DIGGING IN SAND CRABS (DECAPODA, ANOMURA, HIPPOIDEA): INTERLEG COORDINATION

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Summary

Sand crabs (Decapoda, Anomura, Hippoidea) are highly specialised for digging into sand using their thoracic legs. Using video-recording and electromyography, we examined the digging leg movements of three species of sand crabs belonging to two families: *Blepharipoda occidentalis* (Albuneidae), *Lepidopa californica* (Albuneidae) and *Emerita analoga* (Hippidae). The digging patterns of all three species are similar. The ipsilateral legs 2 and 3 are tightly coupled and shovel sand forward from underneath the animal, whereas the movements of leg 4 are more variable, apparently stirring up sand and providing the purchase for rearward descent into the sand. The digging patterns of *B. occidentalis* and *L. californica* resemble each other more than either resembles that of *E. analoga*. In the albuneids, leg 4 cycles at the same frequency as legs 2 and 3, and both albuneid species switch gait from bilateral alternation to synchrony midway through digging. In *E. analoga*, right and left legs 2 and 3 always alternate. Legs 4 can cycle at about twice the frequency of legs 2 and 3, and they tend to move in bilateral synchrony during high-frequency leg movements (e.g. at the start of digging); their bilateral coupling becomes variable during low-frequency movements. Sand crab digging may have originated as a modified form of walking, but this behavioural innovation subsequently diverged in the sand crab superfamily.

Key words: *Blepharipoda occidentalis*, crustacean, digging, *Emerita analoga*, evolution, kinematics, legs, *Lepidopa californica*, locomotion, sand crabs.

Introduction

In decapod crustaceans, the ancestral form of locomotion using the legs is almost certainly walking (Hessler, 1981). The leg morphology of the earliest known decapod, *Palaeopalaemon newberryi* (Schram *et al.* 1978), is similar to that of modern astacideans (crayfish and lobsters), whose locomotion has been well studied (e.g. Ayers and Davis, 1977; Cruse, 1990; Evoy and Ayers, 1982; Jamon and Clarac, 1995; Macmillan, 1975; Müller and Cruse, 1991; Pond, 1975; Sillar *et al.* 1987). Palinurans (spiny lobsters; e.g. Chasserat and Clarac, 1983; Clarac and Chasserat, 1983; Clarac, 1984; Müller and Clarac, 1990*a*) and thalassinideans (mud shrimps) are apparently similar in many respects, but there is tremendous diversity in the patterns of walking behaviour in decapods. Brachyuran crabs walk in all directions, but typically walk sideways when moving quickly (Burrows and Hoyle, 1973; Clarac, 1977; Clarac *et al.* 1987; Daumer *et al.* 1963; Evoy and Fourtner, 1974; see Sleinis and Silvey, 1980, for an example of a forward-walking crab), but some can also use their legs to swim (Hartnoll, 1970; Spirito, 1972). Within the anomurans, hermit crabs (Superfamily Paguroidea) walk while carrying gastropod shells (Herreid and Full, 1986), and squat lobsters and porcelain crabs (Superfamily Galatheoidea) apparently walk in any direction with equal ease

(Z. Faulkes and D. H. Paul, personal observations). Sand crabs are unusual because they have lost the ability to walk and instead use their legs to dig rapidly backwards into sand. Albuneid sand crabs also move their legs rhythmically when swimming, although their swimming ability is poor compared with swimming by uropod beating in hippids (Paul, 1981*a*).

We are interested in sand crab digging as an example of how a 'new' behaviour pattern originates and evolves. To understand this evolutionary problem, we examined both sand crab digging behaviour (this paper; Faulkes and Paul, 1997*b*; Z. Faulkes and D. H. Paul, in preparation) and its neural basis (Faulkes and Paul, 1997*a*) so that we could compare digging in sand crabs with the locomotor behaviour of other decapods. Sand crab digging may be homologous to walking: both are forms of locomotion using the thoracic legs, and members of the taxa most closely related to the sand crabs walk (see Fig. 1F,G). The interleg coordination in the mole sand crab (*Emerita* spp.; family Hippidae), however, differs from the walking patterns in most other decapods: the fourth pair of legs cycles at approximately twice the frequency of the second and third pairs (Trueman, 1970; this study). Such a difference in coordination could argue against the homology of walking and digging.

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Digging in *Emerita*, however, may not be representative of all sand crabs; for example, the abdomen and tailfan are highly modified for uropod beating in hippids, whereas in albuneids their neuromusculature and their use in swimming more closely resemble those of macruran decapods (Paul, 1981*a*,*b*, 1991). Further, interleg coordination in *Emerita* has only been described in general terms for the ipsilateral legs, and not at all for the bilateral pairs of legs (Trueman, 1970).

We examined the digging leg movements of sand crabs of both families (Fig. 1): the spiny sand crab *Blepharipoda occidentalis* (Albuneidae), the pearly sand crab *Lepidopa californica* (Albuneidae) and the mole sand crab *Emerita analoga* (Hippidae). All three sand crab species show some similarities in how they dig, but there are several differences between the digging patterns of the albuneids and *E. analoga*, which are correlated with other familial differences. Abstracts of this work have been published (Faulkes and Paul, 1995; Faulkes *et al.* 1991).

Materials and methods

The sand crabs *Blepharipoda occidentalis* Randall and *Emerita analoga* (Stimpson) were collected in Monterey Bay, California; *Lepidopa californica* Efford were collected near Santa Barbara, California. All were housed in the University of Victoria's recirculating seawater system. All experiments were conducted in accordance with Canadian Council of Animal Care guidelines.

