PENETRATION OF WATER INTO BLIND-ENDED CAPILLARY TUBES AND ITS BEARING ON THE FUNCTIONAL DESIGN OF THE LUNGS OF SOLDIER CRABS *MICTYRIS LONGICARPUS*

By DAVID P. MAITLAND[1,*] AND ARTHUR MAITLAND[2]

[1]*School of Biological Science, University of New South Wales, PO Box 1, Kensington, New South Wales 2033, Australia* and [2]*Department of Physics and Astronomy, University of St Andrews, North Haugh, St Andrews, Fife KY16 9SS, Scotland*

Summary

Soldier crabs, *Mictyris longicarpus* Latreille, inhabit intertidal sand-flats of Eastern Australia. Their gill chambers are modified for both water circulation and air-breathing. Water circulates through the lower gill compartments. The upper regions of the gill chambers are air-filled and function as lungs. The deep vascular parenchyma lining the upper gill chambers, or lungs, is penetrated by a regular series of fine branching airways. Scanning electron micrographs of lung architecture are shown. Measurements relating to lung structure were made on plastic casts.

Because of the lung's design, water circulating through the lower gill compartments does not interfere with lung function. The airways are blind-ended and non-anastomosing, acting in effect as air-filled capillary tubes sealed at one end. A mathematical model and explanation show how the air trapped within this lung structure substantially reduces water penetration, despite surface tension (capillary) processes. This same lung design also facilitates the shedding of the lung cuticle at each moult.

Introduction

Soldier crabs, *Mictyris longicarpus*, are small to medium, round-bodied crabs (males typically reach 14 g and 2.5 cm carapace width) living on sheltered intertidal sand-flats around the coasts of Australia (McNeill, 1926). They are remarkable for their habit of emerging *en masse* at low tide to 'march' across the sand-flats in huge 'armies' as they systematically rake the surface layers of sand for food (Cameron,

*Present address: Department of Physiology, Medical School, University of Witwatersrand, Parktown, Johannesburg, South Africa 2193.

1966; Quinn, 1983). As a soldier crab feeds, water (pumped from the branchial chambers) is used to separate food particles from sand (Cameron, 1966; Quinn, 1980, 1983, 1986).

Soldier crabs appear to be obligate air-breathers, obtaining over 90 % of their oxygen requirement *via* sophisticated lungs developed within their branchial chambers (Maitland, 1987; Farrelly and Greenaway, 1987). The lungs are complex structures formed from a regular series of branching finger-like airways which penetrate the deep vascular parenchyma lining the branchiostegites (lateral extensions of the carapace covering the gills) and portions of the epibranchial septa (membranous partitions which partially separate the gills below from the lungs above; Quinn, 1980; Maitland, 1987; Farrelly and Greenaway, 1987). In this paper we describe plastic casts of the lung and examination with a scanning electron microscope which reveal that the lung consists of a system of non-anastomosing, blind-ended, air-filled capillary tubes. The gill compartments have been found always to contain water (Quinn, 1980, 1983, present study). This water may reach the airways of the lung as the crab changes its orientation. Since oxygen diffuses about 10 000 times more slowly through water than through air (Dejours, 1981), the lung will cease to function effectively by aerobic respiration if substantial amounts of water enter it. The question we address, therefore, is how an air-filled lung exposed to water in such close proximity does not flood. To this end, we develop a model which simulates the architecture of the soldier crab's lungs and use it to derive formulae to describe the extent to which water at various tidal depths may penetrate a system of non-anastomosing, blind-ended, air-filled capillary tubes. The non-anastomosing feature of the lung design also facilitates the shedding of the lung cuticle at each moult.

Materials and methods

Adult male soldier crabs, *Mictyris longicarpus*, were collected at low tide on intertidal sand-flats around Botany Bay in Sydney, Australia. Crabs were dug out of their sand retreats (about 30 cm below the surface) and were kept for up to a week in fresh damp habitat sand exposed to natural light and ambient temperatures (20–30°C).

Lung tissue was observed with a scanning electron microscope (Cambridge S4-10). For these observations, the lung tissue was fixed in 10 % buffered formaldehyde, dehydrated, critical-point-dried, and gold/palladium coated before examination.

