

## Terrestrial adaptations in the Anomura (Crustacea: Decapoda)

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### Abstract

Greenaway, P. 2003. Terrestrial adaptations in the Anomura (Crustacea: Decapoda). In: Lemaitre, R., and Tudge, C.C. (eds), *Biology of the Anomura*. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 13–26.

In this review, morphological, physiological and behavioural adaptations to life on land by anomurans are considered. The most terrestrial group are the Coenobitidae and these have developed terrestrial adaptations broadly similar to those of the terrestrial brachyurans. The coenobitids have developed two evolutionary, terrestrial lines. *Coenobita* spp. retain the protective gastropod shell and this has placed a set of constraints on morphological, physiological and behavioural development particularly in regard to gas exchange, osmoregulation and excretion. *Birgus* do not carry molluscan shells after the juvenile stages and, freed from its constraints, reach larger size and have developed terrestrial adaptations that closely parallel those of the brachyuran land crabs. Shell retention by *Coenobita* has resulted in development of novel abdominal gas exchange organs whilst purine excretion by *B. latro* seems to be unique amongst land crabs. Crabs of both genera are well adapted to life on land in terms of sensory, respiratory, excretory and osmoregulatory functions and they can also moult, mate and lay eggs effectively on land. Several species have the functional ability to live in a range of habitats from rainforest to arid scrubland but their penetration of these habitats is limited to small islands or to a narrow coastal strip. This is probably due to the retention of pelagic larval stages and to the lack of molluscan shells of suitable dimensions and strength in inland situations, which restrict the range to a manageable distance from the sea.

### Keywords

Crustacea, Anomura, terrestrial adaptations, *Coenobita*, *Birgus*

### Introduction

On land, the Anomura are represented principally by the Coenobitidae which include 15 species of shell-carrying terrestrial hermit-crabs (*Coenobita*) and the robber or coconut crab *Birgus latro* (Linnaeus, 1767), the largest terrestrial arthropod (to 3 kg). Although there are relatively few species of *Coenobita*, individuals are numerous in tropical and subtropical maritime regions particularly supralittoral areas and small islands, although some penetrate further inland. Certain species are restricted to beaches (e.g. *C. perlatus* (H. Milne Edwards, 1837), *C. scaevola* (Förskal 1775), *C. spinosus* (H. Milne Edwards, 1837), *C. cavipes* (Stimpson, 1838) while several other species may penetrate long distances inland, e.g. *C. clypeatus* (Herbst, 1791) on Curaçao, *C. rubescens* (Greeff) and *C. brevimanus* (Dana, 1852) in rainforest, *C. compressus* (H. Milne Edwards) (de Wilde; 1973; Burggren and McMahon, 1988). *Coenobita rugosus* (H. Milne Edwards, 1837) may live on the beach or penetrate inland in situations where fresh water is available (Yamaguchi, 1938; Vannini, 1976). The closely related Diogenidae also show terrestrial tendencies but typically occupy intertidal and mangrove habitats, e.g. *Diogenes*, *Calcinus*, *Clibanarius*. There are also a number of intertidal amphibious species in the Porcellanidae, that tolerate emersion but are not normally active out of water e.g. *Petrolisthes*.

The adoption of terrestrial habits seems to be a comparatively recent evolutionary development (as with terrestrial brachyurans) and the oldest coenobitid fossils are from the Lower Miocene (Table 1). The coenobitid line of evolution is entirely terrestrial apart from the planktonic larval stages. Successful transition from aquatic to terrestrial life requires a number of physiological adaptations some of which are immediately essential for survival out of water while others are less immediately important and may be developed progressively over a much longer period of adaptation (Table 2).

The reader is also referred to Burggren and McMahon (1988) and reviews in “The Compleat Crab” (Mantel, 1992) for further literature on certain aspects of terrestrial adaptations of anomurans.

### Gas exchange

Anomurans have developed a number of different adaptations for aerial gas exchange some of which are convergently similar to those described for brachyurans (Burggren, 1988; McMahon and Greenaway 1999) and others, such as the novel abdominal respiratory organ, that are unique and have developed as a response to living in a mollusc shell.

Table 1. Origin of terrestrial anomurans. T<sub>1</sub> are aquatic and can survive brief emersion with some limited degree of terrestrial activity. T<sub>2</sub> are amphibious and voluntarily active out of water for substantial periods e.g. air-breathing intertidal crustaceans. T<sub>3</sub> are amphibious species resident, and principally active, on land but which require regular immersion in standing water (often in burrows) and water is required for breeding (e.g. supralittoral species and amphibious freshwater forms). T<sub>4</sub> are terrestrial species which do not require immersion in standing water but which need periodic access to water for reproduction (from Greenaway, 1999). Fossil data from Glaessner (1969).

Infraorder Anomura	Terrestriality	Earliest Fossil
Superfamily Coenobitoidea		
Family Coenobitidae	T <sub>3</sub> – T <sub>4</sub>	Lower Miocene
Family Diogenidae	T <sub>1</sub> – T <sub>3</sub>	Upper Cretaceous
Superfamily Galatheaidea		
Family Porcellanidae	T <sub>1</sub>	Upper Cretaceous

The gill number and area in brachyuran crabs decreases as terrestriality increases (e.g. McMahon and Burggren 1988; Greenaway, 1999) and this trend is also evident in the phyllobranch gills of the Coenobitidae. *Birgus latro* has the smallest weight specific gill area measured for any terrestrial decapod (area (mm<sup>2</sup>) = 152.1 x mass (g)<sup>0.686</sup>) (Greenaway, 1999) and they play little role in oxygen uptake (Greenaway et al., 1988). Instead, oxygen uptake by *B. latro* occurs across the large, evaginated, branchiostegal lungs (Cameron and Mecklenburg, 1973; Greenaway et al., 1988) supplied with venous blood from the ventral sinuses (Semper, 1878; Harms 1932), a development parallel to that seen in the larger terrestrial brachyurans. The cuticle and epidermis making up the lung membrane are extremely attenuated (Harms, 1932; Storch and Welsch, 1984) and blood is directed to the exchange surface by connective tissue partitions similar in organisation to those described for brachyuran land crabs (e.g. Farrelly and Greenaway, 1993). Evidence gained from direct measurements of pre- and post-branchial CO<sub>2</sub>, from the distribution of carbonic anhydrase and from experimental gill ablation is supportive of a strong

continued role of the gills in CO<sub>2</sub> elimination. However, this is supplemented by pulmonary excretion and during exercise CO<sub>2</sub> elimination is equally partitioned between the two organs (Smatresk and Cameron, 1981; Greenaway et al., 1988; Morris and Greenaway, 1990).