We video-taped *B. occidentalis* and *E. analoga* making digging movements in sea water, using a Panasonic Super-VHS PV-S770 camera (NTSC format; 30 frames s^{-1}). This camera has an electronic 'shutter' so that the exposure time for each frame was less than 1 ms of the 33.3 ms interval between frames. We placed a mirror in the filming tank, angled at 45° to the camera, to video-tape side and ventral views of the animals simultaneously. The animals were hand-held *via* a plastic 'flag' glued to their carapace or tethered by EMG leads (see below). Because *L. californica* are small (Fig. 1), they were video-taped with a Panasonic WV-CP210 camera, which has a shorter focal distance but no electronic shutter, and only one view (side or ventral) of an individual *L. californica* was video-taped at a time. The video tape was analysed frame by frame. Most analyses were carried out by hand, sometimes using Eshkol–Wachman movement notation (Eshkol, 1980). Once we had determined what the patterns of movement were, we re-examined other video-taped sequences of leg movement to confirm that the patterns were consistent across individuals. We digitised some sequences of *B. occidentalis* and *E. analoga* with a Peak 5 movement analysis system (Peak Performance Technologies, Inc.; 60 fields s^{-1}).

We recorded electromyograms (EMGs) from the leg

Fig. 1. (A,B) Two albuneid sand crabs, *Blepharipoda occidentalis* (side view) and *Lepidopa californica* (dorsal view). The fourth legs are splayed to the side, whereas legs 2 and 3 are held underneath. (C) The hippid sand crab *Emerita analoga* swimming by uropod beating. The legs are held streamlined against the underside of the thorax. (D,E) The three sand crab species differ markedly in size. (D) *B. occidentalis* (upper; carapace length approximately 50 mm) and *L. californica* (lower; carapace length approximately 10 mm). (E) *E. analoga* (upper; carapace length approximately 25 mm) and *L. californica*. (F) A squat lobster, *Munida quadrispina* (carapace length approximately 20 mm). This species belongs to Galatheoidea, which is thought to be the sister taxon to the sand crab superfamily Hippoidea. Leg morphology in galatheids is similar to that of other walking crustaceans. (G) Hypothesised sand crab phylogeny (based on Bowman and Abele, 1982; Schram, 1986). *Blepharipoda* and *Lepidopa* are not thought to be closely related genera within the family Albuneidae (Efford, 1969), which contains seven other genera.
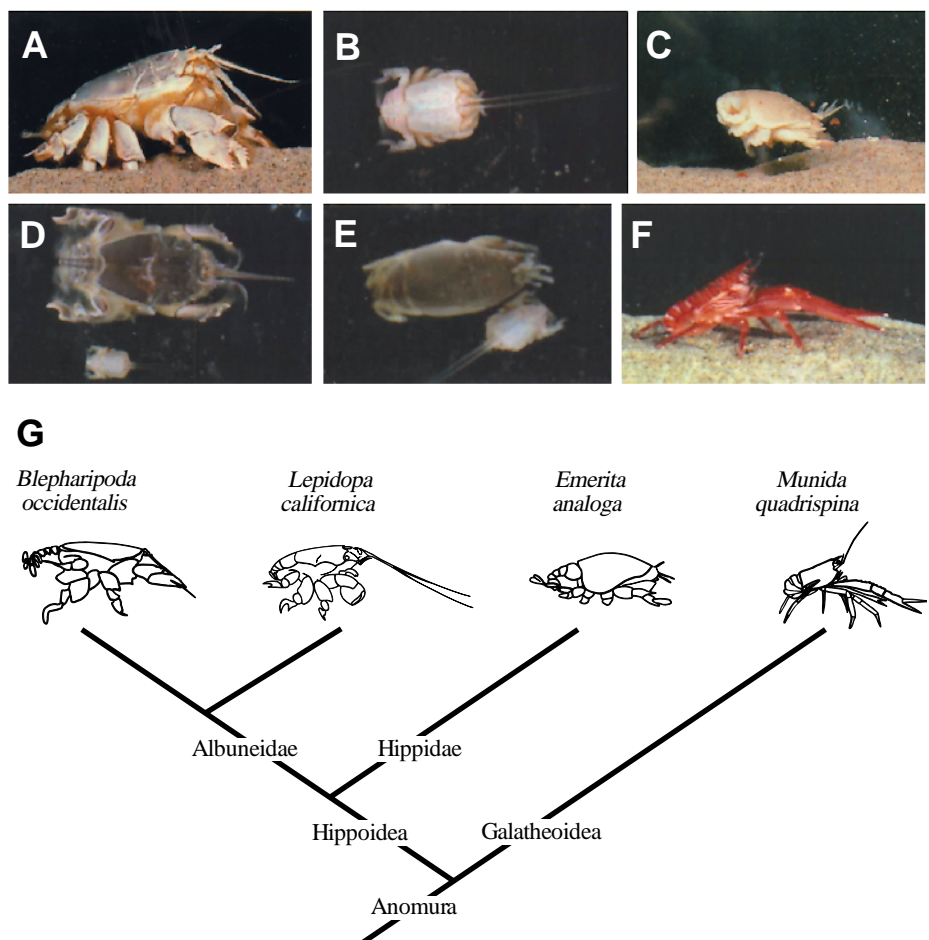
muscles of animals making digging movements above sand and while digging into sand. We drilled small holes in the exoskeleton, inserted two fine Teflon-coated silver wires (A&M Systems, Inc.) into the leg muscles, and glued the electrodes in place. EMGs were recorded on a Vetter D1 reel-to-reel frequency-modulated (FM) tape recorder, and transferred to an IBM-PC compatible computer, using a Labmaster TL-1 analogue to digital converter and the software package Axotape 2 (Axon Instruments, Inc.).

Thoracic legs are designated as left or right (L or R) and are numbered from anterior to posterior; e.g. left claw=L1. In anomurans, the fifth, most posterior pair of legs (legs 5) are small and are not used in locomotion (Haig and Abbott, 1980), so their movements were not analysed. Similarly, legs 1 make only secondary contributions to digging (i.e. sand crabs can dig without them), and sand crabs do not make a full range of movements with these legs when held in sea water, so movements of legs 1 were not examined.

The *period* is the duration of one complete cycle of events (e.g. the movement of a leg forwards and backwards). The relative timing between two repeating events is expressed as *phase* (ϕ), calculated as:

$$\phi = (\text{onset}_{\text{test}} - \text{onset}_{\text{reference}})/\text{period}_{\text{reference}}.$$

Phases of 0 and 1 both mean that two events began at the same time.

