

THE LOCOMOTOR TOOLBOX OF THE SPANNER CRAB, *RANINA RANINA*  
(BRACHYURA, RANINIDAE)

BY

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ABSTRACT

Digging is not a well-understood form of locomotion, and it poses different mechanical problems than other forms of locomotion (e.g., walking). The spanner crab (*Ranina ranina*) digs into sand, primarily using its pereiopods. Above sand, pereiopod movement is variable, with four different movement patterns revealed by tip trajectories. The most common pattern of pereiopod movement above sand is the pattern apparently used for digging: pereiopods 2 and 3 shovel sand forward from underneath the animal, while pereiopod 4 shovels in the opposite direction, pushing the posterior end down into the sand. When above sand, each pair of pereiopods moves in bilateral alternation, but *R. ranina* switches gait to bilateral synchrony as it descends into sand. The abdomen is also rhythmically active during digging, despite being small and relatively stiff. *Ranina ranina* can also locomote forward on top of the substrate by punting with pereiopods 2 and 3. Although many aspects of digging in *R. ranina* are similar to those of digging by other crustaceans, particularly anomuran sand crabs, *R. ranina* has retained a wider behavioural repertoire.

RÉSUMÉ

S'enfoncer dans le substrat n'est pas une forme de locomotion bien comprise, et pose des problèmes mécaniques différents des autres modes de locomotion (comme par exemple la marche). Le crabe *Ranina ranina* s'enfonce dans le sable, utilisant en premier ses péréiopodes. Au-dessus du sable, le mouvement des péréiopodes est variable, avec quatre modèles de mouvement différents, révélés par les trajectoires des extrémités. Le modèle le plus commun du mouvement du péréiopode au-dessus du sable est celui apparemment utilisé pour s'enfoncer : les péréiopodes 2 et 3 rejettent le sable de dessous l'animal vers l'extérieur, tandis que le péréiopode 4 opère en sens inverse, poussant la partie postérieure de l'animal dans le sable. Quand l'animal est sur le sable, chaque paire de péréiopodes se déplace latéralement dans un sens et dans l'autre alternativement, mais *R. ranina* change de mouvement, suivant une synchronie bilatérale quand il descend dans le sable. L'abdomen est aussi actif en rythme, quand l'animal s'enfonce, en dépit de sa petite taille et de sa relative raideur. *Ranina ranina* peut aussi se déplacer vers la surface du substrat en ramant avec ses péréiopodes

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2 et 3. Bien que de nombreux aspects de l'enfoncement chez *R. ranina* soient analogues à ceux d'autres crustacés, en particulier des crabes de sables anomoures, *R. ranina* a développé un répertoire comportemental plus étendu.

## INTRODUCTION

Sand is common in aquatic environments and many aquatic organisms, such as decapod crustaceans, have found ways to use sand as a living place. Some decapod crustaceans exploit sandy habitats by building burrows (Correia & Ferreira, 1995; Nickell & Atkinson, 1995; Babcock et al., 1998; Hasiotis et al., 1998; Kowalewski et al., 1998; Bird & Poore, 1999; Felder, 2001). Other decapods adopt a different approach to living in sand: they dig through it instead of excavating a lasting structure. Examples of digging decapods include sand crabs (Trueman, 1970; Faulkes & Paul, 1997a, b, 1998), slipper lobsters (Jones, 1988; Faulkes, 2004, in press), and true crabs (Skinner & Hill, 1987). Nonetheless, digging is seldomly acknowledged as an important locomotor behaviour for many crustaceans, despite substantial research on crustacean locomotion, in particular walking (Clarac, 2002). Anomuran sand crabs and mole crabs (superfamily Hippoidea) currently provide some of best studied examples of digging (Faulkes & Paul, 1997a, b, 1998). All known sand crab and mole crab species in all three families (Albuneidae and Blepharipodidae, referred to collectively here as non-hippid sand crabs, along with the Hippidae, referred to here as hippid mole crabs; Boyko, 2002) are so highly specialized for digging that they cannot walk. When above sand, they swim by rowing the pereopods and tailflipping in non-hippids, or by uropod beating in hippid mole crabs. Although the non-hippid sand crab and hippid mole crab families differ in digging behaviour (e.g., different patterns of coordination between the pereopods and abdomen; Faulkes & Paul, 1997a), some features are common to both. Previously, I hypothesized that digging in the sand crab and mole crab families was homologous. An alternative explanation is that digging in the sand crab and mole crab families is similar because of convergence, i.e., there are a limited number of ways to dig into sand rapidly that are biomechanically efficient (Boyko, 2002). It is difficult to predict how animals should dig, because digging will be unlike other forms of locomotion due to the drastically different challenges that sand presents to organisms compared to air or water. Sand is heavy, and will create far greater loads on pereopods than air or water. The behaviour of granular materials, like sand, is more complex than that of air or water: sand can switch between solid-like and liquid-like properties, for example (Jaeger et al., 1996). To the best of my knowledge, the physics of wet sand have not been studied in detail. Thus, digging by non-anomuran species helps test hypotheses about the evolution