Lung airway dimensions

To minimize problems arising from tissue shrinkage and the like, dimensions of the lung airways were measured directly from plastic replicas of freshly removed lung tissue. Measurements were made with a Wild M5 binocular microscope with an eyepiece graticule and *camera lucida*.

The plastic replicas were made by pouring Batson's no. 17 corrosion compound (kit 7349, Polysciences, Warrington, PA, USA; shrinkage is less than 1%, Bennett, 1988) over the luminal surface of freshly removed branchiostegites (on which most of the lung is formed). A thinned solution of the compound was used consisting of 4 ml of monomer base, 1 ml of methylmethacrylate, 1 ml of catalyst and four drops of promoter. Before polymerization commenced, the preparation (compound plus lung) was evacuated to 8 kPa for a few seconds to remove trapped air from the compound and the lung airways. Full atmospheric pressure was then restored to force the compound into the evacuated lung airways. After setting, the cast was split from the calcified shell of the branchiostegite and immersed in a macerating solution of 20% NaOH (w/v) plus 0.3 mol l^{-1} EDTA. After repeated washing and maceration, the last traces of cuticle were removed by immersing in full-strength 'Domestos' (a household bleach) prior to washing and drying. Some casts were coated with gold/palladium and photographed under the scanning electron microscope.

Vestibule diameter was measured in eight male crabs whose live body masses spanned the range 1.1 g to 10.5 g. Excised branchiostegites (right side only) were dipped in a 1% Methylene Blue solution for 2 min to delineate clearly the perimeter of each vestibule. Sixty vestibules covering the posterior and middle regions of the lung were drawn from each crab with the aid of a *camera lucida* at 64× magnification. From these drawings, the average vestibule diameter was calculated for each individual.

Water volume

The volume of water held within the branchial chambers of non-feeding soldier crabs was determined as described by Maitland (1990).

Contact angle for Mictyris cuticle

As is well known, surface tension forces determine whether a liquid will wet a solid. For the case of a liquid lying on a solid in the presence of a vapour, the surface tension forces are γ_{LV}, γ_{SV}, γ_{SL}. Each force is normal to the line that is the boundary between the vapour (V), the liquid (L) and the solid (S). Surface tension is sometimes defined as the force per unit length of the boundary. The forces are, respectively, tangential to the liquid/vapour surface, the solid/vapour surface and the solid/liquid surface. The angle between γ_{LV} and γ_{SL} is the contact angle, θ. The contact angle between sea water and the surface of soldier crab cuticle was measured from a 5 μl drop of sea water placed on the surface. Surfaces for which θ was measured were the luminal surfaces of excised lungs (the inside surface of the branchiostegite, see Fig. 2A) and the external smooth carapace cuticle located between the branchial chambers on the dorsal surface of the crab. The drop of water was photographed in profile and θ was measured from 30× enlargement prints on both sides of the drop and the average value was found for three drops

(three crabs: 1 drop on the dorsal surface of each crab and 1 drop on the lung surface of each crab).

Results and discussion

Ecology and behaviour

Soldier crabs live on sheltered sand-flats between the neap tide levels. Prior to being submerged at high tide, crabs bury themselves beneath the sand (Fig. 1) in a 'corkscrew' fashion. This behaviour traps a pocket of air within a cavern 4–5 times the volume of the crab (Fig. 1A). Crabs digging with their right side travel downwards in a clockwise spiral, excavating sand from the floor of the cavern and plastering it onto the roof. In this way the trapped pocket of air is taken below to a depth of between 10 and 30 cm, or to the level of the water table (Fig. 1B). The air cavity remains intact beneath flooded sand. The process is reversed (sand removed from above and placed below) when crabs emerge again at the next low tide (Cowles, 1915; McNeill, 1926). Laboratory observations made during the study reported herein on crabs burrowing against a glass-sided tank, and field observations made during the excavation of crabs from the sand, confirmed the reports of Cowles and McNeill. At high tide in the Sydney area, crabs within their air caverns may be covered by up to about 2 m of water (Marine Services Board of New South Wales Tide Tables).
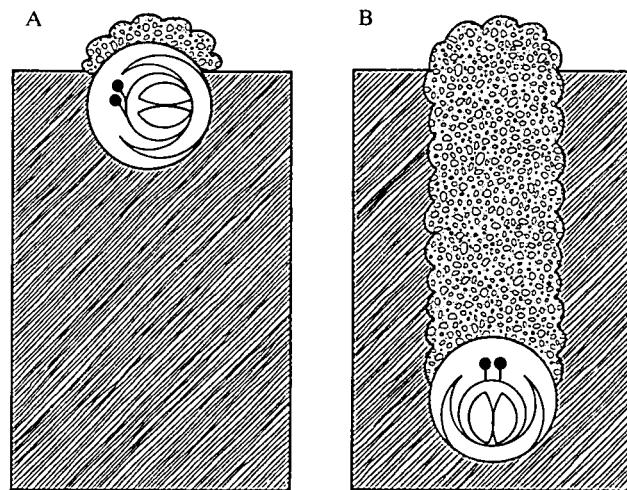

