Respiration and Circulation in Land Crabs:
Novel Variations on the Marine Design[1]

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SYNOPSIS. Both the "true" crabs (Brachyura) and hermit crabs (Anomura) include species that show numerous behavioral, morphological, and physiological specializations permitting terrestrial life. This paper examines respiratory and circulatory adaptations for air breathing in these land crabs. Respiratory specializations include modification of gas exchange structures for air breathing (gills and elaborated branchial chamber linings), ventilatory mechanisms permitting effective air pumping, an elevated hemolymph oxygen capacity, and a primarily CO_2- rather than O_2-sensitive ventilatory control system. The qualitative aspects of hemolymph oxygen transport and metabolic rate are apparently unchanged from that of marine crabs. While the basic cardiovascular morphology of land crabs appears similar to that of marine forms, there is considerable elaboration of the vasculature of the branchial chamber lining, which in some species includes a unique double portal system. Cardiac output is lower in land crabs (probably related to their higher hemolymph O_2 capacity), but insufficient data on hemolymph pressures prevent comparisons with marine forms. In general, land crabs have modified (sometimes extensively) existing structures and processes found in their marine relatives rather than evolving structures for terrestrial life de novo. Accordingly, land crabs present a useful model for the evolution of terrestriality, showing that even subtle anatomical changes can result in the large changes in physiological function necessary for the terrestrial invasion.

INTRODUCTION

The evolutionary transition of animals from water to land has been the subject of much study (and considerable speculation) in the last decade (see monographs by Randall et al., 1980; Little, 1983, 1990). Land crabs have been central in the study of the arthropod invasion of terrestrial habitats, but have also served as useful models with which to investigate the terrestrial invasion generally (see Vol. 8, American Zoologist, 1968; Vol. 218, Journal of Experimental Zoology, 1981; Burggren and McMahon, 1988a). Living on land requires numerous specializations, in large part because the properties of air and water are so very different (Little, 1990; Burggren and Roberts, 1991). The respiratory system, and related elements of the cardiovascular system, in particular, have become specialized for a terrestrial existence. This paper discusses these specializations from the perspective of how the basic pattern of marine brachyuran and anomuran crabs has been modified during the water-land transition.

RESPIRATION: COMPARISON OF TERRESTRIAL AND MARINE FORMS
Morphology of gas exchange organs

The morphology of the respiratory organs of most species of land crabs[2] is extensively modified from that of marine and intertidal species. Modifications have occurred in both gill structure and in the branchial chamber within which the gills reside. However, it is important to emphasize that in most cases

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[2] Here a land crab is defined as a crab (brachyuran or anomuran) that possesses behavioral, morphological, physiological and/or biochemical adaptation permitting extended activity out of water.

the respiratory adaptations to terrestrial life represent modification of respiratory structures common to all crabs, rather than the appearance of structures that have arisen *de novo.*

The dominant feature of the gills of terrestrial crabs is their reduced surface area relative to marine forms. This results from reduction in both number of gills and number of lamellae on each gill (see McMahon and Burggren, 1988, for earlier literature). The reduced respiratory surface area of the gills of terrestrial crabs is thought to be an adaptation to reduce evaporative water loss. However, reduction of gill surface area also potentially reduces the available area across which the exchange of ions and respiratory gases can occur. In many species (*e.g.,* the coconut crab, *Birgus lato*), the posterior gills, which contain the preponderance of cells responsible for ion exchange with branchial chamber water, show less proportionate reduction than anterior gills, indicating that the gills may retain an important role in hydromineral regulation.

The basic pattern of gill structure in marine crabs depends upon the buoying nature of water to prevent the delicate gill lamellae from collapsing and adhering to each other. When the gills of marine crabs are exposed to air, the collapse of the lamellae greatly reduces effective gill surface area. To prevent this, the gill lamellae of many terrestrial crabs, both brachyuran and anomuran, are sclerotized to provide greater stiffness and may have small projections from their surfaces that act as spacers, keeping the lamellae vertically aligned and preventing them from collapsing on each other (for references see Burggren and McMahon, 1988*b*).

