*	645±249*	532±220*	–	–	–	–
Ocypode ceratophthalma	8	153±139*	570±216*	425±242*	–	–	–	–
Holthuisana transversa	16	97±99*	237±91*	140±74*	–	–	–	–

*Significant P–A, P–V or A–V difference, P<0.05.
P, pulmonary haemolymph; A, arterial (pulmonary + branchial) haemolymph; V, venous haemolymph.

partial pressure of oxygen, than mixed (gills and lungs) arterial haemolymph from the pericardial sinus, in every species except *Gecarcoidea natalis* (Tables 1, 2), indicating that significant oxygen loading had occurred in the lung. The lower oxygen content of arterial blood indicated that the pulmonary concentrations were considerably diluted by haemolymph of lower oxygen content returning from the gills. Thus, in these species, the lung was clearly the major site of oxygen uptake. In *G. natalis* there was no significant difference between pulmonary and arterial haemolymph in either P_{O_2} or oxygen content, but both were significantly higher than in venous haemolymph. The absence of a branchial dilution effect in this species indicates a similar oxygen content in pulmonary and branchial haemolymph, suggesting that a similar level of oxygenation occurred in both the gills and the lungs. Another possible explanation is that there was no flow through the branchial circuit; however, this is extremely unlikely given the highly nodulated structure of the gills, which function to increase surface area and to maintain both perfusion and ventilation of the lamellae.

Carbon dioxide excretion

The pattern of carbon dioxide excretion was more complex than that for oxygen uptake and is treated on a species by species basis below. No significant differences were found between mean values for carbon dioxide content of arterial, pulmonary or venous haemolymph in either *Ocypode cordimanus* or *Holthuisana transversa*, although the trend of the data indicated loss of CO_2 from both lungs and gills (Tables 3, 4). Values for P_{CO_2} were not measured for these species, but a significant increase in pH across the lung of *Ocypode cordimanus* was indicative of a loss of CO_2 by that route (Table 5).

In *Mictyris longicarpus*, both pulmonary and arterial haemolymph had a significantly lower CO_2 content than venous haemolymph, which indicated a loss of CO_2 across both lungs and gills. There was no significant difference between the mean values for CO_2 content of arterial and pulmonary haemolymph although, in individual crabs, pulmonary C_{CO_2} tended to be lower than arterial C_{CO_2}.

In *Geograpsus grayi* and *Gecarcoidea natalis*, both pulmonary and arterial C_{CO_2} values were significantly lower than venous values, but no significant difference in mean CO_2 content was found between pulmonary and arterial haemolymph (Tables 3, 4). A similar pattern was found for P_{CO_2} measurements, and there was a significant increase in pH across the lung. This indicates that both the gills and the lungs contribute to the excretion of CO_2.

In *Cardisoma hirtipes*, there was no significant difference in the mean CO_2 content of pulmonary and venous haemolymph, suggesting that only negligible amounts of CO_2 were excreted across the lungs. However, despite a significant drop in CO_2 content in pericardial haemolymph compared with venous haemolymph, there was no significant difference between pulmonary and pericardial C_{CO_2} values, suggesting that, although most CO_2 is lost across the gills, a small quantity is also lost across the lungs (individual data for pulmonary C_{CO_2} generally fell between arterial and venous values). P_{CO_2} data

Table 3. *Carbon dioxide content and partial pressure of pulmonary (P), arterial (A) and venous (V) haemolymph in rested crabs*