Fig. 1. Prior to flooding by the tide, soldier crabs (*Mictyris longicarpus*) construct an 'igloo'. (A) In each igloo, a pocket of air is trapped around the crab and this pocket is taken downwards as the crab transfers sand from the floor to the ceiling of the pocket. The subterranean air chamber thus created (B) provides shelter until the next low tide. The crabs bury themselves between 10 and 30 cm below the surface of the sand.

Lung architecture

Although the data presented below apply primarily to the lung lining the branchiostegites, the lung formed on the epibranchial septum is essentially similar, although less well developed (Maitland, 1987; Farrelly and Greenaway, 1987).

The surface area of the respiratory epithelium lining the branchiostegites is amplified by a variable number of invaginations, or 'vestibules', per square millimetre (Fig. 2A). In a 1.1 g crab the range is between 8 and 11 vestibules mm^{-2}, while in a 10.5 g crab it is between 1 and 4 vestibules mm^{-2} (these ranges refer to the number of complete vestibules falling within a scaled 1 mm×1 mm square grid placed over a *camera lucida* image of the lung surface). Vestibules also vary in diameter, both within and between individuals. For example, in a 10.5 g crab, vestibules range between 220 and 810 μm in diameter, but are on average 440±120 μm (±s.d.; N=60). Average vestibule diameter was found to increase with increasing body mass according to the relationship:

$$y = 180m^{0.34} \ (r=0.978),$$

where y is vestibule diameter (μm) and m is body mass (g).

Vestibules penetrate a short distance into the lung before subdividing into primary, secondary and tertiary respiratory airways oriented at right angles to the branchiostegite. Plastic casts of these airways provide a clear picture of their architecture (Fig. 2B). The air columns terminate against the branchiostegite as blind-ended tubes 35–80 μm in diameter (Fig. 2B). Each vestibule leads into its own discrete system of airways and there are no anastomoses between one vestibular airway system and the next (Fig. 2B,C). Air columns are spread evenly across the surface of the branchiostegite (Fig. 2D).

Lung airways (i.e. linear lung depth) increase in length with increasing body mass according to the relationship:

$$y = 420m^{0.33} \ (r = 0.922, N = 15, \text{male crabs only}),$$

where y is airway length (μm) and m is body mass (g).

Capillarity and lung design

All of the many hundreds of soldier crabs collected were found to have water in their branchial chambers. The total volume of water carried by non-feeding soldier crabs increases with increasing body mass according to the relationship:

$$w = 97m^{0.92} \ (r = 0.91; N = 32; \text{male crabs only}),$$

where w is the volume of water (μl) and m is the body mass (g). Thus, a crab of mass 10 g carries about 0.8 ml of water. This water circulates in the lower regions of the branchial chambers. Although the lung is located above this water level and is partially isolated from it by the epibranchial septum, in some circumstances (e.g. during burrow construction when a crab turns on its side or upside down) water could gain access to the lung region. Since the lung consists of a large number of
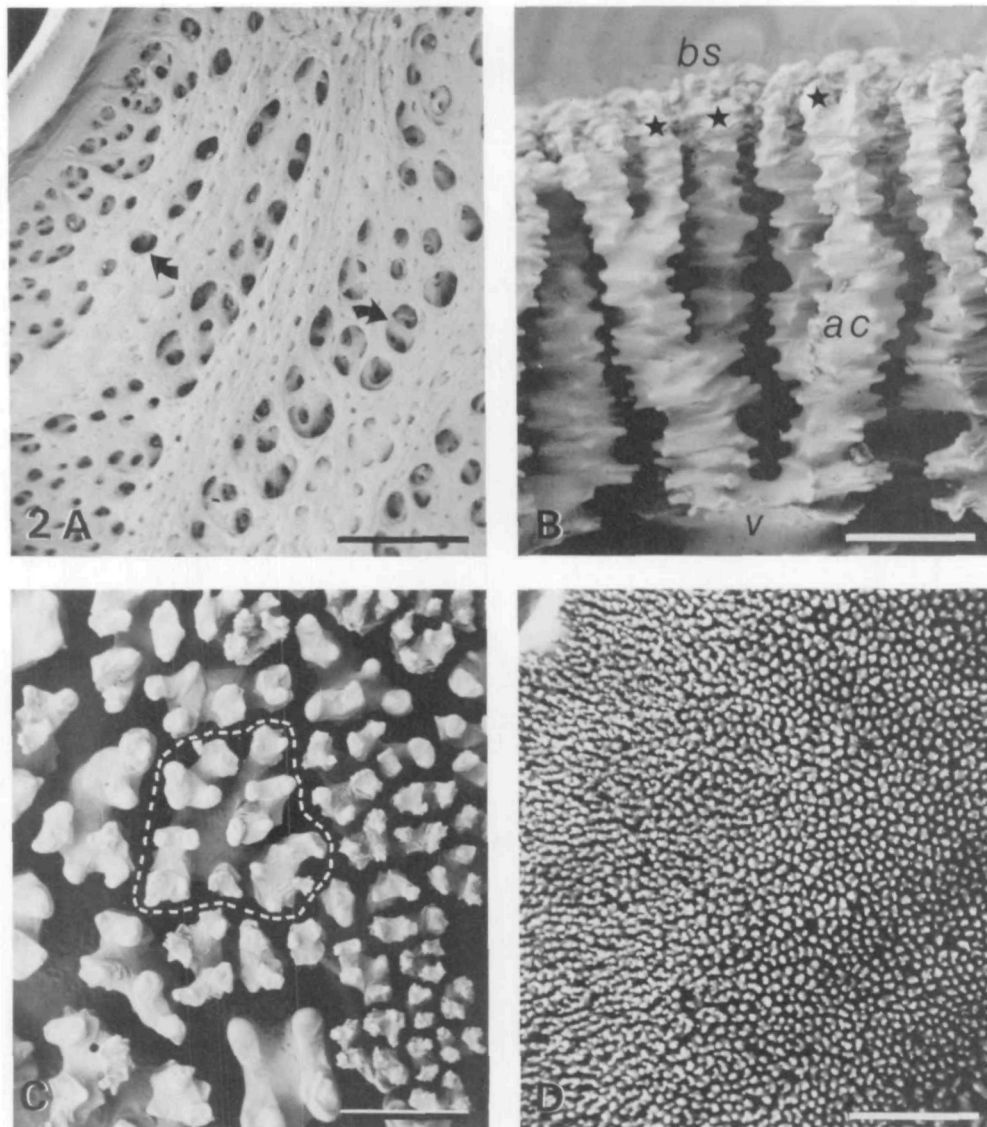
Fig. 2. Scanning electron micrographs of the lung architecture of *Mictyris longicarpus*. (A) Luminal surface of the lung lining the inside surface of the right branchiostegite (dorsal is top right, anterior is top left). Each vestibule (curved arrows) opens into a discrete system of blind-ending respiratory air columns. Scale bar, 1 mm. (B) Plastic cast of air columns lining the branchiostegites (luminal surface towards the bottom, branchiostegal surface, *bs*, at the top). Vestibules (*v*) lead into parallel branching air columns (*ac*) oriented at right angles to the branchiostegite and terminating against it as narrow, blindending tubes (stars). Note the absence of cross-connecting airways between adjacent air columns. Scale bar, 200 µm. (C) Plastic cast of air columns viewed from the branchiostegal surface. Here, the plastic has only partially filled