Many terrestrial crabs exhibit major anatomical modifications of the branchial chambers. The branchial chambers are highly enlarged in many terrestrial species (*Cardisoma guanhumi, Gecarcinus lateralis, Dilocarcinus dentatus, Birgus latro*) when compared with marine forms of similar body mass, and the ratio of gill to branchial chamber lining surface area appears to decrease progressively when examining progressively more terrestrial crabs (McMahon and Burggren, 1988). In some land crabs, the branchial chamber lining remains relatively smooth, but in many terrestrial forms the inner surface of the branchial chamber is highly convoluted (*e.g., Ocypode quadrata*) to provide further enhancement of surface area (Farrelly and Greenaway, 1987; Greenaway and Farrelly, 1990; see McMahon and Burggren, 1988, for earlier literature). In *Birgus latro,* the inner surface of the laterally expanded branchial chamber forms numerous small projections ("treelets") that undoubtedly increase many-fold the surface area of the branchial lining. Some of the most extensive branchial chamber modifications occur in *Eudianella iturbi, Pseudothelphusa garmani,* and *Mictyris longicarpus.* The branchial chamber lining in these species is much thicker in many other crabs but is highly perforated by tiny pores (Innes *et al.,* 1987), giving a "sponge-like" microanatomical appearance superficially resembling the parabronchi of bird lungs.

A unique adaptation for gas exchange occurs in the Scopimerinae, a group of ocypodid air breathing crabs (Maitland, 1986). The Australian sand bubbler crab *Scopimara inflata,* for example, shows little modification to its gills or branchial chamber. However, single large oval patches on the meral segments of each walking leg show greatly reduced cuticular and epidermal layers (Fig. 1). Hemolymph spaces lay directly underneath these patches, which form respiratory surfaces with an air-hemolymph diffusion distance for respiratory gases of less than 1 μm. Preventing gas exchange across these patches reduces total oxygen consumption by up to 60% (Maitland, 1986). *Dotilla,* another member of this group, has similar respiratory patches located on the ventral thoracic sternal plates rather than on the walking legs (Maitland, 1986).

Ventilatory mechanisms

The ventilatory pumps propelling water through the branchial chamber in marine crabs are the paired scaphognathites, flattened "paddles" formed from the expodites of the second maxillae (McMahon and Wilkens, 1983). The complex, four-phased beat of the pump generates a flow of water in through the Milne-Edwards openings at

the base of the limbs, though the branchial chamber, past the scaphognathite, and out via the exhalent canals near the base of the third maxillipeds. Occasional periods of reversed scaphognathite beating produce a reversal of this water flow.

Both brachyuran and anomuran land crabs continue to employ scaphognathite beating as the primary ventilatory pump for propelling air through the branchial chambers. The scaphognathites are highly efficient at air pumping (Cameron and Mecklenberg, 1973; McMahon and Burggren, 1979; Burggren *et al.*, 1985), and can sustain a continuous, relatively non-pulsatile posterior-to-anterior flow of air through the branchial chamber (Fig. 2). Total air flow through the branchial chambers tends to be considerably lower than branchial water flow in marine species (see McMahon and Wilkens, 1983; McMahon and Burggren, 1988), probably because of the higher O_2 capacitance of air compared to water. Periods of reversals occur during air pumping in land crabs, just as during water pumping by marine species. Periods of apnea are quite common in air breathing crabs, as they are in water breathing crabs. In short, there appears to be little modification of the basic scaphognathite pumping mechanism when air replaces water as the respiratory medium.

In land crabs such as *Cardisoma*, the branchial chambers often contain some water even when animals are breathing air. When *Cardisoma* stands in shallow (1 cm) water, they will sometimes show postural modifications (raising or lowering the carapace to move the inhalant channels below or above the surface of the water) that control whether water or air is aspirated into the branchial chamber at the limb bases (Burggren *et al.*, 1985). Such postural changes are often associated with alternating periods of forward and reversed scaphognathite beating. While the physiological effects of this behavior are unknown, the splashing and bubbling of branchial chamber water may moisten the superior aspects of the gills and branchial chamber lining, as well as enhance water and ion exchange between branchial chamber water and hemolymph. The semaphore crab, *Heloecius cordiformus*, similarly appears to splash
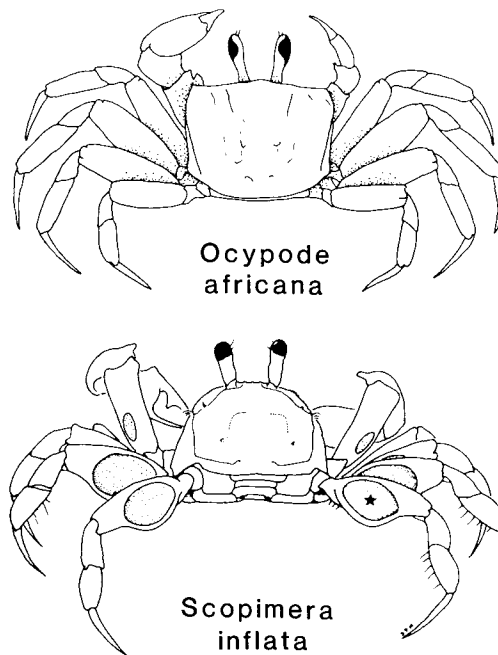