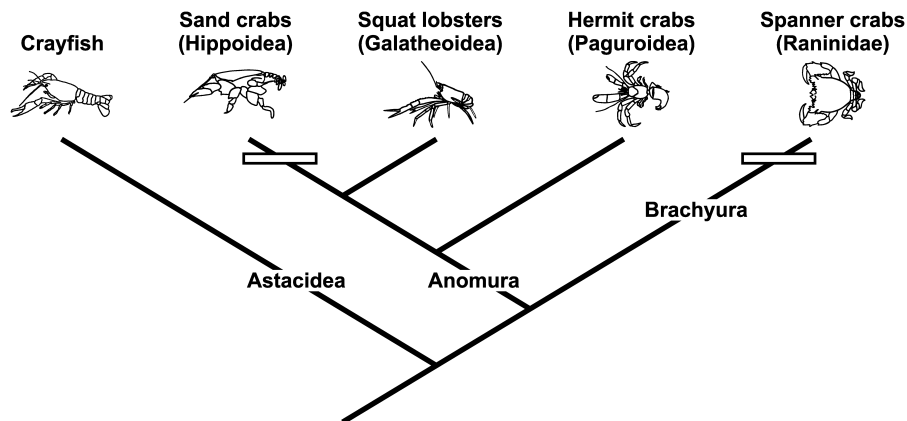


Fig. 1. Phylogeny of digging decapods (Scholtz & Richter, 1995; Schram, 2001; Ahyong & O'Meally, 2004). Although the infraorders Anomura and Brachyura are thought to be sister taxa, the placement of the sand crabs next to several anomuran taxa containing mostly walking species (e.g., squat lobsters and hermit crabs) indicates that similarities between Hippoidea and Raninidae are not homologous. White bars highlight digging taxa. Names of infraorders in branches of tree; names of relevant lower level taxa (superfamilies and families) above animals. Animals not to scale.

of digging behaviour (Boyko, 2002; Paul et al., 2002), and generate hypotheses about biomechanical principles that might explain digging.

*Ranina ranina* (Linnaeus, 1758) is a large digging crab species (commonly known as the “spanner crab” in Australia) that shares many morphological similarities with non-hippid sand crabs (Boyko, 2002; Paul et al., 2002). The pereopods of *R. ranina* and of non-hippid sand crabs are robust and broad, with flattened dactyls, while most walking decapods have slender, pointed pereopods. The abdomen in *R. ranina* is freely moving, albeit small and without uropods (Števcíć, 1973), and is more similar to the sand crabs' mobile tails than the inflexible, fused abdomens of most adult brachyuran crabs. The carapace of *R. ranina*, like that of sand crabs, is slightly longer than wide, whereas that of many brachyuran crabs is wider than long. Based on such likenesses, early taxonomic work suggested that raninid crabs were closely related to sand crabs, but these similarities were recast as convergent adaptations to digging (Števcíć, 1973). Given the relationship between these two taxa, and particularly that walking taxa, such as squat lobsters and hermit crabs, are the closest relatives of sand crabs and mole crabs (Scholtz & Richter, 1995; Schram, 2001; Ahyong & O'Meally, 2004), it is extraordinarily unlikely that digging behaviour in *R. ranina* and hippoid crabs is homologous (fig. 1). This study will examine *R. ranina* digging to assess the similarities with other digging species, and to suggest common mechanisms of digging.