	C_{CO_2} (mmol l^{-1})				P_{CO_2} (kPa)			
Species	*N*	P	A	V	*N*	P	A	V
Gecarcoidea natalis	10	13.9±2.5	14.2±2.8	14.8±2.5	9	1.75±0.32	1.81±0.27	2.13±0.25
Cardisoma hirtipes	12	17.7±1.8	17.4±2.4	18.1±2.0	13	1.95±0.39*	1.75±0.25	2.07±0.36
Geograpsus grayi	20	11.4±3.3	11.6±3.3	12.2±2.9	6	1.11±0.33	1.03±0.27	1.33±0.35
Geograpsus crinipes	10	12.9±1.7*	12.5±1.7	12.9±1.8	8	1.37±0.24	1.33±0.20	1.59±0.24
Mictyris longicarpus	11	17.6±3.5	17.8±3.6	18.2±3.2	–	–	–	–
Ocypode cordimanus	28	14.8±3.8	15.6±3.5	16.1±3.6	–	–	–	–
Holthuisana transversa	14	12.8±2.5	13.4±2.0	14.1±2.2	–	–	–	–

*Indicates a significant difference between pulmonary and arterial values (P<0.05).
All values are means ± S.D.

Table 4. *Mean values (± S.D.) for pulmonary–arterial, pulmonary–venous and arterial–venous differences in haemolymph carbon dioxide content and partial pressure for rested crabs*

	C_{CO_2} differences (mmol l^{-1})				P_{CO_2} differences (kPa)			
Species	*N*	P–A	P–V	A–V	*N*	P–A	P–V	A–V
Gecarcoidea natalis	10	–0.30±1.20	–0.88±0.57*	–0.59±0.97†	9	–0.07±0.16	–0.39±0.29*	–0.32±0.29*
Cardisoma hirtipes	12	0.28±1.39	–0.35±1.17	–0.62±0.97*	13	0.2±0.17*	–0.12±0.23*	–0.32±0.19*
Geograpsus grayi	20	–0.14±0.49	–0.74±1.13*	–0.60±1.10*	6	0.08±0.08	–0.23±0.16*	–0.31±0.17*
Geograpsus crinipes	10	0.34±0.38*	–0.02±0.41	–0.36±0.44*	8	0.04±0.13	–0.21±0.11*	–0.25±0.15*
Mictyris longicarpus	11	–0.19±0.64	–0.60±0.52*	–0.41±0.70†	–	–	–	–
Ocypode cordimanus	28	–0.78±5.17	–1.30±5.21	–0.52±5.02	–	–	–	–
Holthuisana transversa	14	–0.67±3.26	–1.32±3.34	–0.65±2.98	–	–	–	–

*Significant P–A, P–V or A–V difference, P<0.05.
†Significant P–A, P–V or A–V difference, 0.10>P>0.05.
P, pulmonary haemolymph; A, arterial haemolymph (pulmonary+branchial); V, venous haemolymph.

showed that both pulmonary and arterial haemolymph had significantly lower CO_2 tensions than venous haemolymph. A small but significant increase in pH also occurred across the lungs, which again indicated some loss of CO_2 across this route. P_{CO_2} values of pericardial haemolymph were significantly lower than pulmonary values, which suggests that the gills are more important in CO_2 excretion than are the lungs, but that the lungs are making a small contribution.

In *Geograpsus crinipes*, arterial C_{CO_2} was significantly lower than pulmonary C_{CO_2}, indicating that branchial excretion is greater than pulmonary excretion. Although pulmonary and venous C_{CO_2} were not significantly different, there was a small difference in P_{CO_2}, suggesting that the lungs may contribute a small amount to CO_2 excretion (Tables 3, 4). No significant pH differences were found across the lungs, but the sample size for these measurements was very small (N=3). The data are consistent with the gills representing the major route of CO_2 excretion in *G. crinipes*, while the lungs may play a minor role.