The gills of *Coenobita* are also markedly reduced (Harms, 1932) and weight specific gill area of *C. scaevola* (expressed per unit live weight) is of the same order as for *B. latro* (Achituv and Ziskind, 1985). However, the mollusc shells in which hermit crabs live physically constrain development of branchiostegal lungs. Consequently these lungs are small, lack surface amplification, have relatively long blood/gas diffusion distances and a poorly organised blood supply compared to lungs of *B. latro* (Harms, 1932; C.A. Farrelly, pers. comm.). With gills reduced and lung development restricted, the coenobitids have developed a third site for aerial gas exchange, the dorsal surface of the abdomen. The attenuated cuticle and epidermal cells covering this region form a thin respiratory membrane in contact with the air carried in the upper part of the mollusc shell. The membrane receives a rich supply of venous blood via a highly organised network of respiratory vessels and oxygenated blood passes forwards to the pericardium where it mixes with blood returned from the gills and branchiostegites (Bouvier, 1890; Harms, 1932; Greenaway, 1999; Farrelly and Greenaway, 2001). It is not clear how the air in the shell above this respiratory organ is renewed but the carapace movements described by a number of authors (e.g. McMahon and Burggren, 1979) might drive convective exchange of shell air. The ventral surface of the abdomen is frequently bathed in shell water and is not modified for aerial gas exchange. The shell water could potentially act as a dump for respiratory CO<sub>2</sub> but as its CO<sub>2</sub> capacity is small this function will be limited.

A fourth type of gas exchange organ has developed in certain evolutionary lines of porcelain crabs (*Petrolisthes*). These species have oval patches of very thin cuticle on the meral joints of their walking legs similar to the “gas windows” described in certain small burrowing, intertidal brachyurans (Maitland, 1986). At least in larger species of *Petrolisthes*, these

Table 2. The requirement for physiological and behavioural changes on emergence from water. T<sub>1</sub> – T<sub>4</sub> as in Table 1; T<sub>5</sub> are fully terrestrial species able to conduct all biological activities on land (Greenaway, 1999).

Physiological function	Immediate requirement for physiological or morphological adaptation on emersion?	Grade at which adaptation is essential
Oxygen uptake	Yes, morphological modifications required immediately	T <sub>1</sub>
CO <sub>2</sub> output	Yes, required immediately	T <sub>1</sub>
Salt regulation	No, if water is regularly available for immersion	T <sub>3-4</sub>
Evaporative water loss	No, if water is available in microhabitat as behavioural regulation will suffice	T <sub>4</sub>
Nitrogen excretion	No, if emersion periods are relatively brief	T <sub>4</sub>
Temperature regulation	No, temperature can be regulated behaviourally if water or shelter available	–
Sensory reception	Sound – not immediate	T <sub>3</sub>
	Photo – immediate	T <sub>2</sub>
	Chemo – Loss of aquatic chemoreception compensated by vision	T <sub>2-3</sub>
Locomotion and support	No, pre-adapted to support on land or utilise support of mollusc shell	T <sub>2</sub>
Moulting	No, not if animal can moult in water	T <sub>4</sub>
Reproduction	Yes, commonly needs at least behavioural changes and often some morphological and physiological adaptation	T <sub>1-5</sub>

play a demonstrable role in aerial gas exchange, particularly at higher temperatures, and they may allow the animals to remain aerobic during emersion at low tide (Stillman and Somero, 1996; Stillman, 2000). The selective pressures favouring development of gas windows have not been clearly identified. In brachyurans they are associated with small body size and burrowing habits that may favour selection for external gas exchange sites rather than bulky lungs (Maitland, 1986). The extreme flattening of the carapace of *Petrolisthes*, which allows exploitation of shallow cavities beneath littoral rocks and stones, may place similar constraints on lung development in porcellanids.

Ventilation of the gills and lungs of coenobitids is effected by the scaphognathites. In *B. latro* the ventilation rate is determined by alteration of the frequency of beating of the scaphognathites and stroke volume remains more or less constant over the frequency range. Control of ventilation is primarily by CO<sub>2</sub> and scaphognathite frequency is linearly related to the PCO<sub>2</sub> of the inspired air. There is also a secondary stimulation in response to low partial pressures of oxygen (<90 Torr) in inspired air (Cameron and Mecklenburg, 1973; Smatresk and Cameron, 1981) so that the pattern of control of breathing is similar to that of terrestrial animals generally. By contrast ventilatory response of *C. clypeatus* to PCO<sub>2</sub> is low, even at high partial pressures, and the primary control of ventilation is by PO<sub>2</sub> (McMahon and Burggren, 1979), a scenario similar to that in water breathing animals. These authors suggested that *Coenobita* might retain aquatic respiratory patterns by circulation of shell water over the gills but there are no behavioural or physiological data that support this. The animals will commonly encounter elevated PCO<sub>2</sub> both while retracted into the shell for long periods and when buried in the sand during diurnal periods of inactivity (Vannini, 1975b; Achituv and Ziskind, 1985). An alternate explanation for their insensitivity to CO<sub>2</sub> may be that it is an adaptation to high environmental CO<sub>2</sub> (common in burrow-dwelling animals) rather than retention of "aquatic" gas exchange. Vertical movements of the carapace have been described in *B. latro* and in *Coenobita* but are not believed to contribute in any systematic or significant manner to gas exchange by gills or lungs, which are well ventilated by the scaphognathites (Borradaile, 1903; Harms, 1932; Cameron and Mecklenburg, 1973; McMahon and Burggren, 1979). The enhanced frequency of carapace movements during hypoxia and hypercapnia, reported in *C. clypeatus*, may, however, be concerned with ventilation of the abdominal respiratory organ. In resting animals ventilation is not continuous, particularly in *Coenobita*, and given the high oxygen content and diffusion rate of oxygen in air, diffusion may provide adequate delivery of oxygen to the respiratory surface between bouts of ventilation.

The coenobitids have developed a number of features that are characteristic of terrestrial air-breathers, elevated partial pressure of CO<sub>2</sub> (PCO<sub>2</sub>), high bicarbonate levels and carbon dioxide-based ventilatory control (in *B. latro*) although oxygen affinity and arterial oxygen tensions are not obviously different from those of aquatic decapods.

About 90% of oxygen transported by the blood of coenobitids is carried by haemocyanin with only around 10% in

simple solution (Wheatly et al., 1986; Greenaway et al., 1988). Oxygen capacity is at the upper end of the range for decapod crustaceans (1.85 mmol.L<sup>-1</sup> in *B. latro*, 1.51 mmol.L<sup>-1</sup> in *C. compressus*). The respiratory pigments of coenobitids have oxygen affinities that lie in the midrange of values for aquatic decapods; P<sub>50</sub> = 12–19 Torr in resting and exercised *Coenobita* and 13.6 Torr at 30°C in resting *B. latro* (Morris and Bridges, 1986; Morris et al., 1988). The oxygen tension (PO<sub>2</sub>) of oxygenated (arterial) blood of resting crabs reflects this moderate affinity; *B. latro*, 44 Torr, *C. compressus* 14 Torr. Arterial PO<sub>2</sub> of *B. latro* falls during exhausting exercise but in *C. compressus* it doubles whilst venous PO<sub>2</sub> remains unchanged. The oxygen affinity of the haemocyanin of *B. latro* exhibits a large Bohr shift between pH 8–7.3 and a sharply decreased response below this pH range. This facilitates oxygen delivery during exercise but ensures that oxygen loading is not compromised at the lower pH values engendered by severe exercise (Wheatly et al., 1986; Greenaway et al., 1988). In *B. latro*, the pigment is highly and uniformly sensitive to temperature over a wide range (Morris et al., 1988) but as the species normally lives in stenothermal tropical forests the affinity is unlikely to be adversely affected by temperature. In *Coenobita*, haemocyanin is largely insensitive to temperature within its preferred range (25–30°C) although sensitive at higher and lower temperatures (Morris and Bridges, 1986). Most species of *Coenobita* occupy more exposed habitats than *B. latro*, and experience a wider range of temperature, so that it is advantageous to have consistent oxygen affinity over their normal temperature range for activity. The haemocyanins of coenobitids are insensitive to the usual chemical modulators of oxygen affinity utilised by aquatic decapods (lactate, urate, Mg<sup>2+</sup>) and the animals rely more on mechanical means (ventilation and perfusion) to modulate oxygen delivery. *Birgus latro* can increase ventilation >5 × in exercise (Smatresk and Cameron, 1981; Greenaway et al., 1988).