This work has appeared in abstract (Faulkes, 2001).

## MATERIALS AND METHODS

Nine adult spanner crabs, *Ranina ranina*, ranging in carapace length from 109 to 128 mm, were purchased from local seafood suppliers (Briarry's Seafood Connection, Queen Victoria Market, Melbourne). They were housed in a heated ( $\sim 22^{\circ}\text{C}$ ) aquarium in the seawater system at the Department of Zoology, University of Melbourne.

Range of joint movement was measured on an individual that had recently died by manually flexing and extending each joint of the pereopod.

Because digging cannot be seen through sand, digging movements and coordination were inferred in two ways: videotaping animals making putative digging-like movements in water, and recording electromyograms (EMGs) from individuals while being held in water and while actually digging in sand (Faulkes & Paul, 1997a, b, 1998). Behavioural observations and EMG recordings were carried out in a tank measuring about 0.5 m high  $\times$  0.75 m square. Animals were videotaped through a Hi8 video camera (Sony Hi8 Handycam, model CCD-TR705E), with an electronic shutter that limited the exposure of each field of video to 1/250 s, so images were sharp. The camera was linked to a Super-VHS video recorder (Panasonic NV-SD430). This video recorder was used for the initial analysis of the tape (PAL format, temporal resolution 20 ms). The videotape was later converted to a digital video disc (DVD; NTSC format) for further analyses. To record EMGs, I inserted fine silver wires (127  $\mu\text{m}$  diameter), Teflon-coated except for the tip, into small holes in the exoskeleton, made using a needle. The wires were cemented into position using cyanoacrylate glue and wax, and ran to a more rigid "saddle" made of heavier wax glued to the carapace. The EMG signals were amplified, filtered (Seewiesen filters), digitized (TL-2 interface analog-digital board, Axon Instruments, Inc.; 1-1.5 kHz sampling rate), and recorded on a computer using Axotape 1.2 (Axon Instruments, Inc.). Off-line EMGs measurements were made with Axotape 2.0.

## RESULTS

## Pereopod morphology

Decapod pereopods are numbered from anterior to posterior (i.e., the chelae are the first pair of pereopods, or pereopods 1). In *Ranina ranina*, pereopod 5 is slightly anterior and dorsal to the fourth pair. In addition to its unusual dorsal location, pereopod 5 differs from pereopods 2-4 in other ways. First, pereopod 5 is less flexible than the more anterior pereopods, particularly at the proximal joints (table I). Second, the proximal joints are oriented such that elevator muscles cause promotion in pereopod 5 instead of elevation.

## Digging

All the pereiopods are active during digging in *Ranina ranina*, but pereiopods 2, 3, and 4 are the prime movers. The first pereiopods (the large chelipeds) move rhythmically, but make minor contributions to digging. They are depressed relative to the body at the start of a digging sequence, which forces the posterior end of the animal down into the sand. The claws also force sand away from the mouthparts, so that once the animal is submerged in sand, there is an unobstructed path for water flow for respiration. The fifth pair of pereiopods probably contributes less to digging than pereiopods 2, 3, and 4, as suggested by the limited range of joint movement (table I).