the vestibules, revealing how the air columns are compartmentalised into fields, each field (dotted line) arising from a separate vestibule (this was also confirmed in complete casts, by teasing the columns apart and tracing their origins). Thus, in life, the air columns are evenly spread over the branchiostegite as shown in D. Scale bars, C, 450 µm; D, 2 mm.
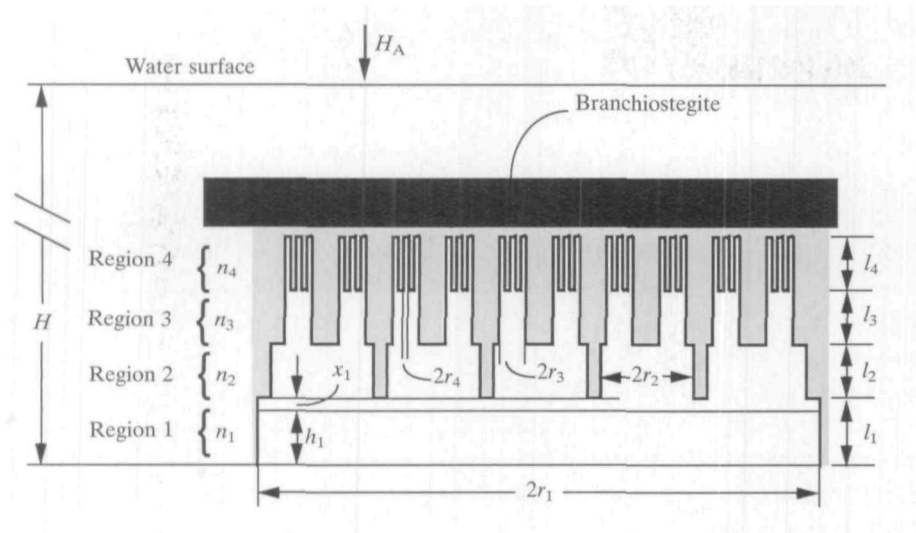
Fig. 3. A stylised diagram showing a section through the lung of the soldier crab, *Mictyris longicarpus* (orientation as in Fig. 2B). The model shows a single vestibule (region 1) and its associated tiered branching system of airways (regions 2–4). Clear areas are air-filled, while blood flows within the shaded areas. Each vestibule (region 1) of radius r_1 and length l_1 leads into five airways (region 2) of radius r_2 and length l_2. Each of the airways in region 2 leads into two airways (region 3) of radius r_3 and length l_3. Finally, each tube in region 3 leads into three blind-ended tubes (region 4) of radius r_4 and length l_4. As water penetrates the vestibule it occupies an increasingly greater proportion of length h_1. The remainder of the vestibule (which remains air-filled) has a length x_1. The vestibule lies beneath a tidal depth H and H_A is the atmospheric pressure in pascals. The respective numbers of tubes in each of lung regions 1, 2, 3 and 4 are n_j, where $j=1, 2, 3$ or 4. Representative measurements are given in Table 1.