Series B – oxygen uptake in lungs with and without portal systems

Crabs with portal systems

This group comprised the gecarcinids, *Gecarcoidea* and *Cardisoma*, and the two species of *Geograpsus*. In all but *Geograpsus crinipes*, oxygen content of the haemolymph increased significantly between each vessel system from afferent to efferent (Table 5; Fig. 1B). In *G. crinipes*, the mean values also increased from afferent to efferent, but significant differences were only found between the afferent system and the first portal system and between the first portal system and the efferent system, i.e. no significant difference was found between the first and second portal systems and between the second portal system and the efferent system. These inconsistencies are due perhaps to the small sample sizes and large variances. The percentage saturation of the efferent haemolymph was high in all four species, averaging around 74 % with a mean afferent–efferent difference of 51 % (Table 6). The pattern of oxygen uptake across the lung was very similar in the different species, with saturation rates dropping off progressively through each lacunar (capillary) system. Nearly half (47 %) of the total oxygen uptake by the haemolymph occurred during transit through the first lacunar system (between the afferent system and portal system 1), around 34 % was picked up in the second system (between portal systems 1 and 2) and only 20 % was taken up in the third system (between portal system 2 and the efferent system) (Table 6).

Crabs without portal systems

The ocypodids have lungs with simpler vasculature, the afferent system interdigitating directly with the efferent system so that there is only one lacunar gas-exchange system compared with three in the previous group. Oxygen contents differed significantly between afferent and efferent haemolymph in both species of *Ocypode*, with a mean saturation of 85 % and an average increase between afferent and efferent systems of 59 % (Tables 5, 6; Fig. 1A).

Table 5. *Pulmonary gas variables of resting crabs (means ± S.D.)*

	Pulmonary pH			Pulmonary oxygen content (μmol l^{-1})					
Species	*N*	Aff	Eff	*N*	Aff	P1	P2	Eff	Hc-O_2max (μmol l^{-1})
Gecarcoidea natalis	20	7.546±0.063*	7.566±0.051	18	266±93*	551±182*	704±189*	804±261	925±139
Cardisoma hirtipes	15	7.508±0.066*	7.551±0.067	15	313±177*	594±198*	808±299*	958±212	1453±231
Geograpsus grayi	8	7.662±0.072*	7.704±0.051	10	213±73*	433±82*	616±55*	860±112	991±206
Geograpsus crinipes	3	7.662±0.132	7.603±0.229	4	179±89*	397±75	639±223	800±120	959±230
Ocypode cordimanus	31	7.492±0.122*	7.573±0.132	21	200±94*	–	–	706±151	880±297
Ocypode ceratophthalma	8	7.608±0.089	7.646±0.105	8	274±71*	–	–	908±202	955±177

*Denotes a significant difference between the marked and next listed vessel system (P<0.05).

Aff, Afferent lung system; P1, first portal system; P2, second portal system; Eff, efferent lung system; Hc-O_2max, theoretical maximal oxygen-carrying capacity of the haemolymph estimated from the concentration of haemocyanin in the haemolymph.

Table 6. *Oxygen saturation of the various vessel systems within the lung*

	Percentage saturation				Difference in percentage saturation				Percentage of total O_2 saturation gained in each lacunar system		
Species	A	P1	P2	E	P1–A	P2–P1	E–P2	E–A	L1	L2	L3
Gecarcoidea natalis	28±11	53±14	72±19	79±25	25	19	7	51	49	37	14
Cardisoma hirtipes	22±13	42±19	58±28	68±23	20	16	10	46	44	35	22
Geograpsus grayi	23±9	49±15	67±15	83±9	26	18	16	60	43	30	27
Geograpsus crinipes	19±9	43±5	59±14	67±5	24	16	8	48	50	33	17
Ocypode cordimanus	23±11	–	–	80±17	–	–	–	57	100		
Ocypode ceratophthalma	29±7	–	–	90±11	–	–	–	61	100		

A, afferent system; P1, first portal system; P2, second portal system; E, efferent system; L, lacunar systems.

Discussion

The role of the gills and lungs in gas exchange

Measurements of differences between venous, arterial and pre- and post-pulmonary blood gases have been used to indicate the relative efficiency of the gills and lungs in gas exchange, as discussed below, although to apportion gas exchange unequivocally it is necessary to measure blood flow to the two respiratory organs as well as blood gases.