When viewed from the side, the tips of pereiopods 2, 3, and 4 are all capable of circling either clockwise or counter-clockwise (fig. 2), although they do not do so with equal probability. From the left view, pereiopod 2 tends to describe a clockwise trajectory, while pereiopod 4 tends to move counter clockwise. Pereiopod 3 always circled in the same direction as one of its neighbours, i.e., pereiopod 3 did not circle clockwise while both pereiopod 2 and 4 were circling counter clockwise. The modal pattern (figs. 2A, 3) accounted for 40% of filmed locomotor sequences, and is the same tip trajectory pattern seen in sand crabs (Faulkes & Paul, 1997a). In this modal pattern (fig. 3), the forward stroke of pereiopod 2 typically leads pereiopod 3, and the dactyls form oppositions (Eshkol, 1980) when pereiopod 3 stops moving relative to the body. Oppositions between pereiopods are maintained while pereiopods 2 and 3 are both moving backwards, and released when pereiopod 2 begins moving forward again. This reduces drag caused by moving the pereiopods backwards through the sand. A similar pattern of opposition occurs in sand crabs (Faulkes & Paul, 1997b).

When above sand, the left and right pereiopods move in bilateral alternation, which is the modal pattern of pereiopod coordination in decapod crustaceans (Clarac, 1984; Cruse, 1990). During digging, the pereiopods change coordination

TABLE I  
Range of joint movement in pereiopods of *Ranina ranina* (Linnaeus)

Joint	Pereiopod				
	1 (Cheliped)	2	3	4	5
Thorax / Coxa	90°	100°	90°	70°	30°
Coxa / Basi-ischium	120°	90°	100°	90°	40°
Basi-ischium / Merus	30°	20°	20°	Minimal	Minimal
Merus / Carpus	100°	90°	90°	80°	70°
Carpus / Propodus	110°	90°	90°	80°	80°
Propodus / Dactylus	70°	90°	90°	110°	110°