Oxygen consumption (MO<sub>2</sub>) of terrestrial coenobitids is within the range for other terrestrial crabs (McMahon and Burggren, 1988) and oxygen consumption (MO<sub>2</sub>) increases with temperature (Q<sub>10</sub> 2.6–2.7 in *C. clypeatus* and *C. rugosus*) (Burggren and McMahon, 1981). Oxygen delivery keeps pace with elevated metabolism due to the temperature sensitivity of haemocyanin, elevation of arterial PO<sub>2</sub> and modulation of ventilation and perfusion (McMahon and Burggren, 1988). The MO<sub>2</sub> can be elevated 3.4 fold over resting levels in *C. compressus* (Wheatly et al., 1985). The coenobitids appear to be specialised for endurance locomotion and on treadmills *C. compressus* voluntarily maintains walking speeds of 0.02–0.03 km.h<sup>-1</sup> for periods as long as 5h and distances up to 150 m. Respiratory and circulatory adjustments to exercise are complete within 30 min of the onset of exercise and thereafter activity is aerobic with no accumulation of lactate (Wheatly et al., 1985). On firm substrates in the field, sustained aerobic exercise at speeds of 0.23 km.h<sup>-1</sup> (max. 0.4 km.h<sup>-1</sup>) is also common (Vannini, 1976; Herreid and Full 1986a,b). *B. latro* too, can cover long distances (Greenaway, 2001). The coenobitids are less able to sustain high levels of exercise and *B. latro* rapidly becomes refractory when high levels of exercise are enforced. When threatened in the field, animals may

“crouch” (Helfman, 1977a) or move rapidly for just long enough to back into crevices or climb trees and they seldom “run” unless caught in the open. *Coenobita* retreat into their shells when threatened rather than attempting to escape but *C. variabilis* and *C. compressus* will often run and are known to abandon their shells when pursued (A.W. Harvey, pers. comm.). The shell carried by hermit crabs doubles the metabolic cost of locomotion at slow walking speeds but this cost falls as speed increases and is  $\sim 1.3 \times$  the shell-less rate when higher speeds are maintained (Herreid and Full, 1986b).

### Salt and water balance

Salt and water regulation of land crabs have been reviewed by Greenaway (1988) and Wolcott (1992) and the reader is referred to these papers for details of earlier work.

**Water gain.** The mechanism of water uptake is related to the habitat and osmoregulatory practices of species and individuals. The more terrestrial anomurans avoid immersion and utilise fresh water from pools, rainwater, dew and damp substrates. The water is taken up by the chelae and passed to the densely setose third maxillipeds (Vannini, 1975b; Greenaway, 1988) from which it may be then ingested or passed to the reservoir of shell water via the branchial chambers (de Wilde, 1973). Beach-dwelling coenobitids drink seawater or extract it from damp sand and often immerse themselves to flush the shell. *Coenobita rugosus* in Somalia make use of fresh water from damp sand following rain but in dry weather migrate nightly to the beach from dry foraging areas in sand dunes in order to access damp sand in the intertidal zone. *C. clypeatus* is reported to ingest damp, friable limestone for its water content (de Wilde, 1973).

**Water requirements.** A few quantitative studies have been made of water usage by terrestrial anomurans but most have been laboratory studies in which the conditions of measurement may not reflect field requirements. Water usage in the laboratory by *B. latro* is 16–20 mL.kg<sup>-1</sup>.d<sup>-1</sup> (Greenaway et al., 1990) but in the field rates are much higher ( $\sim 48$  mL.kg<sup>-1</sup>.d<sup>-1</sup>) and this has also been reported for brachyurans (Greenaway, 1994; 2001). Drinking by shelled hermits in the laboratory has been measured (de Wilde, 1973), but the data are not in a format that facilitate comparison and fluid ingested may be partitioned between the gut and shell water making it difficult to distinguish between turnovers of body and shell water. Drinking rates of coenobitids increase rapidly with the salinity of the drinking water (de Wilde, 1973; Greenaway et al., 1990) as a result of the inability of the crabs to produce excretory fluid that is significantly hyperosmotic to the haemolymph. Thus when saline water is provided for drinking, intake must be considerably enhanced, as much of the volume gained is needed to excrete the salt load and the net gain of pure water, required to replace evaporative loss, is small. Tolerance of saline water is thus critically dependent on the rate of evaporative loss (Taylor et al., 1993).

Water requirement is to a large extent a function of evaporative water loss which in turn depends on cuticular permeability and crab behaviour. Intertidal hermit crabs (*Clibanarius*)

have high evaporative water loss rates which increase further ( $\times 3$ ) if the animals are removed from their shells (Herreid, 1969a). In *Coenobita scaevola* removal from the shell increased evaporative loss by only 11% (Achituv and Ziskind, 1985) and the terrestrial hermits may have a lower permeability. Tolerance to water loss is reportedly high (50% body water) in the intertidal *Clibanarius vittatus* (Young, 1978) but lower (30%) in *C. clypeatus* (de Wilde, 1973) and *Petrolisthes elongatus* (H. Milne Edwards, 1837) (20.8%) (Jones and Greenwood, 1982).

**Water reserves.** The water carried in the shell of terrestrial hermit crabs can amount to 30–50% of the wet weight of the animal (de Wilde, 1973). This water has an osmotic concentration similar to that of the blood and is used as a reservoir to replace evaporative losses and may be added to or replaced during drinking or immersion. *Coenobita* spp. also have two distensible sacs of the abdominal wall which expand after drinking and can accommodate considerable increase in volume of the haemolymph (de Wilde, 1973).

**Behavioural regulation of water loss.** Like many terrestrial animals, coenobitids modify their behaviour to minimise evaporative water loss, particularly under hot and dry conditions, and they characteristically are most active in the higher nighttime humidities. They detect and orient to water vapour (Vannini and Ferretti, 1997) and in experimental humidity gradients, *C. clypeatus* selects areas of maximum humidity whilst avoiding wet substrates (de Wilde, 1973). Although coenobitid species are primarily nocturnal, sudden rises in daytime humidity, or a brief shower, often initiate diurnal activity (Ball, 1972; de Wilde, 1973; Vannini, 1976; Alexander, 1979).