Typically in locomotor research, a complete cycle of leg movement is divided into a power stroke (providing propulsive force; e.g. 'stance phase' in walking) and a return stroke ('swing phase' in walking). In this case, we could not divide digging leg movements into power and return strokes *a priori*, because the legs of the sand crab move through the substratum as it digs. Power and return strokes were determined by examining leg tip trajectories of digging movements made in sea water; movements so defined should be capable of explaining the normal backward descent of the animal into sand. The leg movements that were most rapid and presented the greatest surface area were defined as the power stroke, because such movements would provide propulsive force. Leg movements in sea water that were slower and presented a smaller surface area were defined as the return stroke.

Results

Sand crabs dig into sand backwards, tail-first. Both *B. occidentalis* and *L. californica* can also swim backwards by rowing legs 2 and 3 while tailflipping (Paul, 1981*a*). Both species readily make these rhythmic, digging-like movements with legs 2 and 3 when held in sea water above sand. Legs 4, in contrast, seldom move rhythmically when the animals are held in sea water; EMGs indicate, however, that they make large and regular movements when digging (data not shown; Faulkes, 1996; Z. Faulkes and D. H. Paul, in preparation). *E. analoga* do not move any of their legs when swimming backwards by uropod beating, but could be coaxed, by touching the legs, into making rhythmic, digging-like movements for
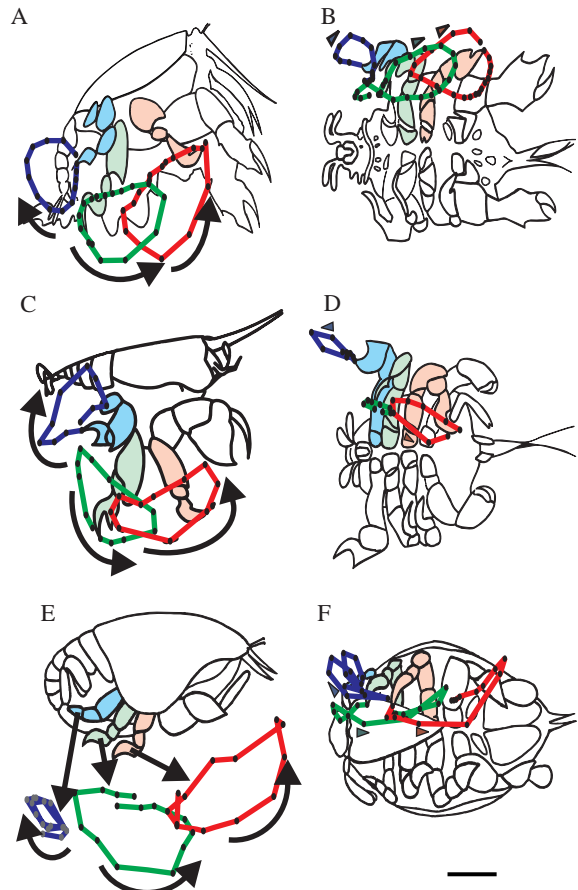

Fig. 2. Leg tip trajectories in sea water. (A,C,E) Legs viewed from the side. (B,D,F) Legs viewed ventrally. (A,B) *B. occidentalis*, (C,D) *L. californica* (antennae truncated), (E,F) *E. analoga*. Dots show the position of the dactyl tips in successive video frames. In all three species, the directions of the tip trajectories viewed from the side are similar for legs 2 (red) and 3 (green) and opposite to the tip trajectory of leg 4 (blue): in this view (A,C,E), the tips of legs 2 and 3 circle counterclockwise, whereas leg 4 circles clockwise. C and D are traced from separate video sequences. The counterclockwise trajectory of leg 4 shown in D is an example of the variability in the movements of leg 4; leg 4 in *L. californica* frequently circles in the same direction as leg 4 in *B. occidentalis* and *E. analoga*. Note that, in E and F, leg 4 has cycled twice in the time that legs 2 and 3 take to complete one cycle. In E, the animal is offset from the trajectories and is shown on a slightly smaller scale than the trajectories. E and F are traced from different video sequences, and F is a composite of two video sequences, one for legs 2 and 3, and another for leg 4. Temporal resolution (A–D,F) 33.3 ms (i.e. one video frame); (E) 16.7 ms (i.e. one video field). Scale bar (shown in F): approximately 20 mm (A,B), approximately 5 mm (C,D), approximately 10 mm (E,F).

video-recording when tethered in sea water above sand. All three species can make a seamless transition from digging-like movements (i.e. swimming) above sand to digging into it, and the continuity of EMG patterns (see Fig. 5 and below) suggests that the same basic motor pattern operates in both media.

Tip trajectories

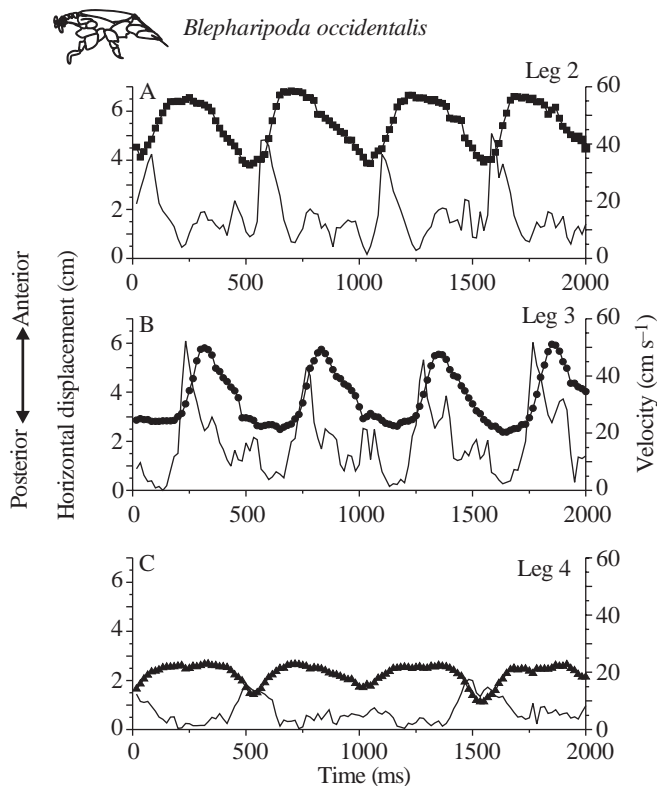The tip trajectories of homologous legs are similar in all