fine capillary tubes, these tubes could be expected to flood as a result of capillary effects whenever water makes contact with the luminal surface of the lung. Water, however, that is experimentally placed upon the lung surface fails to penetrate the vestibular airways.

In seeking a physical basis to explain these observations we note that, while it is common knowledge that water readily penetrates a capillary tube that is open at both ends, water penetration into a complex system of non-anastomosing, blind-ended airways or tubes (Fig. 3), which may be used to simulate a crab lung, has not been considered. In essence, it is the compression of air trapped in the blind-ended tubes that produces a force to oppose that of surface tension and thus effectively prevent the tubes from flooding. This explanation may be convincing in the case of a crab that maintains a normal upright posture within the burrow, but an active crab makes many changes of orientation. During these changes, with water lying on the surface of the lung, trapped air might be expected to travel as a bubble along a lung 'capillary' and thus escape from the lung airways to leave those

airways flooded as water replaces the air. However, we show below that this expectation is unlikely to be realized.

Contact angle for Mictyris cuticle

Sea water was found to wet the external carapace cuticle of the solder crab, with a contact angle of 41° (40.8±3.3°; mean±s.d.; $N=6$). However, θ was 83° (82.8±1.7°; mean±s.d.; $N=6$) for sea water in contact with lung cuticle. This increase in θ for lung cuticle could be due either to the presence of a water-proofing substance or it could result from a cavitation or 'bubble' effect caused by the air trapped within the vestibules beneath the drop of water. Rough or cavitated surfaces are known to increase contact angles (McIver and Schurch, 1987). For the present study, we chose to take θ for lung cuticle to be 41° because we are uncertain as to the true cause of the increase in θ for lung cuticle and because this is a 'worst-case scenario'.

Air bubbles

First we note that, if air is to escape from a submerged capillary tube, water must take its place. In the general case of air trapped in a tube of narrow bore by water which wets the tube, surface tension forces hold the upper surface of the bubble together against the Rayleigh–Taylor instability (Rayleigh, 1883; Taylor, 1950) if the radius of the tube is less than a critical value, r_c. At tube radii greater than r_c, the upper surface of the bubble will be disrupted by the Rayleigh–Taylor instability and water will fall to the lower surface of the bubble. At tube radii less than r_c, if the air bubble is to move, water must move around the sides of the bubble as a film between the tube wall and the bubble. A quantitative account of this movement would involve specialist considerations of thin film formation, viscosity and the like which would take us beyond what we believe to be appropriate for this paper. However, we note that detailed analysis and experiments by Bretherton (1961) have shown that a bubble of air will not rise in a vertical capillary tube of radius r (m) and sealed at one end if we have,

$$\frac{\rho g r^2}{T} < c,\qquad(1)$$

where c is a constant, ρ is the density of sea water ($1025\ \mathrm{kg\,m^{-3}}$ at 15°C), g is the gravitational acceleration ($9.81\ \mathrm{m\,s^{-2}}$) and T is the net surface tension given by:

$$T = \gamma_{LV}\cos\theta.\qquad(2)$$

To calculate T for the case we consider, we shall use $0.073\ \mathrm{N\,m^{-1}}$ for γ_{LV} and 41° for contact angle θ. Values of c lying between 0.15 and 1.5 have been reported. Bretherton shows that the value of c is 0.842 and refers in his paper to a private communication from H. L. Goldsmith and S. G. Mason to the effect that c is 1.27.

Barr (1926) gives 0.15 for the value of c. We have used a much-simplified theory, based on considerations of a spherical bubble subjected to surface tension and buoyancy forces, to show that the bubble is unable to escape from the tube if the following inequality is satisfied:

$$2\pi r T > (4/3)\pi r^3 \rho g.$$ (3)

From this we obtain 1.5 for c. Depending on conditions, we see that the value of c probably lies between 0.15 and 1.5.

Inequality 1 shows that air remains trapped in a capillary tube of a lung in such a way that it cannot be replaced by water if the tube radius satisfies the inequality:

$$r < \sqrt{(cT/\rho g)}.$$ (4)

From the point of view of lung architecture, the value of 0.15 given by Barr (1926) is the most pessimistic value of c. With this value, together with the above values for ρ, g and T, we get:

$$r \leqslant 0.9 \, \text{mm} \qquad (\text{or } r_c = 0.9 \, \text{mm}).$$

Inequality 1 with any of the other values for c allows larger values for r without bubble escape. Thus, a crab at low tide that is oriented most unfavourably on its side (e.g. during burrow construction), with the lung vestibules uppermost and covered by water, cannot lose air from the vestibules if the radii of the vestibules are less than 0.9 mm (with Barr's value for c). The largest vestibules in the largest soldier crab found in our studies had radii of less than 0.5 mm. Given that air cannot escape from vestibules covered by water, we determine below the extent to which water might penetrate the lungs' airways as a result of compression of the trapped air.

Complex blind-ended capillary tubes

Although the detailed branching topology associated with each vestibule within the lung varies both within and between animals, the overall topology is essentially similar. For purposes of the calculations to follow, this branching topology can be simplified as shown in Fig. 3. The length of the vestibule (region 1) is l_1 and its radius is r_1. Five airways (the range was found to be from 3 to 9), each of length l_2 and radius r_2, lead from the vestibule. From each of the airways of region 2 arise two (or sometimes three) airways of length l_3 and radius r_3. Finally, each tube of region 3 leads into three (or more) blind-ended tubes of length l_4 and radius r_4 (region 4 of Fig. 3). To generalize, we denote a region by N, the number of branches in each region by n_N, length by l_N and radius by r_N. If M is the number of regions present, the possible values of N are $1,2,..,M$. In large crabs (over 9 g), M may be 5.