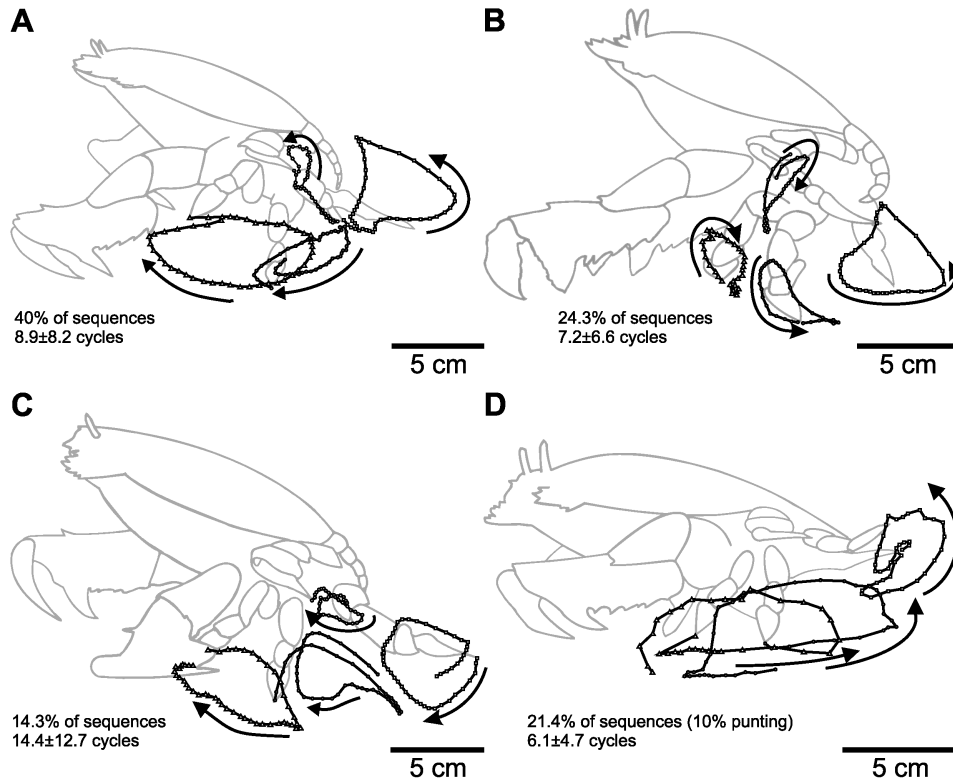


Fig. 2. Tip trajectories of *Ranina ranina* (Linnaeus, 1758) pereiopods traced from: A-C, individuals held in water; and, D, individual punting forward along bottom of aquarium. Note that each pereiopod is capable of circling clockwise or counter-clockwise in this view. Inset text: percent of locomotor behaviour (from 70 observed locomotor sequences) in which trajectories of pereiopods 2, 3, and 4 are the same as shown (i.e., in C, pereiopods 2, 3, and 4 circle clockwise), and the average number of cycles making up the observed locomotor sequences (mean  $\pm$  standard deviation). Interval between dots = 20 ms.

from bilateral alternation to bilateral synchrony (fig. 4). This alternation can be directly observed in the claws, which are often visible when this gait switch occurs. Electromyograms show that the more posterior pereiopods also switch from bilateral alternation to synchrony (fig. 4). As can be seen in figs. 4 and 5, the EMGs are complex, often changing from single bursts per cycle when an individual was above sand to two bursts per cycle as an individual dug into sand. The interpretation of two burst per cycle, rather than two separate cycles, was supported by watching the EMGs while an individual was digging: the visible movements of the carapace, and sounds made by pereiopods contacting the glass bottom of the aquarium, indicated that two distinct muscle bursts occurred for one cycle of the pereiopods.

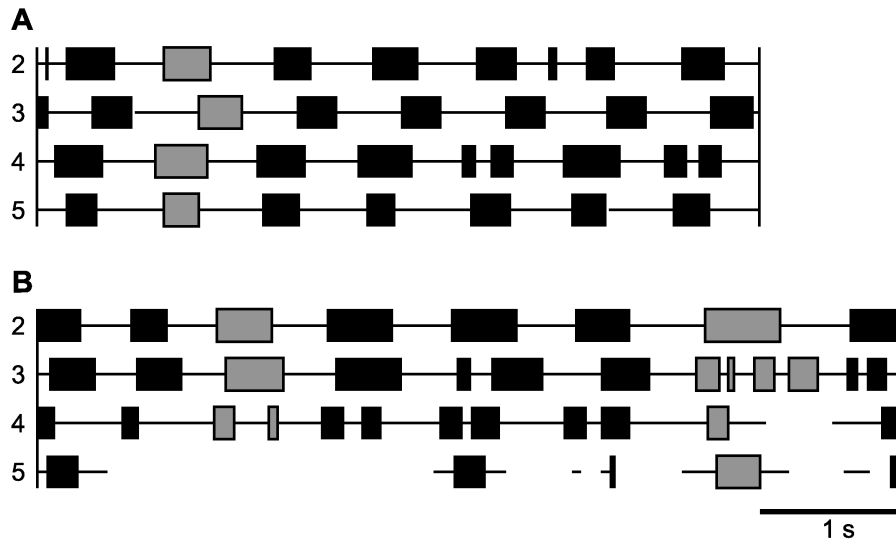


Fig. 3. Two representative sequences of forward and backward movements of individual pereopods from *Ranina ranina* (Linnaeus, 1758) held in water. Single cycles highlighted to show modal pattern (first highlighted cycle in each) and variability (second highlighted cycle in B). The frequency of pereopod 4 is not higher than that of the other pereopods: a single cycle of pereopod 4 can have more than one forward movement because the path of pereopod 4 is often not elliptical (see, e.g., fig. 2A).

The abdomen never moves rhythmically during locomotion above sand. EMGs reveal that it does do so during digging, however, cycling at about the same frequency as the pereopods (fig. 5).

#### Punting and swimming

While above sand, *Ranina ranina* can punt (Martinez et al., 1998) with pereopods 2 and 3 to locomote forward on top of a substrate (fig. 6). *R. ranina* moves forward using thrust generated by pereopods 2 and 3 pushing off from the substrate, with periods of gliding between. Often none of the pereopods was in contact with the substrate at any given moment, and the duty factor was correspondingly low; for example, in fig. 6B, the pereopods contact the substrate 35.3% to 47.0% of the time. Pereopods 4 and 5 are positioned such that they do not contact the substrate during walking, but they are often rhythmically active during punting. The rapid, large amplitude movements of pereopod 4 suggest that it may generate hydrodynamic thrust or lift. It is not clear how the movements of pereopod 5 influence punting.