Fig. 3. Forward and backward movements of legs in *B. occidentalis* (line and symbol) and leg velocity (line only) in sea water. (A) Leg 2, (B) leg 3 and (C) leg 4. On the left vertical axis (horizontal displacement), larger numbers are towards the anterior of the animal. The highest velocities of legs 2 and 3 occur during the forward movement, whereas leg 4 moves most rapidly during a transition from backward to forward movement. The velocity of leg 4 is lower and more variable than that of legs 2 and 3.
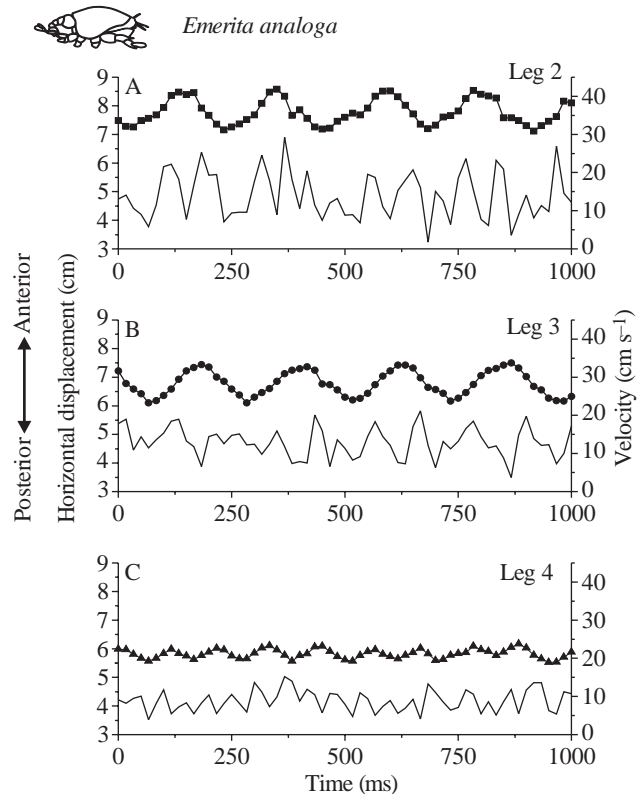
Fig. 4. Forward and backward movements and velocity of legs in *E. analoga* in sea water. The same analysis and representation are shown as in Fig. 3. The power and return strokes in legs 2 and 3 are almost equal in velocity. Note the greater frequency of leg 4 than of legs 2 and 3.

three sand crab species when the animals make digging-like movements above sand (Fig. 2). The cycle of legs 2 and 3 consists of a forward-directed power stroke and a backward-directed return stroke. During the power stroke, the leg swings rapidly forwards and away from the body, with the dactyls in an 'open' (extended) position and the broad surfaces facing forwards, which would increase the resistance of sand on the legs when digging. During the return stroke, the legs are brought closer to the body with the dactyls in a 'closed' (flexed) position, thereby decreasing surface area and resistance. In sand, legs 2 and 3 would function like shovels, scooping sand out from underneath a digging animal. In *B. occidentalis*, the return stroke speed of legs 2 and 3 is slower than that of the power stroke (Fig. 3), but in *E. analoga*, the two portions of the cycle can have nearly the same speed during very vigorous leg movements (Fig. 4).

The tip trajectory of leg 4 is distinct from those of legs 2 and 3 (Fig. 2). When viewed from the right side, the tip of leg 4 circles clockwise whereas the tips of legs 2 and 3 circle counterclockwise. The different tip trajectories result from a very different sequence of joint movements (Z. Faulkes and D.

H. Paul, in preparation; Faulkes, 1996) and not simply from the difference in the shape of leg 4 compared with legs 2 and 3 (Fig. 1A,B). In the albuneids, the movement of leg 4 is not readily divisible into power and return strokes, because its overall movement is much more variable, and its speed more uniform, than those of the other legs (Fig. 3), even when it is making relatively large-amplitude movements (which are always smaller than those made by legs 2 and 3 in all three species; Figs 2, 3). The most rapid part of the movement of leg 4 in *B. occidentalis* occurs when the leg tip is at its most posterior and the leg is moving dorsally and laterally, as it reverses direction from backwards to forwards (Fig. 3C). Its tip trajectory incorporates a substantial lateral component and is not easily represented in two dimensions (Figs 2, 3). The smaller, more complicated excursions of leg 4 in all three species, compared with those of legs 2 and 3, suggest that legs 4 contribute to digging by creating a thixotropic effect (i.e. liquefying the sand) and by providing purchase, by extending laterally, so that the shovelling movements of legs 2 and 3 cause the the rear end of the animal to be pushed down into the sand. *E. analoga* with legs 4 amputated submerge themselves more slowly and less steeply than before amputation (D. H. Paul, unpublished observations). If leg 4 circled in the same direction as legs 2 and 3, the resulting forces would presumably propel the animal directly backwards.

In *E. analoga*, the movements of legs 4 are coupled with, and complementary to, uropod beating movements and may be divisible into power and return stroke components on the basis of how they function in tandem with the uropods (Faulkes and Paul, 1996*b*). Currently, however, we do not have a sufficiently clear understanding of how legs 4 move in *E. analoga* to make this distinction, because *E. analoga* seldom row their legs above sand, and when they do, the spatial and temporal resolution of the video recordings limits detailed analysis of the rapid movements of these small legs.

The leg movements we video-taped in tethered animals in sea water would appear to function well for digging into sand. To ensure that the leg movements in these two situations were truly comparable, we video-taped and recorded EMGs from animals making leg movements in sea water and recorded EMGs from the same individuals digging in sand. The patterns of movement and muscle activity correlate well, and the EMG patterns are similar in sea water and in sand; i.e. muscles that act as synergists during leg movements in sea water continue to act as synergists during digging into sand. Simultaneous video/EMG records were made for all muscles in leg 2; one example is shown (Fig. 5). The motor outputs to single legs in sea water and in sand are compared in detail elsewhere (Faulkes, 1996; Z. Faulkes and D. H. Paul, in preparation).