Oxygen uptake

The lungs of all species studied were clearly effective in oxygen uptake as both the concentration and the partial pressure of oxygen in pulmonary haemolymph were significantly higher than in venous blood. Pericardial haemolymph (mixed pulmonary and branchial) had a lower oxygen content and partial pressure than pulmonary haemolymph in every species (except *Gecarcoidea natalis*), indicating a dilution of oxygen-rich pulmonary haemolymph with low-oxygen branchial return, i.e. the lungs of air-breathing crabs are more efficient in oxygen uptake than are the gills. This finding is not surprising, given that the lungs have a blood/gas diffusion distance some twenty times less than that across the gills (Storch and Welsch, 1975; Taylor and Greenaway, 1979; Farrelly and Greenaway, 1992, 1993). A similar situation obtains in air-breathing fishes (Hughes and Weibel, 1976). In *G. natalis*, similar levels of oxygenation occurred in pulmonary and pericardial haemolymph, indicating that the gills and lungs were equally effective in oxygen uptake. This is perhaps not surprising as the gills of this species show the most extreme modifications for air-breathing of any crab yet described. Numerous floral-like nodules, lined by a relatively thin epithelium are present on each lamella and provide a large additional surface area to that of the lamellae themselves (Farrelly and Greenaway, 1992). Similar structures in *Gecarcinus lateralis* (Cameron, 1981) suggest a similar capability. In contrast, the gills of most air-breathing crabs, though modified to remain erect in air, are lined with a thick transporting epithelium which functions primarily in ion regulation (Farrelly and Greenaway, 1992) and have a relatively small surface area (Gray, 1957; Hawkins and Jones, 1982; Farrelly and Greenaway, 1992).

Mean oxygen content of post-pulmonary blood was lower than Hc-O_2max in all species (Tables 5, 6). There may be several reasons for this. First, Hc-O_2max is based on the copper content of the blood and this measurement may overestimate haemocyanin-bound copper and thus Hc-O_2max (Greenaway *et al.* 1988). Second, crabs may well not oxygenate the haemolymph fully under resting conditions if O_2 delivery is adequate to meet demand at lower saturations. Certainly, the afferent (venous) supply to the lungs was 20–30 % saturated with oxygen, indicating a large venous reserve.

Carbon dioxide excretion

Elimination of CO_2 is determined by factors very different from oxygen uptake and in the species examined was apportioned rather differently between gills and lungs. In both *Gecarcoidea natalis* and *Geograpsus grayi*, the lungs and gills played an equal role in CO_2 excretion, and in *Mictyris longicarpus* the lungs are possibly more efficient than the gills. In contrast, the branchial route was clearly the most important route of CO_2

excretion in *Cardisoma hirtipes* and *Geograpsus crinipes*, although some pulmonary exchange was indicated. Interestingly, the latter two species are both ecologically and behaviourally strongly associated with water, although they do not carry water in their branchial chambers. For example, *C. hirtipes* has access to water in the bottom of its burrow and *G. crinipes* often forages around freshwater seepage areas and coastal cliffs (C. A. Farrelly and P. Greenaway, personal observation). Such a regular association with available water sources may encourage the use of water as a CO_2 sink as it is flushed through the branchial chambers (see Wood and Randall, 1981*a*,*b*).

Some loss of CO_2 across the lungs of these air-breathing crabs must occur by simple diffusion down its partial pressure gradient, as the lungs have a very short blood/gas diffusion distance and are permeable to gases. However, the bulk of CO_2 entering the haemolymph becomes hydrated to bicarbonate and its excretion is then limited by the speed of the rehydration reaction to molecular CO_2 as the blood passes through the lung. Significant rehydration during lung transit requires catalysis by carbonic anhydrase, and thus the function of the lungs in CO_2 excretion is largely dependent on the presence of this enzyme. Though absent from crustacean haemolymph, carbonic anhydrase has been found in the membrane fraction of gills (Burnett and McMahon, 1985) and in the branchiostegites of air-breathing crabs (Morris and Greenaway, 1990; Henry, 1991), where it is believed to convert haemolymph HCO_3^- into CO_2 for excretion. Carbonic anhydrase has not been found in the branchiostegites of aquatic crabs (Henry, 1991). The presence of carbonic anhydrase in the membrane fraction of the lungs of landcrabs provides further supportive evidence for the developing role of the lung in CO_2 excretion. Henry (1991) did not find carbonic anhydrase in the lung of *Cardisoma guanhumi*, a close relative of *C. hirtipes*, which may explain the relatively small loss of CO_2 found in the lung of this species. *Cardisoma*, with its regular access to water, appears to be maintaining an aquatic pattern of branchial CO_2 excretion.