FIG. 1. The meral segments of the walking legs of the Australian sand bubbler crab, *Scopimera inflata*, have a respiratory surface (indicated by star) produced by thinning of the cuticle and epidermis. (from Maitland, 1986).

water within the branchial chamber and also alter the total amount of branchial water during air exposure (Maitland, 1990).

Ventilation of the branchial chamber in some land crabs appears to be aided by lateral movements of the abdominal mass, which acts like a piston to draw air in and out of the branchial chamber (*e.g.*, *Holthuisana transversa*, Greenaway *et al.*, 1983). *Birgus latro* has muscles that elevate the branchial chambers (see McMahon and Burggren, 1988, for details). Changes in volume or conformation of the branchial chamber may well alter air flow through the branchial chamber, and could even generate a gas flow (albeit quite transient) independent of the scaphognathites. Movement of epimeral muscles appears to be responsible for sudden large pressure changes in the branchial chambers of *Coenobita clypeatus* (McMahon and Burggren, 1979), and may similarly alter branchial air flow. Certainly, the movement of water (and presumably air) through the branchial chamber of the semaphore crab, *Heloecius cordiformus*, is
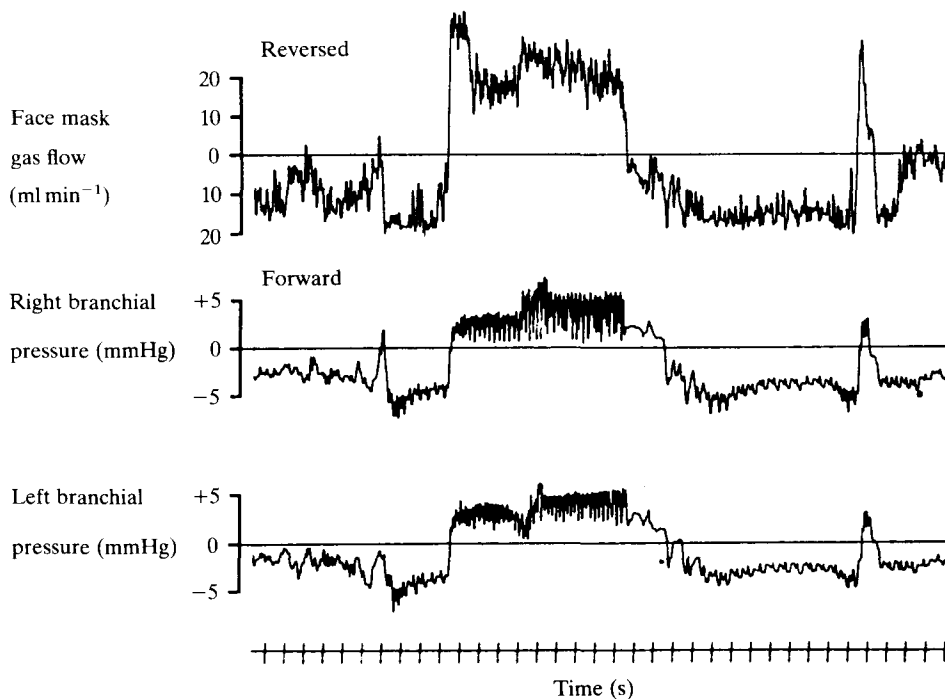
FIG. 2. Simultaneously recorded measurements of branchial air pressure (right and left branchial chamber) and air flow out the exhalant canals in the land crab *Cardisoma guanhumi*. Note the 10 second period of reversed scaphognathite beating in the middle of the record. (from Burggren *et al.,* 1985).

achieved by contraction of muscles that directly alter branchial chamber volume (Maitland, 1990).