By considering Fig. 3 together with Boyle's law and surface tension, it can be shown that the depth of water H that will cause water to penetrate all regions up to

Table 1. *Representative dimensions of a vestibule and airway system as depicted in Fig. 3*

l_N	r_N	n_N
$l_1 = 125\,\mu m$	$r_1 = 175\,\mu m$	$n_1 = 1$
$l_2 = 200\,\mu m$	$r_2 = 75\,\mu m$	$n_2 = 5$
$l_3 = 125\,\mu m$	$r_3 = 50\,\mu m$	$n_3 = 12$
$l_4 = 190\,\mu m$	$r_4 = 31\,\mu m$	$n_4 = 31$

N, region of the lung, from 1 (the vestibule) to 4 (the blind-ended tubes adjoining the branchiostegite).

l is length, r is radius and n is the number of branches in each region.

region N and a distance h_N into region N leaving distance x_N and the remaining regions unflooded is given by:

$$H_{xN} = \frac{H_A\left(n_N h_N r_N^2 + \sum_{j=1}^{N-1} n_{N-j} l_{N-j} r_{N-j}^2\right)}{n_N x_N r_N^2 + \sum_{j=1}^{M-N} n_{N+j} l_{N+j} r_{N+j}^2} - h_{0N}, \tag{5}$$

where H_A is the depth of water that produces a pressure of 101 kPa (10.33 m for one standard atmosphere) and h_{0N} is given by:

$$h_{0N} = \frac{2T}{\rho g r_N}. \tag{6}$$

The constraints are $N-j \geq 1$ for the numerator and $N+j \leq M$ for the denominator. Terms corresponding to values of $N \pm j$ outside these and the summation limits given are not possible. In deriving equation 5, we have omitted the terms such as $\pm (h_N + l_1 + ... + l_{N-1})/H_A$ because H_A is about 10 m and $(h_N + l_1 + ... + l_{N-1})$ is less than 1 mm. Table 1 gives measurements taken from a randomly selected tube system associated with a single vestibule in a 5 g crab.

Of course, the tubes do not have a uniformly circular cross section and the walls are not uniformly cylindrical, but the data are adequate for the purposes of estimating depths H_1, H_2 and H_3 (the tidal depth H which will totally flood regions 1, 2, 3, respectively). Using Fig. 3 with values for n as given in Table 1, and the measured values for tube lengths and radii with $\theta = 41°$, equation 5 gives the following values: $H_1 = 2.72$ m, $H_2 = 11.2$ m, $H_3 = 23.21$ m, when each region is fully flooded (that is, when $x_1 = x_2 = x_3 = 0$). In the study area (Botany Bay, Sydney), the highest recorded tide during the year 1986–1987 was 2 m (as noted above). Clearly, therefore, under normal circumstances, water cannot penetrate very far into the soldier crab lung vestibules, even at high tide.

Moulting

Some of the soldier crabs brought into the laboratory attempted to moult so it

was possible to study how the cuticle lining the lungs is shed. The non-anastomosing blind-ending architectural design of the lung appears to be important, and, like pulling fingers out of a glove, the old cuticle is withdrawn from the lung (direct observation).

By necessity, if the lung were made of anastomosing tubes, the cuticle would need to have specialized breakage zones incorporated within the branches to enable the cuticle to be shed. Such breakage zones were not found in the soldier crab lung. In general, arthropod respiratory structures avoid this problem by utilising non-anastomosing designs. Thus, insect tracheae (Wigglesworth, 1972), isopod pseudotracheae (Hoese, 1983) and tick spiracular structures (Pugh *et al.* 1988) are all invaginated, non-anastomosing, tree-like structures.

Moulting allows an arthropod to grow. In soldier crabs, moulting also allows the lungs to be maintained in a healthy condition. Some crabs, particularly older individuals (increased intermoult interval), were found with vestibules blocked with sand grains. However, these could be removed along with the old cuticle at the next moult.

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