Speed

Both above and below sand, the speeds of the leg movements are inversely correlated with species size. When making digging movements in sea water, the legs cycle back and forth at frequencies of approximately 1.5–2 Hz in *B. occidentalis*, approximately 3–4 Hz for leg 2 and 3 in *E. analoga* (leg 4 is faster, approximately 3–8 Hz; see Figs 4, 8C) and approximately 4–7 Hz in *L. californica*. This ranking persists when animals dig (Fig. 6), but the differences are reduced because all three species slow down as they dig, presumably because of the resistance of the sand (Fig. 7). Most of the *B. occidentalis* used in this work had carapace lengths of approximately 40–60 mm (larger individuals may have carapace lengths up to approximately 80 mm), compared with approximately 22–28 mm for *E. analoga* and approximately 10–14 mm for *L. californica* (close to maximum size for the latter two species).

Ipsilateral coordination

The ipsilateral coordination of legs 2 and 3 is very similar in all three species (Figs 8, 9). Legs 2 and 3 are strongly coupled, with leg 3 starting to move forward shortly after leg 2 ($\phi_{3\ in\ 2} \approx 0.2$; Fig. 9) both in sea water (Fig. 9A) and in sand (Fig. 9B). Legs 2 and 3 also form and break 'oppositions' (i.e. two limbs are near but not touching; Eshkol, 1980) at the same point in their movement cycles in all three species: the two legs form an opposition when leg 3 stops moving forward, which is 'broken' when leg 2 starts to move forward (Fig. 8).

When albuneids are held in sea water, the movements of leg 4 are much more variable than those of legs 2 and 3 (note pauses in Fig. 8A) and may not occur at all, but regular EMG bursts are recorded from leg 4 when an individual is digging (data not shown; Faulkes, 1996; Z. Faulkes and D. H. Paul, in preparation). Nevertheless, when leg 4 does move, either in sea water or in

Fig. 5. A comparison of motor output in sea water and in sand in *B. occidentalis*. (A) Combined video analysis of the individual joint movements of leg 2 in sea water and EMG records from the closer and extensor muscles, made simultaneously. Boxes indicate movements of individual joints, with the muscle that should be responsible for moving the joint indicated in each box. (B) EMGs from the same individual digging in sand. In both media, the closer acts as a return stroke synergist and the extensor as a power stroke synergist, and the two muscles alternate. Same vertical scale for EMGs in A and B. Thick boxes, power stroke leg movements; thin boxes, return stroke leg movements. Leg segments: Cx, coxa (most proximal); B-I, basi-ischium; M, merus; C, carpus; P, propus; D, dactyl (leg tip). Muscles: REM, remotor; PRO, promotor; ELE, elevator; DEP, depressor; EXT, extensor; FLX, flexor; STR, stretcher; BND, bender; OP, opener; CL, closer.

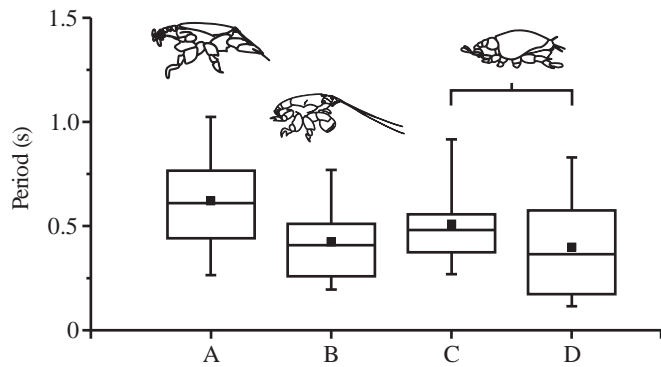*Blepharipoda occidentalis*

67 ms
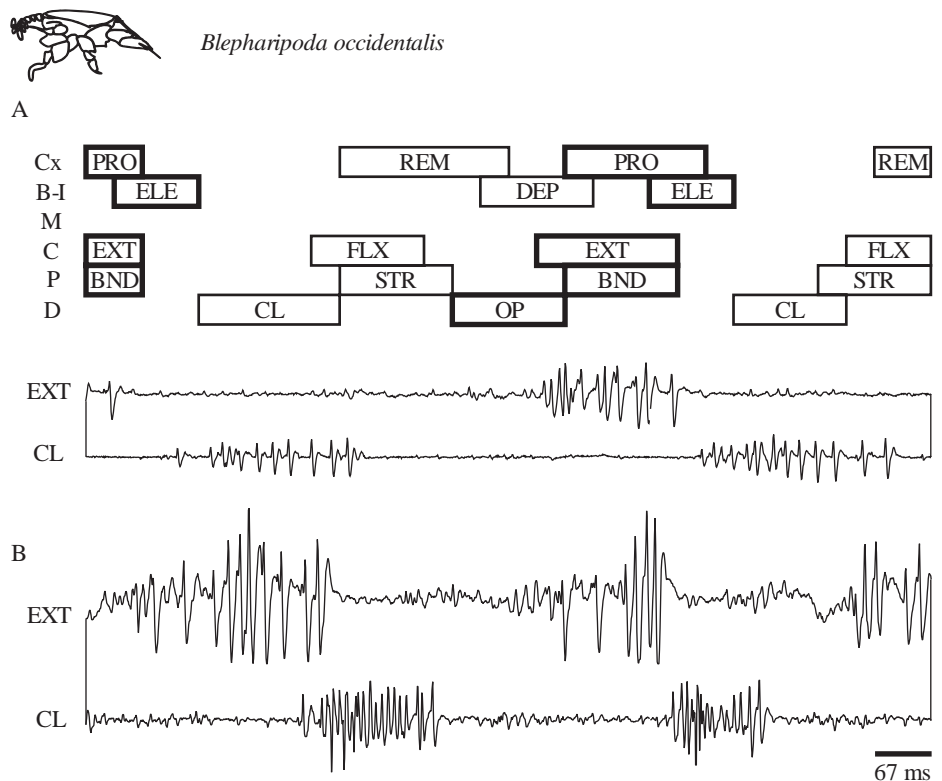
Fig. 6. Comparison of frequency of leg movements in the three sand crab species in sand. Box chart of EMG periods from (A–C) leg 2 bender in (A) *B. occidentalis*, (B) *L. californica*, (C) *E. analoga* and (D) leg 4 stretcher in *E. analoga*. The means are significantly different (one-way ANOVA, $F=30.1$, $P<0.05$). The bottom of the vertical line is the fifth percentile; the bottom of the box is the twenty-fifth percentile; ■, mean; the middle box line is the fiftieth percentile (i.e. median); the box top is the seventy-fifth percentile, the top vertical line is the ninety-fifth percentile. Sample size: A, C, D, three digs each from three animals; B, three digs each from two animals.