Metabolic rate

Perhaps reflecting the relative ease with which it is measured, oxygen consumption (MO_2) has been measured in at least 4 species of terrestrial anomurans and 8 species of terrestrial brachyurans (see McMahon and Burggren, 1988, for references). MO_2 is highly variable, ranging from about 1 up to 6 μMol $O_2 \cdot$g wet mass$\cdot$h^{-1}. Generally, no interspecific differences in MO_2 measured at similar temperatures (or corrected for temperature) are apparent when comparing land crabs with marine species. However, metabolic rate of both marine and terrestrial species can be strongly influenced by seasonal effects, body size, physiological state (*e.g.,* molting stage), activity level, and the load of the adopted molluscan shell in the case of hermit crabs, to name but a few factors (see McMahon and Wilkens, 1983; McMahon and Burggren, 1988; Burggren

and Roberts, 1991). Such influences no doubt account for the great variation in metabolic rates reported not only between species, but even for the same species when measurements were made in different laboratories. Studies specifically designed to investigate metabolic rate differences attributable to habitat in crabs contain many potential pitfalls, as any differences that emerge could potentially result from innate phylogenetic differences as well as habitat differences (Burggren, 1991).

Respiratory gas transport

The transport of O_2 and, to a lesser extent, CO_2, by the hemolymph has been investigated in considerable detail in both anomuran and brachyuran land crabs. Like their marine relatives, land crabs use hemocyanin (Hcy) as the respiratory pigment. In both marine and terrestrial species, however, the presence of this respiratory pigment elevates the O_2 capacity of the hemolymph by only 2–3 times. The marine crabs that have

been examined carry a significant fraction of their total O_2 in solution in the hemolymph rather than chemically bound to Hcy (Mangum, 1980), though Hcy remains the primary transport vehicle in resting animals (for review see McMahon and Wilkens, 1983; McMahon and Burggren, 1988). In terrestrial crabs, almost all O_2 transport is due to O_2 bound to Hcy, with dissolved O_2 in solution playing little or no role in O_2 transport (McMahon and Burggren, 1988). Does this mean that there are *qualitative* differences in O_2 transport between terrestrial and marine forms? Probably not. As body temperature rises, the solubility of O_2 in hemolymph decreases even as O_2 demand by the tissues increases, shifting the burden of O_2 transport to hemocyanin. Since almost all terrestrial crabs are tropical or sub-tropical (Wolcott, 1992), their body temperature can be as much as 20°C higher than temperate marine forms (*e.g., Cancer magister*), from which most data have been collected. Thus, the shift in O_2 transport mechanism towards O_2 chemically bound to Hcy and away from O_2 dissolved in solution in hemolymph is in all likelihood a direct result of differences in body temperature rather than a physiological adaptation to terrestrial life per se.

Two specific respiratory characteristics of crab hemolymph—Hcy O_2 affinity and Hcy O_2 capacity—have received considerable attention with respect to putative adaptations to the terrestrial habitat. Modulation of Hcy O_2 affinity by chemical factors is now known to involve numerous hemolymph factors, including urate, lactate, and Ca^{++} (for reviews see Morris, 1990; Burnett, 1992). However, the hemocynanin of terrestrial species seems to be largely insensitive to organic modulators, and in any event the hemolymph concentration of these modulators can depend upon many of the same considerations that affect metabolic rate (mentioned above). Not surprisingly, no clear relationship between Hcy O_2 affinity and the tendency towards terrestriality has been identified in brachyuran or anomuran crabs.

What is clear, however, is that terrestrial crabs generally have a higher total hemolymph O_2 capacity than do temperate marine forms due to higher concentrations of hemolymph Hcy (see McMahon and Burggren, 1988, for a summary of data and references). While the adaptive advantages (if any) of this higher Hcy concentration have not been unequivocally demonstrated, the higher O_2 capacity would allow the same level of tissue O_2 transport for a reduced hemolymph flow through the respiratory organs. Since conserving water is a primary concern of land crabs (Greenaway, 1988; Wolcott, 1992), a reduced hemolymph flow through the gas exchange organs could reduce evaporative water loss in terrestrial forms. Indeed, a decreased cardiac output is characteristic of land crabs (see section below on cardiac output).