Each pair of pereopods moves in bilateral alternation during punting. This alternation is seldom exact; because these animals were freely moving and not constrained to moving in a straight line, they were often turning by stepping

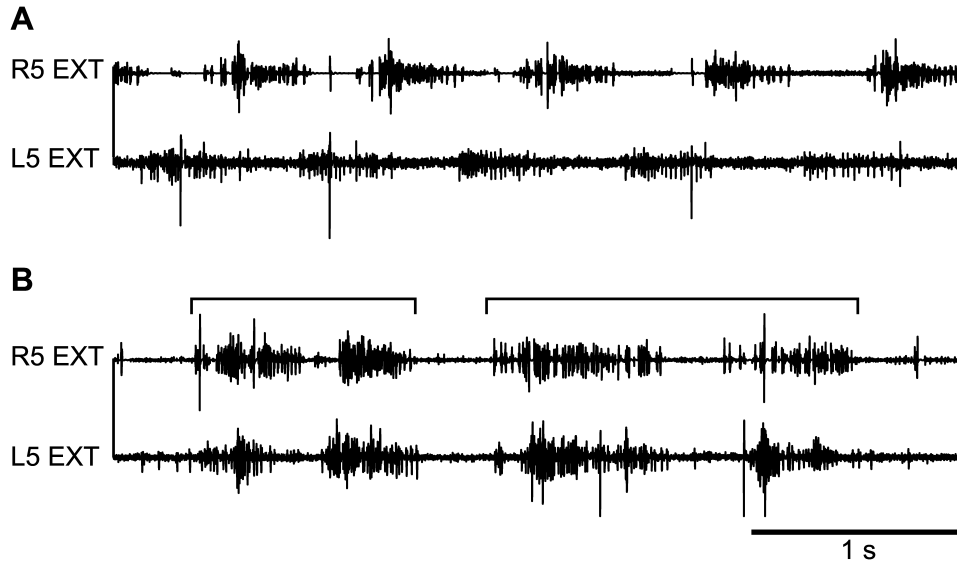


Fig. 4. EMGs from homologous extensor (EXT) muscles in contralateral fifth pair of pereopods in *Ranina ranina* (Linnaeus, 1758): A, individual rowing in water above sand; B, individual digging in sand. The EMGs burst twice per cycle of movement; one cycle indicated by braces above EMGs. Same individual and amplification in A and B.

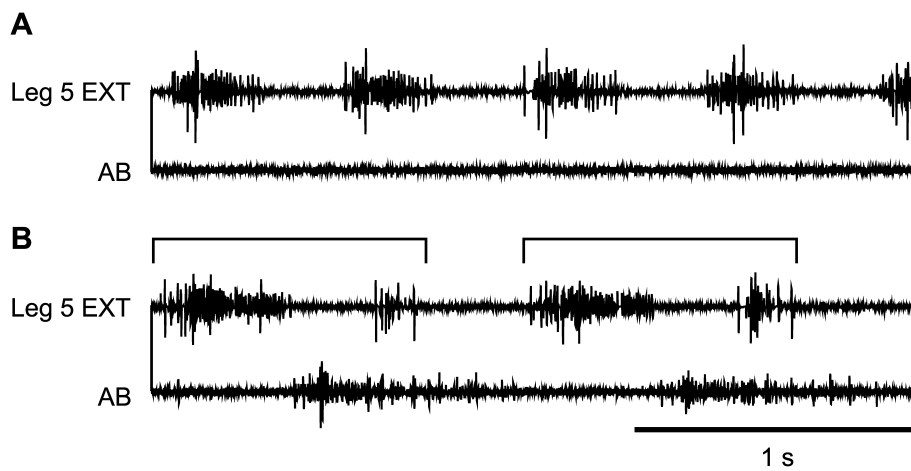


Fig. 5. EMGs from pereopod 5 extensor (EXT) and abdomen (AB) of *Ranina ranina* (Linnaeus, 1758) while: A, above sand; and, B, while digging. The pereopod EMGs burst twice per cycle; one cycle indicated by braces above EMGs. Same individual and amplification for both A and B.

preferentially on one side. Such high variability is characteristic of punting, however (Martinez et al., 1998).