sand, it cycles at the same frequency as the more anterior legs (Fig. 8A,B). The coupling of leg 4 with the more anterior legs may be less crucial than the coupling between legs 2 and 3 for several reasons. First, leg 4 is seldom used during swimming; second, the tip trajectory of leg 4 does not overlap with those of the other legs (Fig. 2), so there is little risk of legs colliding regardless of their phasing; third, leg 4 is not a primary shoveller.

In contrast to leg 4 of albuneids, leg 4 of *E. analoga* (and *E. portoricensis*; Trueman, 1970) can move back and forth at approximately double the frequency of the other legs, i.e. at approximately the same frequency as the beating of the uropods (Figs 4, 8C; Paul and Faulkes, 1995). Such 'double time' movements by leg 4 are very difficult to elicit when an animal is held in sea water, because *E. analoga* swim by uropod beating with their legs held against the underside of the thorax unless something touches the legs. High-frequency, 'double time' EMGs in leg 4 were regularly recorded from digging animals, however, particularly early in a digging sequence. EMGs also showed that the frequency of movement of leg 4 tends to drop to approximately that of legs 2 and 3 as an individual becomes submerged in the sand (note the sharper increase of period in Fig. 7D than in Fig. 7C). The data concerning the exact coupling of leg 4 with the more anterior, ipsilateral legs are equivocal (Fig. 10): no coupling is suggested by depressor muscle EMGs (Fig. 10A), but a loose preference of $\phi\approx0.5$–0.6 (leg 4 phase in leg 2 period) is evident in stretcher muscle EMGs (Fig. 10B). Although in some respects contradictory, both analyses show that the coupling of leg 4 with leg 2 is looser than the coupling between legs 2 and 3 in *E. analoga*.

Bilateral coordination

The bilateral legs of sand crabs typically alternate, although
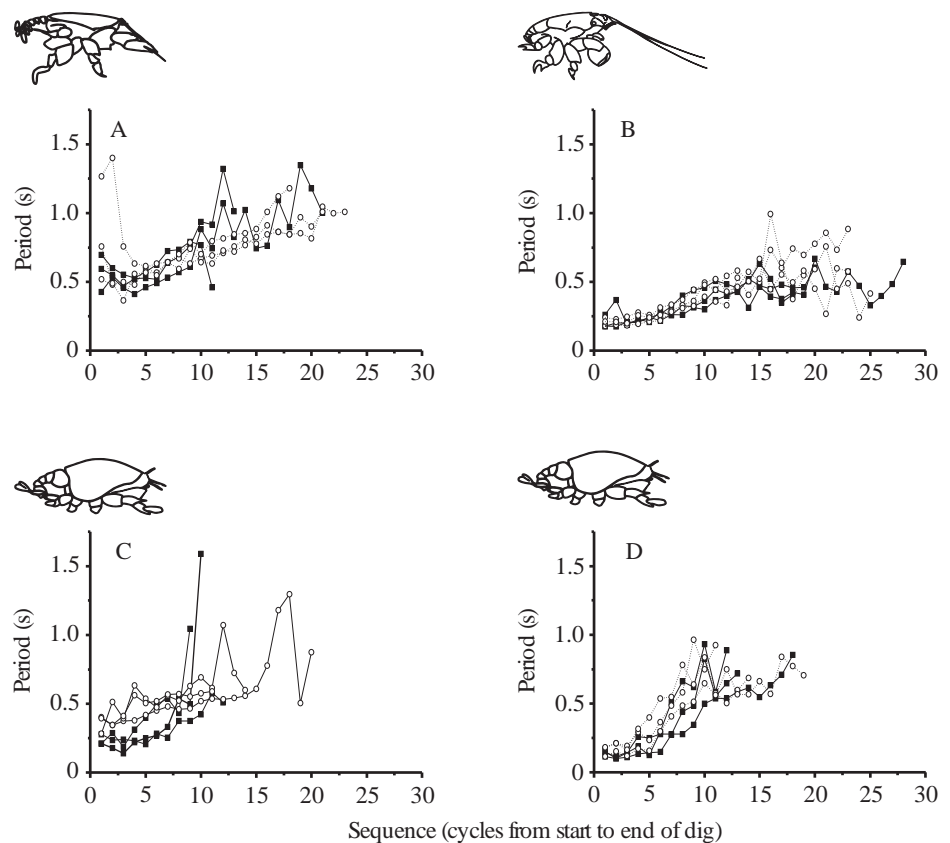