Carbon dioxide transport, a process inherently much more difficult to quantify than O_2 transport, has not been extensively investigated in terrestrial crabs. Partial *in vivo* data (*i.e.,* P_{CO_2} in venous hemolymph or pH of arterial hemolymph) abound, as do *in vitro* measurements of hemolymph carriage of CO_2 (*e.g.,* Morris *et al.,* 1988), but very few studies on land crabs have provided sufficient data to provide the same quantitative approach to CO_2 transport that has been possible for O_2 transport. One general finding is that hemolymph P_{CO_2}, rarely higher than 6 mmHg in aquatic crabs (McMahon and Wilkens, 1983), ranges between 5 and 15 mmHg in terrestrial crabs (see McMahon and Burggren, 1988). This tendency for elevated CO_2 (and thus lower hemolymph pH) with increasing terrestriality is not unique to crabs, but has been observed in virtually every major animal lineage showing either an evolutionary or developmental transition from water to land. Because air has a higher O_2 capacity than water (20–40 times higher, depending upon temperature), air breathing animals can hypoventilate relative to water breathing animals. This hypoventilation, however, leads to an accumulation of CO_2, which is reflected in the higher tissue and body fluid values of P_{CO_2} in terrestrial animals. In the case of land crabs, the higher hemolymph P_{CO_2} even at rest places these animals at greater risk of passing into a respiratory acidosis during exercise, but at least in forms with access to water H^+ ions can be elimi-
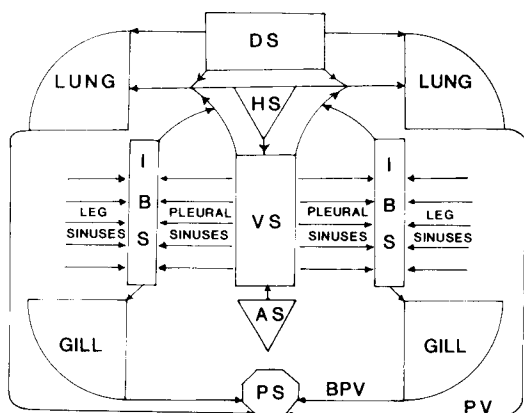
FIG. 3. A highly diagrammatic representation of the venous circulation of the terrestrial crab, *Ocypode cordimanus*. DS, dorsal sinus; HS, hepatic sinus; VS, ventral sinus; IBS, infrabranchial sinus; AS, abdominal sinus; PS, pericardial sinus; BPV, branchiopericardial vein; PV, pulmonary vein. (from Greenaway and Farrelly, 1984).

nated, and most of the accumulating CO_2 is stored temporarily as bicarbonate.

Control of ventilation

One of the central dogmas in comparative respiratory physiology is that, as animals become more and more reliant upon air breathing for gas exchange needs, ventilation of their gas exchange organs is stimulated increasingly by CO_2 and decreasingly by O_2 (Burggren and Roberts, 1991). The control of ventilation has been thoroughly investigated in marine crabs—ventilation is primarily O_2 driven, with CO_2 playing only a minor role in influencing the flow of water pumped through the branchial chamber (see review McMahon and Wilkens, 1983; McMahon and Burggren, 1988). Although relatively few studies have investigated ventilatory control in land crabs, an enhanced respiratory sensitivity to CO_2 has been reported for *Birgus latro, Gecarcinus lateralis* and *Holthuisana transversa* (for review see McMahon and Burggren, 1988). Interestingly, the terrestrial hermit crab *Coenobita clypeatus* remains far more sensitive to O_2 than CO_2 (McMahon and Burggren, 1979). This may reflect the fact that *C. clypeatus*, although occupying a terrestrial macrohabitat, probably makes important and frequent use of its shell water for respiration.

CIRCULATION: COMPARISON OF TERRESTRIAL AND MARINE FORMS

Cardiovascular morphology and the pattern of circulation

The basic cardiovascular pattern of decapod Crustacea is well known (see Burggren and McMahon, 1988*b*, McMahon and Burnett, 1990, and Greenaway and Farrelly, 1990, for current reviews and earlier references). Oxygenated hemolymph is pumped from the heart into a series of posterior and anterior arteries. Hemolymph then passes through the distributing vessels and on to the exchange vessels, which have a diameter comparable to vertebrate capillaries (as small as 2–10 μm in some species!). After perfusing the viscera, hemolymph flows into a ventral sinus, and then flows on into the infrabranchial sinuses which, as the name implies, lie inferior to the gills. The infrabranchial sinuses also receive hemolymph returning from the limbs. Hemolymph from the infrabranchial sinuses flows superiorly into the gills, where it becomes oxygenated. After leaving the gills, the oxygenated hemolymph flows on into the pericardial cavity, where it is aspirated into the heart through several pairs of ostia in the heart wall.