Morphological considerations

The vascularized branchiostegal membranes lining the branchial chambers of air-breathing crabs have clearly become the major site of oxygen uptake, providing an evolutionary parallel to the lungs of pulmonate molluscs formed by vascularization of the mantle chamber (Plate, 1898; Ghiretti and Ghiretti-Magaldi, 1975). However, unlike the pulmonates, air-breathing crabs have retained their gills, which have also become modified for aerial gas exchange. Thus, most air-breathing crabs need to perfuse two respiratory surfaces simultaneously and in parallel.

Only the amphibious members of the superfamily Potamoidea depart from this pattern, e.g. the freshwater landcrabs *Holthuisana transversa* and *Pseudothelphusa garmani*. Both these species are long-term bimodal breathers living in highly seasonal wet/dry climates, where they breathe water for extended periods during the wet season and air during the dry season. These species possess gills that are not modified to remain erect in air. Thus, on emersion, the gills initially trap a layer of water, which prevents effective ventilation. Eventually, however, the lamellae dry out and collapse, retarding both perfusion and ventilation. In *Holthuisana*, 80 % of the haemolymph has been shown to be shunted to the lungs during air-breathing (Taylor and Greenaway, 1984), i.e. the gills of

these species are only poorly perfused when breathing air. It should be noted that this change in perfusion is a slow response, over some days, and is thought to be passively induced by gradual collapse of the gill lamellae as they slowly dry out. In water, the gills become fully functional again, and return of venous haemolymph to the heart is then predominantly *via* the gills. Thus, in these species, pericardial gas variables sampled during air-breathing can be almost exclusively attributed to the lung (discounting the gills), and likewise during water-breathing, can be almost entirely attributed to the gills (discounting negligible contributions from the lung). *Holthuisana*, when water-breathing (i.e. gill respiration), has an arterial oxygen content of 346 μmol l^{-1} (Greenaway *et al.* 1983), which is very similar to that achieved by lung-breathing in air (369 μmol l^{-1}).

Unfortunately, the extremely specialized habit of these potamoid species has not always been understood and this distinctly bimodal pattern of gill and lung perfusion has been indiscriminately and mistakenly applied to all air-breathing crabs, including obligate air-breathers (e.g. Innes and Taylor, 1986; Whiteley *et al.* 1990). In reality, the gills of the obligate air-breathers possess rigid nodulated lamellae that remain erect in air and which are probably well perfused at all times and therefore contribute continuously to the gas content of haemolymph in the pericardial sinus. Maintenance of branchial perfusion in air-breathing crabs is also necessary for the purposes of reabsorption of ions from the urine (Wolcott and Wolcott, 1985*a*, 1988). There is some evidence to suggest that flow-rectifying structures are present in the gill lamellae of some air-breathing crabs (Taylor and Taylor, 1986; Farrelly and Greenaway, 1992), possibly acting to reduce flow through the central regions of the lamellar by shunting around the marginal canal. How effective these structures are in altering perfusion ratios between the gills and lungs and how they might be regulated is completely unknown. The ratio of perfusion of gills and lungs in the obligate air-breathers is not confidently known for any species and therefore the exact importance of each of these respiratory sites cannot be measured. Al Wassia *et al.* (1989), on the basis of a sample size of only two, found a lung:gill perfusion ratio of 4:1 in *Ocypode saratan* whilst air-breathing. Whiteley *et al.* (1990) found a ratio of 3:1 for this species under similar conditions, but re-analysis of their data indicates a ratio of 1.5:1, i.e. 60 % to the lungs and 40 % to the gills. These ratios were based on differences in partial pressures in the pericardial sinus and lungs during air-breathing and in the pericardial sinus measured during enforced water-breathing, on the assumption that the gills alone were perfused. The assumption that branchial performance in water is equal to that during air-breathing is highly dubious, however, as the efficiency of the gills may well vary in different media.