Fig. 7. Sand crabs slow down as they dig. Sequential periods of EMG bursts in leg 2 bender muscle in sand for (A) *B. occidentalis*, (B) *L. californica*, (C) *E. analoga* and (D) leg 4 stretcher in *E. analoga*. Each graph shows three digs each from two individuals (filled symbols and solid lines; open symbols and dashed lines).
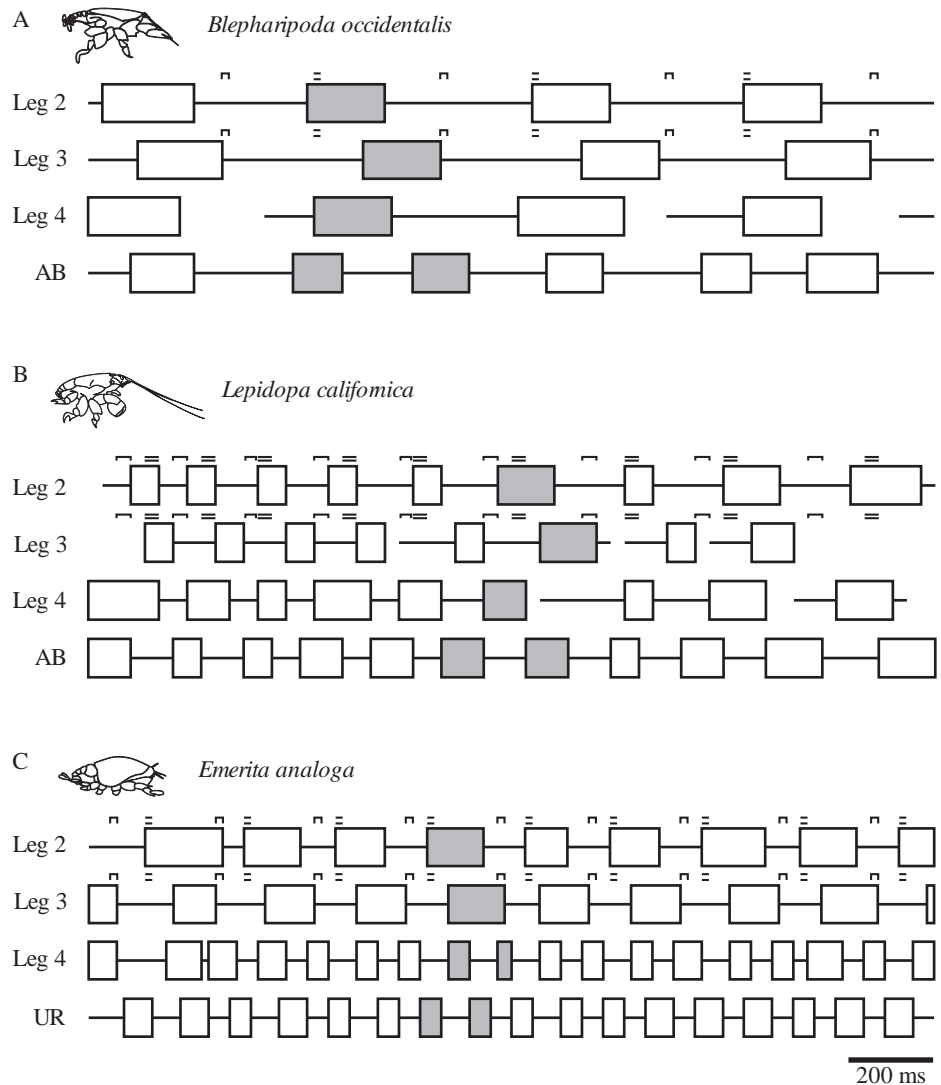
Sequence (cycles from start to end of dig)

Fig. 8. Movement of limbs forwards (boxes) and backwards (lines) relative to the body in (A) *B. occidentalis*, (B) *L. californica* and (C) *E. analoga* making digging-like movements in sea water. Breaks indicate that the limb was still. Shaded boxes highlight forward movements in a representative cycle of locomotion. AB, abdomen; UR, uropods. Symbols (Eshkol, 1980): ⌐, a pair of limbs form an opposition (i.e. close but not touching); =, release of opposition. Temporal resolution: A, C, 16.7 ms (digitised using Peak 5), B, 33.3 ms. Scale bar for all shown in C.

there is a strong tendency for them to be synchronous in some cases. In *B. occidentalis* and *L. californica*, the bilateral legs alternate (i.e. $\phi \approx 0.5$) when the frequency of leg cycling is high (i.e. when making digging movements in sea water and early in digging): when the left leg is moving forwards, the right leg is moving backwards (Figs 11A–D, 12). As an individual digs, the frequency of cycling decreases and legs 2–4 switch gait from bilateral alternation to synchrony (i.e. $\phi \approx 0$ or 1): the left and right legs of each segment move forwards and backwards together (Figs 11A–D, 12). This gait switch usually occurs over a few cycles (approximately 4–5), but can be very abrupt (approximately 1–2 cycles); it is almost certainly triggered by the increasing load on the legs as the animals descend into the sand, although what sensory cue triggers it is unknown. Were the legs to continue to alternate, the increased load would exacerbate the tendency towards zigzag progression imposed by this gait; by switching to moving the legs in bilateral synchrony, this tendency to zigzag would be avoided.

The coordination of the bilateral legs in *E. analoga* is different from that in the albuneids. Both video recordings and

EMGs of *E. analoga* show that legs 1, 2 and 3 always alternate, both in sea water and in sand: they do not switch gait during digging as the albuneids do (Figs 11E, 13A). This may reflect the fact that the tendency for zigzag progression in *E. analoga* is less than in the albuneids, because their leg trajectories are more ventral and closer to the midline (Fig. 2). EMGs show that legs 4, in contrast, often move in bilateral synchrony during digging (Figs 11F, 13B); this was occasionally video-taped in animals suspended in sea water. In contrast to the bilateral synchrony in albuneids, the bilateral synchrony of legs 4 of *E. analoga* normally occurs at the start of a digging sequence rather than at the end (compare Fig. 13B with Fig. 12). As a digging *E. analoga* submerges into the sand and the period of legs 4 increases, the bilateral phasing of legs 4 becomes scattered (Fig. 11F).