The morphology of the circulatory system of a variety of marine crabs has also been scrutinized, using a combination of dissection of fresh tissues and examination of vascular corrosion casts of the hemolymph vessels (see Burggren and McMahon, 1988*b*; Greenaway and Farrelly, 1990; Taylor, 1990). Generally, with the exception of the circulation of the branchial chamber lining, there are no qualitative differences in cardiovascular morphology between terrestrial crabs and closely related marine forms. However, the specialization of the branchial chamber lining in many terrestrial crabs has resulted in great elaboration of the vasculature to this tissue (see Greenaway and Farrelly, 1990). As evident in Figure 3, the branchial chamber (often termed a "lung," but see[3]) receives venous hemolymph directly from the dorsal sinus, hepatic sinus

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[3] The term "lung" is well ensconced in the literature on air breathing crabs, and for convenience sake this usage is retained. However, the current author opines that the term lung should be restricted to specialized,

and ventral sinus, and thus indirectly from virtually every body tissue. Oxygenated hemolymph draining the "lungs" returns to the pericardial sinus where it mixes with oxygenated hemolymph from the gills, and is aspirated into the heart for redistribution to the tissues.

Corrosion casting of the branchial chamber vessels reveals an extensive network of arborizing vessels draining into large "pulmonary" veins. One of the most fascinating aspects of the circulation of the branchial chamber lining in many land crabs is the pattern of microcirculation. Essentially, there is a dual portal system, with hemolymph passing through three discrete series of vascular beds before finally draining into the pulmonary vein (Greenaway and Farrelly, 1990). Whether there is any control over the resistance of any of these vessels is unknown. If such control exists, however, it would provide a mechanism by which hemolymph could be preferentially distributed between the gills and branchial chamber lining. Whatever the mechanism, redistribution of cardiac output from the gills towards the branchial chamber lining occurs when the amphibious crab *Holthuisana transversa* emerges from water (Taylor and Greenaway, 1984). Whether this is a passive response resulting from an increase in branchial resistance caused by collapse of the gills upon air exposure, or an active response involving active muscular regulation of vascular resistance, remains equivocal. Muscular valves regulating flow through the peripheral hemolymph channels of the gill lamellae have been described in the marine crabs *Carcinus maenas* and *Ovalipes catharus* (see Taylor, 1990), but whether similar structures could alter branchial resistance and thus redirect hemolymph flow to the branchial chamber lining is as yet undetermined. Virtually all animals with two or more sites for gas exchange have some way of redistributing blood between these sites, as dictated by ambient conditions, interacting needs of respiration and hydromineral regulation, or needs for acid-base

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distinctive organs that have evolved *de novo* specifically for gas exchange, rather than pre-existing structures (*e.g.,* branchial chambers) merely modified for respiration.

adjustments (Farrell, 1991). Redistribution of cardiac output between anterior and posterior arteries, modulated by neurotransmitters, has now been demonstrated for marine crabs and lobsters (see McMahon and Burnett, 1990). Given all of these observations, it would be surprising if terrestrial crabs did not have a similarly sophisticated ability for altering perfusion between gills and branchial chamber linings.

Cardiac output

Cardiac output is one of the most difficult of all physiological measurements to make in crabs. Nonetheless, data are available for both marine (*Cancer magister, C. productus, Carcinus maenas*) and terrestrial species (*Cardisoma carnifex, Gecarcinus lateralis, Ocypode quadrata* and *Coenobita clypeatus*) (see Burggren and McMahon, 1988b; McMahon and Burnett, 1990, for references). Cardiac output is generally lower in the terrestrial crabs. Low cardiac output has been correlated with a high blood oxygen capacity in both vertebrates and invertebrates (McMahon and Wilkens, 1983). This is because cardiac output can still meet oxygen demand if the blood O_2 capacity is elevated. As mentioned above, the hemolymph O_2 capacity of terrestrial crabs tends to be greater than that in marine crabs, and with similar metabolic rates, this suggests that cardiac output of terrestrial forms should, indeed, be lower.