The trend towards terrestrialization in crabs appears to have involved modification of the gills to facilitate ion-regulation at the expense of gas exchange, a function which is transferred increasingly to the lungs, developed from the branchiostegal membranes. The range in aerobic capacity of air-breathing crabs is comparable to that of aquatic species (O'Mahoney, 1977). However, whether lungs have conferred an actual increase in aerobic capacity in the air-breathing forms over their aquatic ancestors, or have merely provided compensation for loss of gill function, can only be speculated upon and is likely to vary widely between species.

In brachyuran crabs, the branchial and pulmonary circulations run in parallel with each

other (as clearly shown by vascular casts; see Farrelly and Greenaway, 1993), each with separate return vesssels to the pericardial sinus. All haemolymph must pass through either the gills or the lungs before entering the pericardial sinus. Therefore, the pericardial haemolymph is a mixture of haemolymph from these two systems. Thus, if one system has a low oxygen concentration and the other a high one, then the final oxygen concentration will be less than that of the high one. (By contrast, in serially arranged gas exchangers, the final oxygen concentration attained would be determined by the most effective exchanger and, as all blood goes through it, the system overall would be maximally efficient.) Thus, the parallel arrangement of the gill and lung circulations in air-breathing crabs imposes a number of constraints upon the performance of the respiratory system as a whole because the efficiency of the gills in gas exchange directly affects the gas status of arterial blood. The efficiency of the gills in gas exchange cannot be allowed to decrease too far as this would seriously impair the effectiveness of the lung through dilution of blood gases. Gill structure, then, must represent a compromise between osmoregulatory requirements and respiratory needs, and the lungs must function efficiently enough to offset any shortfall from the gills in order to maximize arterial oxygen levels. The effect of multifunctional gill structure (gas exchange plus ionoregulation), with the attendant long blood/gas diffusion distances, is clearly reflected in measures of the index L_{diff} (Piiper, 1982; Innes and Taylor, 1986), which assesses whether gas exchange is limited by either the diffusing capacity of the exchange surface (high L_{diff}, approaching 1) or vascular supply (perfusion-limitation) of the exchange surface (low L_{diff}, approaching 0). L_{diff} values in aquatic crabs breathing water vary between 0.5 and 0.8, while L_{diff} values for terrestrial crabs breathing air range from 0.4 to 0.6 (Taylor and Taylor, 1992). Thus, despite the increased diffusing capacity of the lungs of air-breathing crabs, the overall L_{diff} is compromised by the strongly diffusion-limited gills (see Innes and Taylor, 1986; Taylor and Taylor, 1992). Big improvements in L_{diff} are only observed either in species that have extremely complex lung structures (large surface areas) with extremely reduced gills, e.g. *Mictyris longicarpus* (Farrelly and Greenaway, 1987), or in species that have complex lungs but which do not perfuse the gills during air-breathing, e.g. *Pseudothelphusa garmani* (Innes and Taylor, 1986). The fact that huge improvements in L_{diff} are not observed in most terrestrial crabs again argues that a significant haemolymph contribution from the gills is compromising the overall respiratory performance.

The function of lung portal systems

Both patterns of lung vasculature are able to achieve very high oxygen concentrations in the haemolymph (see Table 1; Fig. 1) and relatively high levels of saturation of haemocyanin (85 % in the portal lungs, 90 % in lungs with a single lacunar bed), and the data on resting crabs did not demonstrate any overwhelming advantage in the function of either lung type. A closer look at the function of the portal systems, however, may suggest an advantage during activity.