**Osmoregulation.** Anomurans are separable, on the basis of their osmoregulatory behaviour, into amphibious, intertidal forms, such as porcelain crabs and diogenid hermit crabs, and the more terrestrial coenobitids. The former are immersed twice daily and are generally either osmoconformers or weak osmoregulators (Davenport, 1972a,b,c; Jones, 1977; Young, 1979; Sabourin and Stickle, 1980) although stronger regulatory ability must be present in *Clibanarius fonticola* (McLaughlin and Murray, 1990) which inhabits freshwater pools.

The coenobitids exhibit a continuum of osmoregulatory behaviour; some species are restricted to supralittoral habitats and drink seawater while others penetrate inland and prefer dilute water (Table 3). In beach-dwelling coenobitids that drink seawater, the inability to produce hyperosmotic excretory fluid and the effects of evaporative water loss and dietary salt intake, result in blood and shell water concentrations hyperosmotic to seawater (Table 3). The main osmoregulatory tactic in these animals is to flush the shell reservoir with seawater at regular intervals either by immersion or by drinking. This allows replacement of fluid losses and facilitates loss of salt from the body fluids to shell water but sets a minimum concentration for the blood similar to that of seawater.

*Coenobita* spp. that live away from the beach do not usually have access to seawater and indeed these species prefer dilute water unless they are depleted of salt (de Wilde, 1973). As the drinking water is dilute the animals can and do maintain

Table 3. Osmoregulation in terrestrial coenobitids. SW = sea water; FW = fresh water.

Species	Distribution	Drinking Water	Blood Conc. mosm	Shell water mosm	Source
<i>C. scaevola</i>	Beach only	SW			Achituv and Ziskind (1985)
<i>C. perlatus</i>	Beaches/atolls, small islands	SW	>SW 1020–1500	>SW 970–1260	Gross (1964), Gross and Holland 1960
<i>C. cavipes</i>	Beach and vicinity	FW/ SW	<SW 865–975	<SW	Gross et al. (1966)
<i>C. rugosus</i>	Beach and vicinity	FW/SW			Vannini (1975b)
<i>C. clypeatus</i>	Beach and inland	FW	<SW 969	<SW 915–945	de Wilde (1973)
<i>C. brevimanus</i>	Coastal forest dense vegetation	FW	<SW 840	<SW ~762–908	Gross (1964)
<i>B. latro</i>	Inland	FW	<SW 650–750	No shell water	Taylor et al. (1993) Greenaway (2001)

shell water and body fluid concentrations well below that of seawater (Table 3). The salt in their shell water must originate from the diet, perhaps via urine released into the shell, and presumably is available to the animal via branchial uptake or ingestion.

The normal ranges of osmotic concentration maintained by coenobitids are well established (Table 3) and it is known that the crabs maintain their shell water isosmotic with the body fluids (summarised in Greenaway, 1988). However the mechanisms of regulation in the shelled hermit crabs have not been studied. Regulation is potentially complex as it may involve exchanges of water and ions between numerous compartments including the shell water, crab tissues, the excretory system and the outside environment. The urine is isosmotic and on release from the antennal organs may potentially be voided, drunk, passed to the branchial chambers for ion recovery or added to the shell water. Similarly, fluid released from the branchial chambers after salt recovery could be voided or added to the shell water. Only drinking and flushing have been examined to date. When crabs of either group have access to waters of differing salinities they can regulate shell water within the preferred range behaviourally by selective drinking and promotion of evaporation (Gross, 1955; 1964; de Wilde, 1973). Crabs have a strong ability to assess the salinity of water bodies and *C. clypeatus* can discriminate differences in salinity of only 0.18–0.36 (de Wilde, 1973), whilst *C. rugosus* can distinguish between airborne odours of fresh and saline water (Vannini and Ferretti, 1997). Although differential drinking may be utilized for osmoregulation by beach-dwelling animals and in atoll populations, it is not useful in the more inland situations where generally only fresh water is available (Wolcott, 1992). There different mechanisms must be used.

Osmoregulation in *B. latro* differs from the patterns seen in other coenobitids as, in the absence of a mollusc shell, the body fluids are regulated directly against the environment. In common with other coenobitids, *B. latro* has a preferred range of blood concentration and is remarkably tolerant of haemoconcentration. In most natural field situations, only fresh water is available for drinking, and *B. latro* maintains its blood concentration in the range 650–750 mosm, with the lower blood concentrations preferred in wet conditions and maintained even if salt intake and excretion are high (Greenaway, 2001). Where only saline water is available (e.g. atolls), the osmotic concentration of the body fluids becomes elevated; the animals will

tolerate concentrations in excess of 1100 mosm for long periods (Gross, 1964; Taylor et al., 1993).

Salt regulation in *B. latro* is convergently similar to that of the terrestrial brachyurans. Urine of similar osmotic concentration and ionic composition to the blood is released from the antennal organs. Some volume recovery occurs by drinking and the residual volume is passed to the branchial chambers where salt recovery conforms to homeostatic needs. Turnover of salt in the field is high (7.8 mmol.kg<sup>-1</sup>.d<sup>-1</sup>) but regulation of body sodium is readily achieved when drinking fresh water (Greenaway, 2001). When dietary salt intake is low, the final excretory fluid is extremely dilute (<10 mmol.L<sup>-1</sup> Na) but, with access to saline water, the animals respond rapidly with increases in intake, in flow and in concentration of the urine and in the concentration of the released excretory fluid. When sea water is drunk, the excretory fluid released is isosmotic or marginally hyperosmotic to the blood (Greenaway et al., 1990; Taylor et al., 1993; Greenaway, 2001). Once elevated, however, blood concentrations can only be reduced if crabs have access to drinking water of lower osmotic concentration than the blood.

Salt resorption from urine released to the branchial chambers is effected by transport mechanisms in the branchial epithelium (Morris et al., 1991) and, as the crab normally drinks only fresh water, a high rate of branchial ion recovery is the default condition. Branchial ion transport is controlled by the blood-borne hormone dopamine. Elevation of the blood concentration is believed to increase the circulating level of dopamine which stimulates an increase of the [cAMP] in the branchial epithelium which in turn results in deactivation of Na<sup>+</sup>K<sup>+</sup>-ATPase (Morris et al., 2000). Thus *B. latro* has developed an ion regulatory mechanism that normally conserves ions by production of a dilute excretory fluid suited to the particular requirements of its normal habitat. When faced with the relatively uncommon circumstance of high salt intake, then branchial transport is down regulated to increase salt output. In situations where *B. latro* has access to both dilute and saline drinking water, e.g. on small islands and atolls, it too can regulate its body fluid concentration by differential drinking (Gross, 1955; Combs et al., 1992).

*B. latro* has developed a flexible system of osmoregulation that combines a high degree of physiological and behavioural regulation of salt and water balance with tolerance of large fluctuations in blood osmolality. These adaptations enable the

species to regulate effectively in environments where only fresh drinking water is available and also on small islands where, seasonally, seawater becomes the sole source of drinking water.

### Nitrogenous excretion

Uniquely amongst the terrestrial crustaceans studied, *B. latro* has adopted a terrestrial excretory pattern and eliminates purines in lengths of white excreta (Greenaway and Morris, 1989). In initial enzymatic analyses, the purine was identified as uric acid (Greenaway and Morris, 1989), but recent HPLC studies have revealed that both uric acid and guanine are present at a ratio of 2:1 (P. Greenaway, pers. obs.). The white faeces are made up of billions of small spherules of purine 1–2 µm in diameter produced by R cells in the tubules of the midgut gland and released periodically into the gut in coordinated bouts of secretion (Dillaman et al., 1999). The purine excreted is synthesised de novo and a key enzyme in this process, xanthine dehydrogenase, is present at high activities in the midgut gland (Dillaman et al., 1999).