While these data suggest a correlation between cardiac output and habitat, choosing closely related, similarly sized species from different habitats is of critical importance when attempting to delineate environmental adaptations from broader, phylogenetic differences (see Burggren, 1991, for discussion and additional references). Comparisons of the large, temperate, sub-tidal brachyuran *Cancer magister* with the small, tropical anomuran *Coenobita clypeatus* may be an inappropriate way to address the question of cardiac output and its relation to habitat.

Hemolymph pressures and baroreceptors

There is a paucity of data on hemolymph pressures at any site in the circulation, in both terrestrial and marine crabs. Thorough, systematic investigations of the
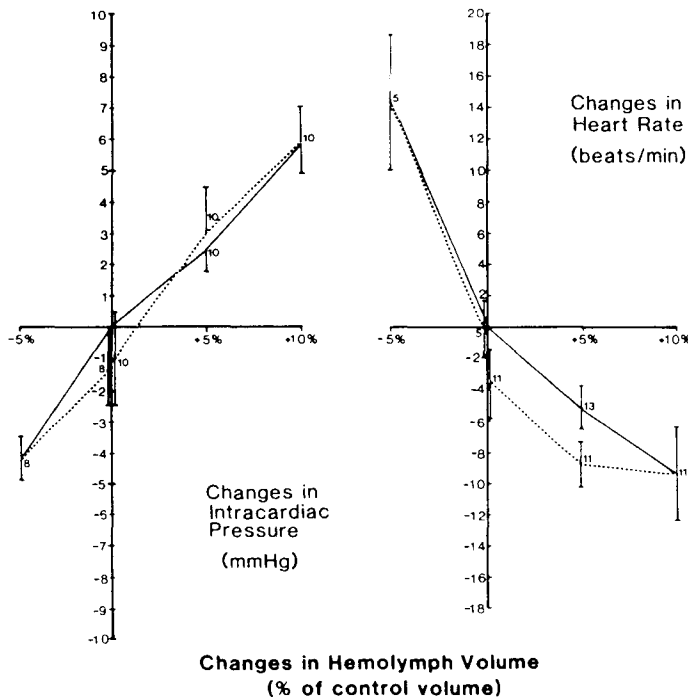
FIG. 4. Changes in intracardiac systolic pressure (left) and heart rate (right) resulting from 5% incremental increases and decreases in hemolymph volume in the land crab *Cardisoma guanhumi*. The solid lines connect mean values (±1 SE) recorded upon first change in hemolymph volume, while the dotted lines connect values recorded during subsequent return to control hemolymph volume. Numbers of crabs contributing to each mean are indicated. ANOVAs indicate significant treatment effects ($P < 0.001$) for both hemolymph pressure and heart rate. (from Burggren *et al.*, 1990).

hemodynamics of the crustacean circulation, involving simultaneous measurement of hemolymph pressures, flows and resistance of peripheral vascular beds are rare (see Reiber, 1992). Certainly, insufficient data exist to make any sort of meaningful comparisons between the cardiovascular systems of terrestrial and marine crabs. Burggren and McMahon (1988b) have speculated on adaptations of the circulation that might be anticipated in crabs making the transition from water to land. Such adaptations might revolve primarily around the fact that the circulation of terrestrial crabs experiences gravitational influences that are completely countered by the water column in marine crabs. Threat postures involving raising the claws as well as postural adjustments during tree climbing (head up, head down) could lead to hemolymph pooling in the venous sinus in terrestrial crabs, leading

to possible redistribution of cardiac output. Even the hydrostatic gradient in the vessels between the dorsal and ventral surfaces of a large land crab could lead to hemolymph pooling. Taylor and Greenaway (1984) report that labelled microspheres injected into the hemolymph of *Holthuisana transversa* in air collected preferentially in the ventral as opposed to the dorsal tissues of the "lungs," suggesting the same type of ventral-dorsal stratification found in the lungs of terrestrial vertebrates. (Hemolymph flow stratification was also found in the lungs of *H. transversa* when submerged in water, but the stratification was less marked than when in air.)