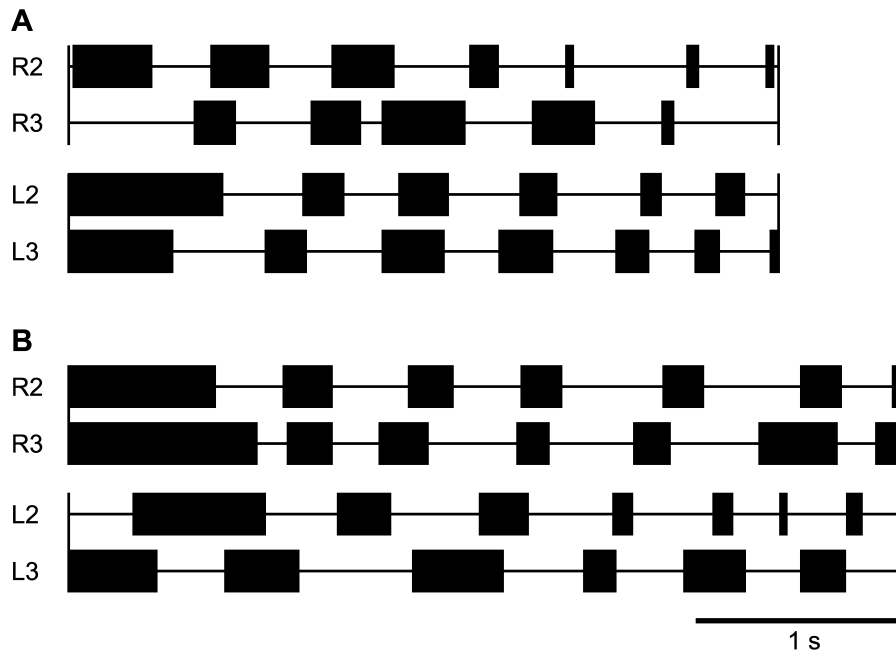


Fig. 6. Two representative walking sequences in *Ranina ranina* (Linnaeus, 1758), each from the onset of walking. Bars = pereiopods touching substrate; lines = pereiopods above substrate.

I recorded *R. ranina* swimming forward using its pereiopods once during this study (data not shown). Fast punting led directly into a short bout of swimming, and there was not a sharp demarcation between the two behaviour patterns. While swimming, the pereiopods cycled at over 3 Hz. The singular nature of this event precludes detailed analysis, but that *R. ranina* can swim has not been previously reported, to the best of my knowledge.

#### DISCUSSION

Digging by *Ranina ranina* is similar to digging by sand crabs and mole crabs, particularly non-hippid sand crabs, in several ways (Faulkes & Paul, 1997a, b, 1998). Thus, it appears that all of these features are related to biomechanical efficiency. First, pereiopods 2 and 3 shovel sand from underneath the animal in the same direction (e.g., clockwise when viewed from the side), while pereiopod 4 pushes the animal's posterior down into the sand by circling in the opposite direction (e.g., counter-clockwise). This combination of movements ensures an animal descends directly down into sand. Second, pereiopods 2 and 3 form an opposition (Eshkol, 1980) at the end of forward movement of pereiopod 3, and break this opposition when pereiopod 2 begins moving forward. The backward

movement of pereopods 2 and 3 while they are closely opposed seems to reduce drag during the return stroke. Third, the abdomen is used to dig, even though the abdomen is small and relatively immobile in *R. ranina*, and *R. ranina* does not move its abdomen rhythmically above sand. Moving the tail even slightly seems to aid digging by liquefying the sand. Fourth, there is a gait switch as animals submerge into sand. The gait switch in *R. ranina* is the same as in non-hippid sand crabs, from bilateral alternation to bilateral synchrony (the hippid gait switch is more complex; Faulkes & Paul, 1997a). The gait switch appears to prevent a zig-zagging descent into sand (Faulkes & Paul, 1997b).