In *Coenobita*, faeces are deposited outside the shell and any faecal elimination of purines or ammonium could readily be established. Excretion of ammonia, either in gaseous form or in excreted fluid, could also be easily assessed but the necessary measurements have not been performed. Excretory products in the blood offer few clues to the excretory mechanism used; urea is not detectable, ammonia levels are reportedly low and although uric acid is somewhat elevated (Henry and Cameron, 1981) this could be connected with purine storage in the tissues. At the present time the mechanism of N excretion is obscure and investigation of the excretory mechanisms employed by the shell-carrying hermits is urgently needed.

Purine is stored in large amounts in connective tissue cells throughout the bodies of *Coenobita* and *B. latro*, (Henry and Cameron, 1981; Greenaway and Morris, 1989) as well as other land crabs (Linton and Greenaway, 1997a). In the brachyuran land crab *Gecarcoidea natalis* (Pocock, 1888), this stored purine is synthesised de novo, and it is likely that synthetic ability is common to the brachyuran and anomuran land crabs that store purines (Linton and Greenaway, 1997b). A storage excretion function has been ascribed to the urate accumulated by *G. natalis* (Linton and Greenaway, 1998; 2000). Although this function is possible in *Coenobita* it seems unlikely in *B. latro* where N is excreted as purine and is not therefore constrained by water availability as in *G. natalis*. The possibility that purine stored in *B. latro* functions as a remobilisable N reserve needs to be investigated.

### Feeding and diet

The terrestrial anomurans are catholic feeders and eat fallen fruits and seeds, mangrove propagules, a wide variety of other plant material, strand line detritus, animal faeces and animal carcasses varying from small invertebrates to fish, giant tortoises, birds, goats and donkeys (Grubb, 1971; de Wilde, 1973; Vannini, 1976; Barnes, 1997a). Much of the normal diet is plant material, but near human habitations resident populations

*C. cavipes* may become reliant on human faeces and refuse (Barnes, 1997a). On Aldabra, *C. rugosus* exploits fresh tortoise faeces (Grubb, 1971). A number of species of *Coenobita* climb bushes and small trees (reviewed by von Hagen, 1977) where it is likely that they forage on plant material or perhaps scale and other insects. In mangroves, however, climbing by *C. cavipes* and *C. rugosus* seems not to be primarily oriented towards feeding (Barnes, 1997b).

*Birgus latro* is a little more selective in its diet but also exploits a wide range of plant and animal materials. It particularly favours high energy plant material notably seeds rich in carbohydrate or lipids (e.g. *Pandanus elatus* (Ridl., 1906), *Calophyllum inophyllum* (Linnaeus, 1753), *Cocos nucifera* (Linnaeus, 1753), *Aleurites moluccana* ((L.) Willd., 1805), and it will rip away and discard the fleshy material of soft fruits such as custard apples (*Annona reticulata* (L., 1753)) and papaya (*Carica papaya* L.) to access the seeds. Fruits and kernels of the sago palm *Arenga listeri* (Becc., 1891) are particularly attractive, as is the carbohydrate-rich pith. *Birgus latro* will climb the tall trunks of *A. listeri*, *Pandanus* and *C. papaya* to reach the fruits but most animals wait for fruit to fall and aggregations of several hundred animals are reported beneath preferred fruiting trees (Hicks et al., 1990). The large chela, which can develop forces of 90 kPa, (Hicks, Rumpff and Yorkston, 1990) is used to open the very hard nuts of *A. moluccana* and *C. inophyllum* and the animals readily open *Macadamia* nuts in the laboratory. Large animals can strip the husk from fallen coconuts and open the hard inner shell at the “eyes”. They investigate, carry away and attempt to open any unusual object and will visit garbage bins hence their common name, robber crab. The crabs are also active predators. On Christmas Island, they feed extensively on the gecarcinid crabs *Gecarcoidea natalis* and *Cardisoma hirtipes* (Dana, 1852), which they stalk or dig out from shallow burrows (Hicks et al., 1990; Greenaway, 2001). On Aldabra they are reported to prey on hatchling tortoises (Swingland in Alexander, 1979) and on the land crab *Cardisoma carnifex* (Herbst, 1794). Foraging is dependent on humidity, and marked or radio-tagged *B. latro* forage infrequently in dry weather but nightly in moist conditions (Reese, 1987; Fletcher et al., 1990b; Greenaway, 2001).

*Birgus latro* stores lipids and glycogen in the R cells of the midgut gland (Chakravarti and Eisler, 1961; Lawrence, 1970; Storch et al., 1982; Dillaman et al., 1999). The midgut gland fills the abdomen and can expand substantially to accommodate food reserves, which may allow survival for more than a year without feeding (Storch et al., 1982).

There is no information on the digestive physiology of *Coenobita* although there are several studies on the masticatory apparatus of hermit crabs (Schaefer, 1970; Caine, 1975; Kunze and Anderson 1979). Recently Wilde and Greenaway (1998, 2001) measured rates of assimilation of nutrients by *B. latro* (Table 4) and these data may be applicable to the family Coenobitidae in general.

*Birgus latro* has a very high ability to utilise fats and storage polysaccharides of both plant and animal origin and additionally can digest significant amounts of plant fibre such as hemicelluloses, cellulose and lignin. Protein assimilation from plant

material is 65–70% and the animals efficiently digest chitin from crab skeletons. *Birgus latro* and probably other coenobitids clearly have the ability to digest a wide range of food materials from plant fibre through to protein and chitin, which helps to explain their catholic feeding habits. It also clarifies some of the more bizarre aspects of feeding in the group, such as feeding on faeces. To coenobitids, vertebrate faeces are a rich food source as they contain undigested plant fibre, mucous and animal protein in the form of sloughed-off intestinal cells and waste enzymes. Additionally, the products of microbial digestion in the lower alimentary tract of vertebrates commonly pass out in the faeces and these, and the microbes themselves, will be utilised by *Coenobita*. Faeces represent a considerably higher quality diet than, for example, shoreline plant detritus. In the long term, eating faeces may entail the risk of becoming a secondary host for vertebrate parasites but the gastric mill may well be an effective protection against many infective stages.

Table 4. Assimilation of food components by *Birgus latro* fed on artificial diets. Data from Wilde and Greenaway (2001, and pers. obs.). Diets consisted of starch, coconut, sunflower seed, hazelnuts and bran ground and blended into an agar base. The crab diet was prepared from dried and powdered *Gecarcoidea natalis* blended in agar.