Indirect evidence for a "baroreceptor," a circulatory mechanoreceptor stimulated by changes in hemolymph pressure, has been gathered in *Cardisoma guanhumi* (Burggren *et al.*, 1990). Increasing hemolymph vol-

ume in increments equivalent to 5% total hemolymph volume by infusing filtered sea water into an infrabranchial sinus caused corresponding increases in intracardiac hemolymph systolic pressure (Fig. 4). As hemolymph pressure increased, heart rate decreased. When hemolymph was removed, hemolymph pressure decreased and heart rate increased. These responses are qualitatively similar to those occurring in a vertebrate circulation in which a baroreflex maintains blood pressure. In fact, the rate of heart rate change in *Cardisoma*, about 2 beats·min·mmHg^{-1}, is within the range reported for vertebrate baroreceptor reflexes, conforming to the contemporary view of the decapod circulation as a relatively complex, efficient system (McMahon and Burnett, 1990). Possession of a sensitive baroreceptor reflex could allow *Cardisoma* to make adjustments in hemolymph pressure (and thus in hemolymph flow) during transient perturbations caused by gravitational effects on hemolymph flow and distribution (Burggren *et al.*, 1990). Recently, Rajashekhar and Wilkens (1991) have manipulated hemolymph pressure in the branchiostegal sinus of the shore crab *Carcinus maenas*. This reflexly alters the action of the dorsal ventral muscles that modify branchiostegal sinus volume, leading these researchers to conclude similarly that a reflex involving the regulation of hemolymph pressure resides in this intertidal crab. Independently, Taylor and Taylor (1991) elucidated the role of the branchiostegal muscles in modifying hemolymph pressure in *Carcinus maenas*, and concluded as had Burggren *et al.* (1990) and Rajashekhar and Wilkens (1991) that a baroreceptor reflex was operating in brachyurans. It would appear that there may be at least two reflexes operant—one regulating hemolymph pressure through heart rate and one through the action of the dorsal ventral muscles on hemolymph-filled sinuses. Whether the baroreceptor reflexes of *Cardisoma* and *Carcinus* are primitive characters shared by all brachyurans, or derived characters that have evolved in response to selection pressures associated with exposure to air that is occasional (*Carcinus*) or frequent (*Cardisoma*), is currently unknown—

other species both marine and terrestrial obviously must be examined in this respect.

CONCLUSIONS

The terrestrial habitat is in many respects a potentially hostile environment that in many animals has required substantial preadaptation for a successful transition from a marine environment (Randall *et al.*, 1980; Little, 1983, 1990; Burggren and Roberts, 1991). Does this need for extensive preadaptation similarly apply to brachyuran decapods? Although the proportion of brachyuran and anomuran crabs that live on land is small indeed, certain genera (especially *Cardisoma, Coenobita, Gecarcinus, Geosarma, Ocypode, Sesarma* and *Uca*) have shown varying degrees of success in invading the terrestrial habitat. In many instances, these crabs have made the transition to air breathing without the evolution of major new cardio-respiratory structures. Gills are still retained and still achieve some gas exchange in most species, and even the spectacular respiratory surfaces formed by the branchial chamber lining in *Birgus* and *Eudianella* represent primarily quantitative modifications (albeit of great degree) to existing structures rather than evolution of qualitatively different structures with separate embryonic origins. Cardiovascular adaptations to the terrestrial habitat are even more equivocal, except for the great elaboration of the vasculature of the branchial chamber lining, most land crabs have a cardiovascular system similar in gross morphology to that of marine forms. Thus, major morphological adaptations do not seem necessary for terrestriality in brachyuran decapods.

If one's goal is to study the evolution of terrestriality, are not land crabs, with their substantial morphology resemblance to their marine relatives (*i.e.*, lack of overt morphological adaptation to land), somewhat of a disappointment? To the contrary, the land crabs offer important lessons about the evolution of terrestriality. Perhaps the most fundamental of these is that major adjustments in organ and systems level morphology are not an absolute necessity for a

successful invasion of land by decapods, particularly when combined with adjustments in behavior that allow exploitation of microhabitats with some marine features. Generally speaking, the evolution of small, even subtle, alterations in morphological characteristics can result in much more profound evolutionary alterations in physiological function—*i.e.*, anatomy and physiology are not as tightly linked as some evolutionary biologists would advocate (see Burggren and Bemis, 1990, for discussion). The terrestrial crabs abound in examples illustrating this point, but perhaps no more graphic is the example of *Scopimera*, in which a thinning of the cuticle (a moderate morphological change) converts the leg from strictly an organ of locomotion to an organ of respiration!

In summary, land crabs hold a fascination for zoologists focusing on changes in respiratory and circulatory function during the evolutionary transition from water to air—as much for what these crabs have managed to do with novel variations on the basic marine theme as for any fundamentally new adaptations that may have arisen.

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