Most oxygen (approximately 50 %) in the portal lungs is picked up in the first pass through lacunae, between the afferent and first portal systems. Around 30 % is picked up in the second set of lacunae and only 20 % in the last set. There were no obvious

morphological differences between the different lacunar systems that would prohibit equal oxygen uptake in each lacunar bed (see Farrelly and Greenaway, 1993). The decreasing rate of oxygen pick-up across the lung was probably a function of the progressively reduced oxygen gradient between the haemolymph and the branchial chamber gases as the haemolymph became more saturated in each consecutive network. During exercise, higher perfusion rates and lower oxygen concentrations of afferent blood may mean that blood would reach the second and third lacunar systems with lower oxygen concentrations and thus higher gradients for gas exchange. Serially arranged lacunar beds may provide a greater opportunity to saturate the haemocyanin under these conditions, thus maximizing oxygen uptake. One might expect such a model to predict a larger aerobic capacity during exercise for crabs with portal lungs compared with crabs without. However, data for *Gecarcinus lateralis*, *Cardisoma guanhumi* and *C. carnifex* (all species with portal lungs) show a mixed aerobic and anaerobic response to exercise, with a low metabolic scope, fairly poor endurance and a long recovery time (Herreid *et al.* 1979, 1983; Wood and Randall, 1981*a*,*b*; Full and Herreid, 1984). Despite this, the gecarcinids are capable of long migrations of up to several kilometres, over several days (Hicks, 1985; Wolcott and Wolcott, 1985*b*). In contrast, the ghost crabs are highly aerobic and have a high metabolic scope and fast recovery time (Full and Herreid, 1983). Interestingly, fiddler crabs (e.g. *Uca cultrimana*, *U. coarctatus* and *U. pugilator*) do not have portal lungs but have a similar arrangement to that in the ghost crabs (von Raben, 1934; C. A. Farrelly, unpublished results) and have a significant dependence on anaerobic metabolism during exercise (Full and Herreid, 1984). *Uca* lacks the corrugations present in the lung lining of the ghost crabs (i.e. has a smaller lung surface area) and therefore may provide a better comparison with the smooth portal lungs of the gecarcinids. The correlation between lung types and respiratory performance is thus still not clear.

It is tempting to think that the serial arrangement of the portal systems down the branchiostegites, combined with a forward-directed ventilation, forms a counter-current exchange system. However, scaphognathite-powered ventilation in air-breathing crabs is relatively slow compared with that in aquatic crabs and is often intermittent in nature, with trapped air acting as a store that can then be drawn upon (Cameron, 1975; O'Mahoney and Full, 1984; Taylor and Davies, 1981). Given the lung's large volume and the notoriously low oxygen extraction rates reported for air-breathing crabs (Cameron, 1975; Taylor and Davies, 1981), it is doubtful whether any substantial gas gradients could be maintained within the branchial chamber. Therefore, it is very unlikely that any counter-current system could be operating.

The question still remains as to why the first set of lacunae in the portal lungs only picks up 50 % of the total oxygen, whereas the single capillary system of the ocypodids is able to pick up 85 %. This may be related to differences in lung structure and, although lung morphometrics appear to be of the same order of magnitude in the different lung types (see Farrelly and Greenaway, 1993), small differences in length or in the thickness of lacunae and in blood/gas diffusion distances may result in significant functional differences. Respiratory performance is also determined by (a) oxygen consumption and aerobic scope; (b) whether exercise is aerobic and/or anaerobic; (c) heart rate and cardiac

output; and (d) the affinity and capacity of the pigment and its modulation during exercise. Differences between these factors may obscure the limitations imposed by the architecture of the different lung types. Detailed studies covering all these aspects are needed before any judgement on the relative merits of the morphology can be made.

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