	High fat diet	% assimilation	
		High carbohydrate	Crab diet
Dry matter	75.5	71.7	64.7
Lipid	96	87.4	70.8
Carbohydrate	98.1	99	89.4
Hemicellulose	68	45	–
Cellulose	52	17	–
Lignin	51	18	–
Chitin	–	–	92.8
C	82.1	72.7	64.5
N	69.4	65.2	–

Coenobitids can detect food odours from distances exceeding 5 m (Dunham and Gilchrist, 1988) but they are attracted preferentially by the odours of foods that they have not eaten recently rather than foods recently eaten. This negative preference induction lasts 6–9 h after a change of foods (Thacker, 1996; 1998) and presumably facilitates avoidance of particular nutritional deficiencies that might be incurred by reliance on a single food type or, alternatively, the accumulation of toxins.

### Thermoregulation

Many coenobitid species occupy tropical beach habitats where high daytime insolation and temperatures enforce nocturnal activity patterns. Where rainfall is low or vegetation cover poor, inland distribution is generally restricted (e.g. *Coenobita scaevola* on Red Sea coasts (Achituv and Ziskind, 1985). Behavioural means are used to avoid overheating. *Coenobita* seek cool, humid daytime refuges under beach debris, or in litter and under shrubs and tree roots at the top of beaches. *Coenobita scaevola* and *C. rugosus* bury themselves up to 20 cm in the sand to avoid direct insolation and as a result body

temperature seldom exceeds 35°C (Vannini, 1976; Achituv and Ziskind, 1985). The more inland species also seek daytime refuges; *C. brevimanus* clusters in groups under logs in rain-forest on Christmas Island and in piles of coconut debris (Gross, 1964), while *B. latro* favours rock crevices, hollow logs and trees (Fletcher et al., 1990b; Greenaway, 2001). Activity is largely nocturnal but often begins before sunset as insolation drops. In cold weather *Coenobita* become inactive and remain buried in the sand or under debris (George and Jones, 1984).

Although behavioural thermoregulation is predominant in the Red Sea species, *C. scaevola*, all shell water has generally been lost by the time crabs emerge from burrows at the end of the day and their first action is to refill the shell with sea water (Achituv and Ziskind, 1985). The evaporation of this water will facilitate heat loss.

### Role of the shell in terrestrial life

The terrestrial hermit crabs live in and carry around a protective molluscan shell, a habit that predated terrestrial life. Shell-carrying provides certain advantages in the terrestrial life of these crabs as it reduces evaporative water loss, provides a reservoir of salt and water that increases survival time under desiccating conditions, allows for foraging further from water sources and removes the immediate need to develop new methods of ionic regulation. Additionally, it assists in thermoregulation and offers protection against predators (Herreid, 1969b; de Wilde, 1973; McMahan and Burggren, 1979; Achituv and Ziskind, 1985).

Dependence on a shell imposes a new set of constraints as well as offering some advantages. Potentially, population size and structure, and particularly penetration inland, may be limited by the availability of suitable shells of marine gastropods. Whilst shell availability may not be limiting in some situations (e.g. Quirimba Island (Barnes, 1999) it is evident from crab behaviour that shells are a limiting resource generally. Thus *C. brevimanus* may attack and kill the muricacean gastropod *Acanthina* in order to obtain the shell (McLean 1974), *C. clypeatus* are reported to collect and stockpile empty mollusc shells for later use (Gilchrist, 1995), and shell exchange amongst conspecifics is common (Hazlett, 1981). Groups of crabs congregate to exchange shells, and the availability of a large vacant shell triggers a cascade of shell exchange with progressively smaller animals taking part until the vacated shell is too small for the remaining participants. Similar behaviour occurs following the death of an individual; *Coenobita* are attracted by the odour of dead conspecifics and aggregate around them. Shell exchange is believed to be an evolutionarily conserved behaviour inherited from marine ancestors (Small and Thacker, 1994). If suitable shells of terrestrial origin are available inland they are utilised; *Coenobita* on Vanuatu and Guam use shells of the introduced land snail *Achatina fulica* (Bowdich, 1822) (Fletcher et al., 1991a; A.W. Harvey, pers. comm.). Occasionally other structures such as small coconut shells or bamboo may be used in place of mollusc shells, but use of structures other than the shells of marine gastropods is rare.

Heavy shells result in high energy expenditure for loco-

motion and in reduced speed and mobility but offer greater protection from predation. Small shells are lighter but may restrict growth and lead to smaller clutch sizes for females. *Coenobita compressus* seems to prefer shells with a high internal volume/weight ratio, which optimises these conflicting requirements (Osorno et al., 1998).

The restrictions imposed by shell dependence probably determine population size, size distribution and inland dispersal. Whilst the mollusc shell is an effective behavioural solution to many of the physiological problems that animals must face on land, it decreases the selective pressures for physiological solutions to these problems and reinforces dependence on shells. *Birgus latro* is the only coenobitid crab that no longer relies on mollusc shells (once past the juvenile stage). Independence from shells removes restrictions on body size and significantly, *B. latro* is the largest of the coenobitids (to 3 kg), and its physiological adaptations to terrestrial life parallel those of brachyuran crabs. These adaptations have not obviously resulted in more effective or widespread penetration of terrestrial habitats than in other coenobitids; *B. latro* is more or less restricted to maritime and island forest habitats, while *C. clypeatus* penetrates both drier habitats and further inland.

### Locomotion and movements

Although coenobitids appear cumbersome and generally carry heavy mollusc shells, they have strong locomotor ability (Herreid and Full, 1988) and are often excellent climbers ascending shrubs, saplings and trees (Barnes, 1997b; von Hagen, 1977). The shelled forms climb with the chelae and the pointed dactyls of the pereopods that hook around small branches or grip the surface. *Birgus latro* has long needle-like terminations of the dactyls of the walking legs and uses these to grip bark on large tree trunks or irregularities in rock surfaces. They can sling themselves upside down from small branches and grip vertical rock faces and overhangs.

The heavily calcified walking legs easily support the large body of *B. latro* which is carried clear of the ground during locomotion although the crab squats on the curled abdomen at rest. *Coenobita* use the chelae and the next two pairs of pereopods in locomotion. An alternating tripod gait is normal, with forward thrust provided largely by the second pereopods (R2, L2) while the first pereopods (chelae) are used mainly in support. The abdomen and mollusc shell are usually carried clear of the ground during locomotion although large shells may be dragged. At rest the shell lies on the ground (Herreid and Full, 1986a).

Hermit crabs are capable of sustained locomotion at slow walking speeds, and journeys up to 500 m in a night have been recorded during breeding migrations (de Wilde, 1973). The foraging range for beach living *Coenobita*, where food and water are co-located, is relatively small; they generally move within a 30 m radius and may have particular home sites and home ranges (Herreid and Full 1986a; Brodie 1998). Where food and water sources are separated, animals may migrate between them nightly (e.g. *C. rugosus*), but longer forays inland occur when the animals are freed from a fixed water source by wet conditions (Vannini, 1976). *Birgus latro* are not fixed in their

foraging pattern and many seem to have a number of home sites that they move between. At other times they appear to be nomadic, and radio-tagged animals may move as much 500 m through rain forest in 24 h (Fletcher et al., 1990b; Greenaway, 2001) to locate fruiting trees.

### Sensory adaptations

Terrestrial animals rely chiefly on vision, olfaction and sound detection to provide information about the environment, and the relevant sensory organs of emergent species must be able to function in air rather than water. Land crabs have developed aerial visual and olfactory systems but appear to show less reliance on sound. Despite functional changes in sensory systems the gross anatomy of the brain remains similar in aquatic and terrestrial species of anomurans (Sandeman et al., 1993).