Based on phylogenetic relationships (fig. 1), the naïve prediction would be that non-hippid sand crab digging would be more similar to hippid mole crab digging than either are to *R. ranina*, but non-hippid digging is more similar to that of *R. ranina* than to that of the related hippids. Thus, the results of this study do not refute the hypothesis that the similarities in digging behaviour of raninids, non-hippids, and hippids are due to convergence. Although the standard working assumption is that similar features are homologous (Brooks & McLennan, 1991), it is absolutely critical to realize that any hypothesis of homology stands or falls based on our understanding of relationships between organisms as a whole (Lauder, 1986, 1991), rather than being determined by any single criterion. Therefore, the hypothesis that similarities in digging in the sand crab and mole crab families are due to homology rather than convergence is still viable. The similarities between raninids, non-hippid sand crabs, and hippid mole crabs invite further investigation into the neuromusculature and central pattern generators related to digging to determine whether the similarities between raninids and non-hippid sand crabs are superficial, or whether the similarities between non-hippid sand crabs and hippid mole crabs are deeper than they first appear.

The main difference between *R. ranina* and non-hippid sand crabs is versatility. *Ranina ranina* has a wide repertoire of locomotor behaviours using the pereopods, including digging, punting (Martinez et al., 1998), and forward swimming. Sand crabs have no equivalent to punting or forward swimming. When above sand, non-hippid sand crabs swim backwards in a way that strongly resembles digging (Faulkes & Paul, 1997a, b, 1998). *Ranina ranina* shows that the ability to dig rapidly through sand does not preclude punting (or walking, presumably). The presence of punting in *R. ranina* and its absence in sand crabs may be due to ecological differences rather than physiological ones. *R. ranina* are opportunistic feeders, and emerge from sand quickly to come to bait (Skinner & Hill, 1986), which suggests that punting is an important part of their foraging ecology. Although there have been suggestions that various non-hippid sand crabs are sediment feeders (Hill, 1979), filter feeders (Lafferty, 1993), or feed on hippids (MacGinitie, 1938; Lafferty, 1993), no data indicate that any non-hippid sand crab

is an active, opportunistic forager like *R. ranina* (cf. Boyko, 2002). Furthermore, *R. ranina* lives in deep water (Skinner & Hill, 1986; Hill & Wassenberg, 1999), whereas sand crabs live in the intertidal swash zone. Although there can be strong tidal currents where *R. ranina* lives (Skinner & Hill, 1986; Hill & Wassenberg, 1999), they do not create the repeated fast accelerations, decelerations, turbulence, flow reversals (Denny et al., 1985), and continual disturbance of sand (Martinez, 1996) seen in the swash zone. In such an unstable environment, punting or walking for any length of time may be effectively impossible, thus imposing a strong selection pressure against punting in sand crabs, but not in *R. ranina*.

As a first step in categorizing digging mechanisms in crustaceans and other aquatic organisms, the major mechanisms used by *R. ranina* might be described as “shovels” and “fans.” A shovel physically moves sand using a flat surface, and moves at moderate speed. The pereopods act as shovels in *R. ranina* and sand crabs (Faulkes & Paul, 1997b). A fan liquefies the sand to facilitate penetration of other limbs and or the body, and moves at higher speeds. The abdomen of *R. ranina* might be viewed as a fan, albeit a modest one compared to the rapid and agile abdomen and uropods of sand crabs (Faulkes & Paul, 1997a). This is no doubt an incomplete list, but provides a starting point for categorizing digging mechanisms in aquatic organisms.

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