*Coenobita rugosus* has ridges on the left chela and second left pereopod that resemble a stridulatory apparatus (Vannini, 1976), and these have also been observed in several other species (A.W. Harvey, pers. comm.). The species is reported to produce chirping sounds (Borradaile, 1903). *Coenobita purpureus* (Stimpson, 1838) make sounds (Imafuku and Ikeda, 1990), as does *C. violascens* (Heller, 1852) when captured (Nakasone, 1988a). *Birgus latro* has been reported to make a continuous ticking sound (Grubb, 1971), but there are no other records of sound production by the species, and Grubb (1971) may have detected scaphognathite activity which can be audible. As some species of *Coenobita* emit sounds it is likely that they also have sound receptors but, although there are anecdotal reports of sensitivity to sound (Borradaile, 1903), visual and vibration sensing cannot be ruled out. Vannini (1976) has suggested that orientation in transdunal migrations of *C. rugosus* may be to either the noise, or vibrations, generated by breaking waves.

Coenobitids have apposition eyes similar to those of other diurnal arthropods (Spears, 1983). On behavioural evidence vision is evidently an important sense, but to date there are no physiological studies on vision in the group.

Olfaction is highly developed and centred on the first antennae. These are in constant palpatory movement when the crabs are active, and the movements maximise the volume of air sampled and perhaps provide directional information on sources of odours. The first antennae of coenobitids differ from those of aquatic decapods as the basal joints are quite long and enable the two sensitive flagella to touch and sample the ground as well as a large volume of air above and around the crab. The sensory units (aesthetascs) of *C. compressus* are short and blunt and more similar to those of terrestrial insects than to those of aquatic decapods, including aquatic hermit crabs, and this may be a familial trait. These differences are believed to be concerned with adaptation for detection of volatile chemicals in air and perhaps with restriction of antennular water loss (Ghiradella et al. 1968a; 1968b). The species also appears to lack aesthetascs on the dactyls although these are present in aquatic decapods.

Both *B. latro* and *Coenobita* detect food from a distance and aggregate around significant food sources. *Birgus latro* seems



particularly effective at detecting fruit and aggregates around opened coconuts, pith of sago palms and fruiting trees. It also quickly detects road kills and other carrion. *Coenobita cavipes* is attracted by a variety of volatile food odours but can detect nonvolatile foods only by contact (Rittschof and Sutherland, 1986). *Coenobita* can also detect water vapour; and species that penetrate inland, such as *C. rugosus* and *C. brevimanus*, can distinguish between the odour of fresh water and sea water, although this sense is poorly developed in beach dwelling species such as *C. cavipes* and *C. perlatus* (Vannini and Ferretti, 1997). Where individuals are numerous, location of food may be facilitated socially with animals locating food sources by observing behaviour of their neighbours rather than by detection of food *per se* (Kurta, 1982).

The coenobitids are characterised by retention of the long filiform second antennae seen in aquatic anomurans. These are highly mobile and seem to be used to investigate and locate solid objects in the environment in a manner similar to that of their aquatic relatives and astacurans. There have been no specific studies on their role in the Coenobitidae.

The coenobitids possess considerable ability to orient, navigate and home (Vannini and Cannicci, 1995). *Coenobita clypeatus* orient to a few preferred breeding sites from wide areas of the hinterland (de Wild, 1973). Populations of *C. rugosus* may occupy a distinct home area in which they remain for periods of a year or more whilst not necessarily occupying any specific home site (Vannini, 1976). Likewise the aquatic diogenid, *Clibanarius laevimanus* (Randall, 1840), forms clusters amongst mangroves between foraging periods, and stays within a home area even though it may change clusters within the area (Gherardi and Vannini, 1992). *Coenobita rugosus* orient to visual cues if landmarks are visible and in uniform environments utilises celestial cues. Orientation to locate the home beach using celestial cues involves learning, since a particular home beach on an island or atoll may face in any direction (Vannini and Chelazzi, 1981). *Coenobita* is also sensitive to directional air movements, and in the absence of other cues they may use wind currents as a source of directional information for navigation (Vannini, 1975a; Vannini and Chelazzi, 1981; Vannini and Ferretti, 1997).

### Moulting and growth

*Birgus latro* is long-lived and grows slowly with maximum size reached only after 40–60 y (Fletcher et al., 1990a; Fletcher et al., 1991b). *Coenobita* too may be long-lived, and lifespan in the larger species exceeds 10 years (Chace, 1972). Longevity and slow growth in litter-eating terrestrial brachyurans have been linked with a low N intake (Linton and Greenaway, 2000) but other explanations for the longevity of coenobitids may be necessary as many coenobitids have an appreciable intake of animal material in the diet.

In preparation for the moult, *B. latro* digs a burrow up to 1 m long and seals itself inside for 3–16 weeks. This period increases with body size. Adults moult annually, usually in the winter months (Held, 1965; Fletcher et al., 1990a; 1991b). Typically premoult animals enter their burrows with their abdomens markedly swollen by food reserves and increased

blood volume. After moulting the animal eats its exuviae, which contribute organic materials and calcium salts needed for the new skeleton. Certain brachyuran land crabs reabsorb calcium from the old skeleton in premoult, store it in the body and reuse it to calcify the new skeleton (Greenaway, 1985; 1993), but there are no data regarding premoult storage of calcium in *B. latro*. As the species moult in burrows and eat their exuviae, significant internal storage mechanisms may not have been developed. The growth increment at the moult in large animals is hard to assess as linear measurements increase only slightly, and the changes in body water, food reserves and abdominal size make mass changes an unreliable indicator of increased size. Reported increases in linear dimensions following moulting are 1–16% with large crabs showing the smallest increments (Held, 1965; Fletcher et al., 1990a; 1991b).

Very little information is available in regard to moulting of *Coenobita*. *Coenobita clypeatus* is reported to hide during the process most of which occurs in the shell (de Wilde, 1973). There is a noticeable reduction in activity for several days prior to the moult and after ecdysis the exuviae are positioned just in front of the mouth of the shell (A.W. Harvey, pers. comm.). During calcification the new soft skeleton of the chelae and other walking legs is moulded to fit the shape of the shell. If the animal increases markedly in size it may no longer fit neatly within the old shell and a rapid trade up in shell size may be necessary to avoid water loss and predators. There is no information available on calcium balance or storage through the moult or on growth increments of *Coenobita*. *Coenobita clypeatus* grows up to 500 g if large-enough shells are available (de Wilde, 1973).

Autotomy of limbs is uncommon amongst the land crabs, and coenobitids are no exception. Autotomy generally only occurs if limbs are severely damaged or infected, and the incidence of missing chelae in *B. latro* is very low (Grubb, 1971). This may reflect the greater importance of the limbs in locomotion and feeding in terrestrial crabs, the major investment in replacing the lost protein from a diet low in nitrogen and the relatively long intervals between moults. It is significant that amongst the terrestrial brachyurans only the carnivorous grapsids readily shed limbs. Given their high N intake and rapid growth rates this is an affordable tactic.

### Reproduction

No terrestrial anomurans complete the reproductive process on land, and all species retain marine larval stages although, as in *Coenobita variabilis* (McCulloch, 1909), these may be abbreviated (Harvey, 1992). Substantial reproductive adaptations to terrestrial life have nevertheless been achieved within the group and location of sexual partners, courtship, mating, and the extrusion and early development of eggs all occur on land. The animals also possess the necessary behaviours to time and orient their breeding migrations to the sea and select particular conditions of lunar and tidal cycles for spawning. Many of these behaviours may differ within a species as the direction of the sea, time of the wet season, and direction and strength of ocean currents may vary within the geographical range.

The spawning period of *B. latro* varies over its distribution

range and probably reflects the seasonal occurrence of favourable weather conditions and ocean currents. Spawning on Christmas Island coincides with the onset and main peak of the wet season, which provide optimal conditions for migration to the coast for spawning. The downward migration is an individual affair but the return journey may involve coordinated groups (Schiller et al., 1991). As mating precedes migration it is likely that males do not migrate to the coast. Mating lasts only a few minutes during which the male lays the female on her back and deposits a mass of spermatophores around the oviducal apertures at the base of the third pereopods (Helfman, 1977b; Schiller et al., 1991). The spermatophores are robust, gelatinous structures about 650  $\mu\text{m}$  high glued to the exoskeleton by the pedestal. A short stalk rises from the pedestal and bears a heart-shaped ampulla, which contains the spermatozoa (Tudge, 1991). Eggs (~ 100,000) are laid after mating and are attached to the pleopods and carried throughout the developmental period (27–29 days) before release into the sea. The crabs release eggs at night between the first and last quarter of the moon. They do not generally spawn from beaches (Schiller et al., 1991) but instead descend cliffs or walk over intertidal platforms until they encounter wet rock or pools. On contact with seawater, the females orient the abdomen towards the water and advance cautiously until wave wash stimulates hatching. Only 1–2 waves are needed for complete hatching of the zoeae. *Birgus latro* usually has four planktonic zoeal stages that are believed to be dispersed primarily by surface currents. The postlarval, megalopal stage is epibenthic, and on reaching the shallow water larvae search for and occupy mollusc shells before emergence onto land. They burrow in sand and metamorphose to the first crab stage that emerges after 3–4 weeks (Reese and Kinzie, 1968). Juveniles may live in mollusc shells until they reach a carapace length of ~15mm and thereafter abandon the shell.

*Coenobita clypeatus* reach sexual maturity in their second year at weights of 1–2 g, although they can reach 500 g in weight. The early onset of sexual maturity may allow self-sustaining populations in areas where large shells are rare or unavailable. Populations of *Coenobita* that live inland migrate to coastal breeding sites where it is believed that mating takes place (Yamaguchi, 1938; de Wilde, 1973). Males are thought to detect females by means of chemosensory and visual clues, and both sexes partially emerge from their shells for mating during which spermatophores, similar to those of *B. latro*, are transferred to the female (Reese, 1987). The smallest females produce around  $10^3$  eggs and the largest adults perhaps  $5 \times 10^5$  (de Wilde, 1973). Eggs are released into the sea about 30 d after laying and *C. clypeatus* avoids immersion during this process (de Wilde, 1973). The larvae hatch in the water as zoeae and take 3–7 weeks to pass through up to five zoeal stages before megalopae appear (Provenzano, 1962; Nakasone 1988b). By contrast *C. variabilis* have only two non-feeding zoeae and reach the megalopal stage in 6–7 days (Harvey, 1992). Megalopae feed in all species and soon begin to search for mollusc shells. With or without shells the megalopae emerge from the water and bury themselves on the beach where they metamorphose and resurface as juvenile crabs (Harvey, 1992; Brodie, 1999). Megalopae will not metamorphose in water, and

there are conflicting reports on survival of megalopae that metamorphose without shells (Harvey, 1992).

Pelagic larvae are important to enable wide distribution of coenobitids. The planktonic stages generally last 2–4 weeks and whether they encounter a terrestrial habitat depends on the direction and strength of ocean currents and prevailing weather conditions. Thus megalopae may return to the home or to neighbouring islands, be dispersed down current to new islands or be transported unpredictably sometimes over very long distances. The possibility of not encountering a suitable island is obviously high; recruitment of *B. latro* appears to be rare, although whether this results from the reclusive fossorial nature of the megalopae, from irregular recruitment, or both, is unclear (Reese, 1987; Schiller et al., 1991). The longevity of *B. latro* means that regular recruitment is unnecessary for population survival, and it may even be an adaptation to erratic recruitment. The distributions of many coenobitid species are very wide, e.g. *B. latro* is distributed throughout the Indian and Pacific oceans. This distribution is thought to be the result of a population explosion in the Pleistocene. Currently the Indian Ocean and Pacific populations appear to be separate, whilst continued genetic exchange persists between Pacific island populations (Lavery et al., 1996a, b).

The life styles of *Coenobita* and *B. latro* diverge after 1–2 years (Harms, 1932; Reese, 1987), when the juvenile *B. latro* abandon shell living and undergo morphological changes to adopt the adult body form.

## Summary

The Porcellanidae, Diogenidae and Coenobitidae have all developed amphibious or terrestrial life styles but only the latter show significant independence from water. Coenobitids conduct essentially all functions on land although they must have access to the sea to release larvae into the water. Terrestrial adaptations developed by coenobitids generally parallel those of terrestrial brachyurans, but as their morphological and behavioural starting points for the colonisation of land differed, some significant differences are apparent between the terrestrial representative of the two groups. The family Coenobitidae has a small number of species but is very successful (in terms of the number of individuals) in tropical maritime and island environments. A number of species have powerful osmoregulatory ability and maintain salt balance with only freshwater to drink but the mechanisms involved require further study. *Birgus latro* has developed purine excretion but the nitrogenous excretory products and their mechanism of elimination in *Coenobita* have not been studied. Aerial gas exchange is enabled by well-developed branchiostegal lungs in *B. latro*, whilst *Coenobita*, constrained by the shells in which they live, have developed a novel abdominal gas exchange organ in addition to gills and lungs. The relative contributions of each to overall gas exchange are unknown. The coenobitids, unlike the brachyuran land crabs, have long filiform second antennae used as touch and mechanoreceptors, and share good visual capability and a well developed olfactory sense in air. Whilst many terrestrial and semi-terrestrial brachyurans have evolved direct development the coenobitids all retain marine

larval stages. This restricts inland penetration, as the animals must be able to migrate back to the coast to shed their larvae into seawater, and is probably responsible for their limited distribution. For *Coenobita*, the situation is aggravated by the relative paucity of large snail shells in inland situations, and the relatively thin walls of these shells that offer little protection against large predators.

From available evidence, it is clear that the terrestrial adaptations made by the coenobitids have allowed them to successfully occupy a number of terrestrial niches ranging from the supra littoral zone to several kilometres inland in habitats that range between semi-desert and rainforest. Further penetration may not be possible without reproductive adaptations to eliminate aquatic larval stages and, for *Coenobita*, probably independence from the necessity to carry a mollusc shell.

### Acknowledgements

I am grateful to Alan Harvey for supplying helpful information on the biology of *Coenobita*.

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