Discussion

The three sand crab species, *B. occidentalis*, *L. californica* and *E. analoga*, are similar in their digging behaviour patterns.
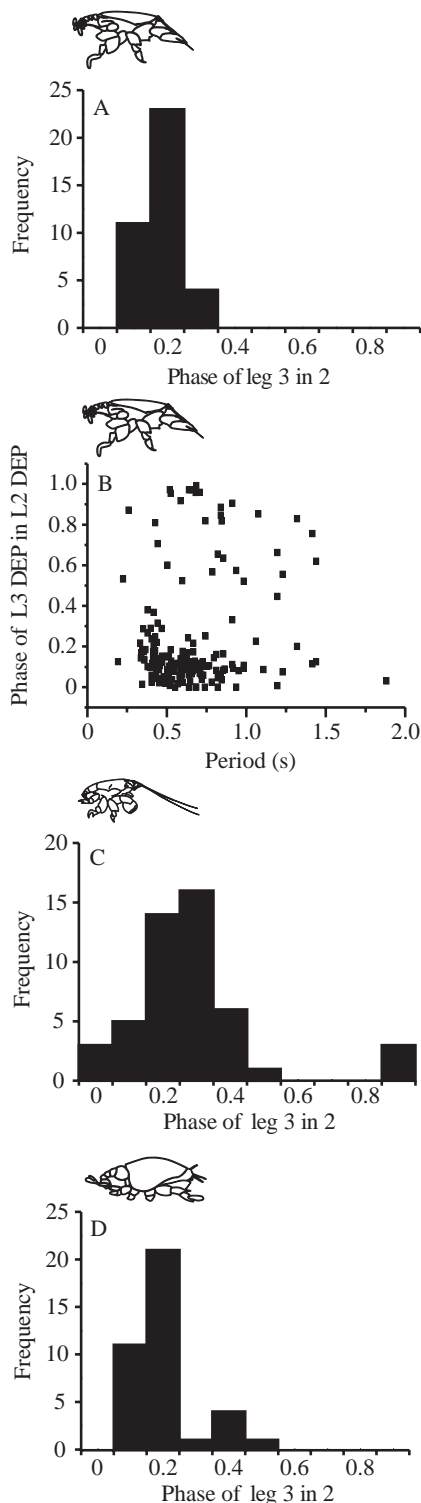
Fig. 9. Coupling of legs 2 and 3 when moving in sea water (A,C,D) and sand (B). (A) Phase histogram of forward movement (from video recordings) of leg 3 relative to forward movement of leg 2 in *B. occidentalis* (*N*=6 sequences from six animals). (B) Phase *versus* period of leg 3 depressor (DEP) EMG onset relative to leg 2 depressor EMG onset during digging in *B. occidentalis* (*N*=6 digs from two animals). (C,D) Phase histograms of legs 2 and 3 in (C) *L. californica* (*N*=6 sequences from three individuals) and (D) *E. analoga* (*N*=8 sequences from three individuals).
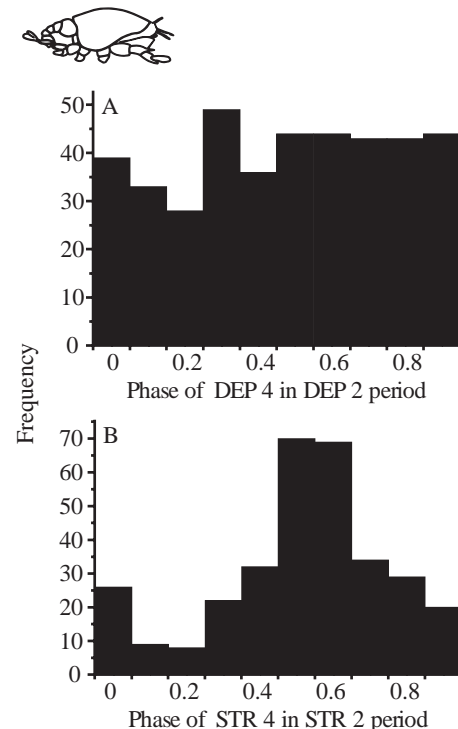

Fig. 10. Coupling of legs 2 and 4 in *E. analoga* during digging. (A) Phase histogram of leg 4 depressor (DEP) EMG burst in ipsilateral leg 2 depressor period; 19 digs from four animals. (B) Phase histogram of leg 4 stretcher (STR) in ipsilateral 2 stretcher period (both left and right legs measured); 25 digs from four animals. A suggests no coupling between the pair of legs, whereas B suggests coupling.

Legs 2 and 3 provide most of the propulsive force during digging, and their ipsilateral coupling is very tight. The movements of leg 4 are less powerful but important in allowing an animal to descend rapidly into sand. The variable movement of leg 4 and its loose coupling with the more anterior legs suggest that the activation of legs 4 may have a higher threshold or be more dependent on sensory input than the activation of legs 2 and 3; it is also possible that there are separate command systems for legs 4 and legs 2 and 3 (Bowerman and Larimer, 1974; Larimer, 1976). Bilateral pairs of legs typically alternate their movement in sand crabs, as in many other crustaceans (Cruse, 1990; Macmillan, 1975; Müller and Cruse, 1991; Sleinis and Silvey, 1980). Nonetheless, bilateral pairs of legs move synchronously under a well-defined set of conditions, although these conditions are not the same for the two albuneids and *E. analoga*.

The equivocal data on the coupling of legs 2 and 4 in *E. analoga* are provocative (Fig. 10). They may reflect differential entrainment effects on the motor output to different segments of leg 4, since there are multiple sources of coordinating input to this leg. Along with the hypothesised coordinating influence from anterior ipsilateral legs, legs 4 in *E. analoga* are coupled with the uropods (whereas the movements of the abdomen do not influence the legs in

albuneids; Faulkes and Paul, 1997*b*). Thus, it is conceivable that the uropod motor system exerts a stronger influence over the circuitry controlling proximal muscles than distal muscles, while legs 2 and 3 influence the circuitry controlling all leg 4 segments. In this case, the timing of proximal leg muscle motor output would receive two coordinating inputs with different frequencies (flattening the phase distribution, as in Fig. 10A), whereas the distal leg muscles would not. Additionally, the stretcher muscle (Fig. 10B) shares its only excitatory innervation with the opener muscle; these two muscles typically generate matching EMGs (Barnes, 1977; Faulkes and Paul, 1997*a*; Z. Faulkes and D. H. Paul, in preparation). The motor output to the shared opener/stretcher excitor may have a more rigid set of timing constraints than the output to the more profusely innervated depressor muscle.

Homology and divergence in sand crab digging

The following similarities between the digging patterns of three species in the two sand crab families provide evidence that digging is a monophyletic, derived character shared among members of the sand crab superfamily. First, the tip trajectories are similar in all three species, with the circling of leg 4 being different from that of legs 2 and 3. Second, the movements of legs 2 and 3 are tightly coupled, leg 3 trailing leg 2 with a phase of approximately 0.3 in all three species. Third, the movements of leg 4 are quite variable and loosely coupled with those of
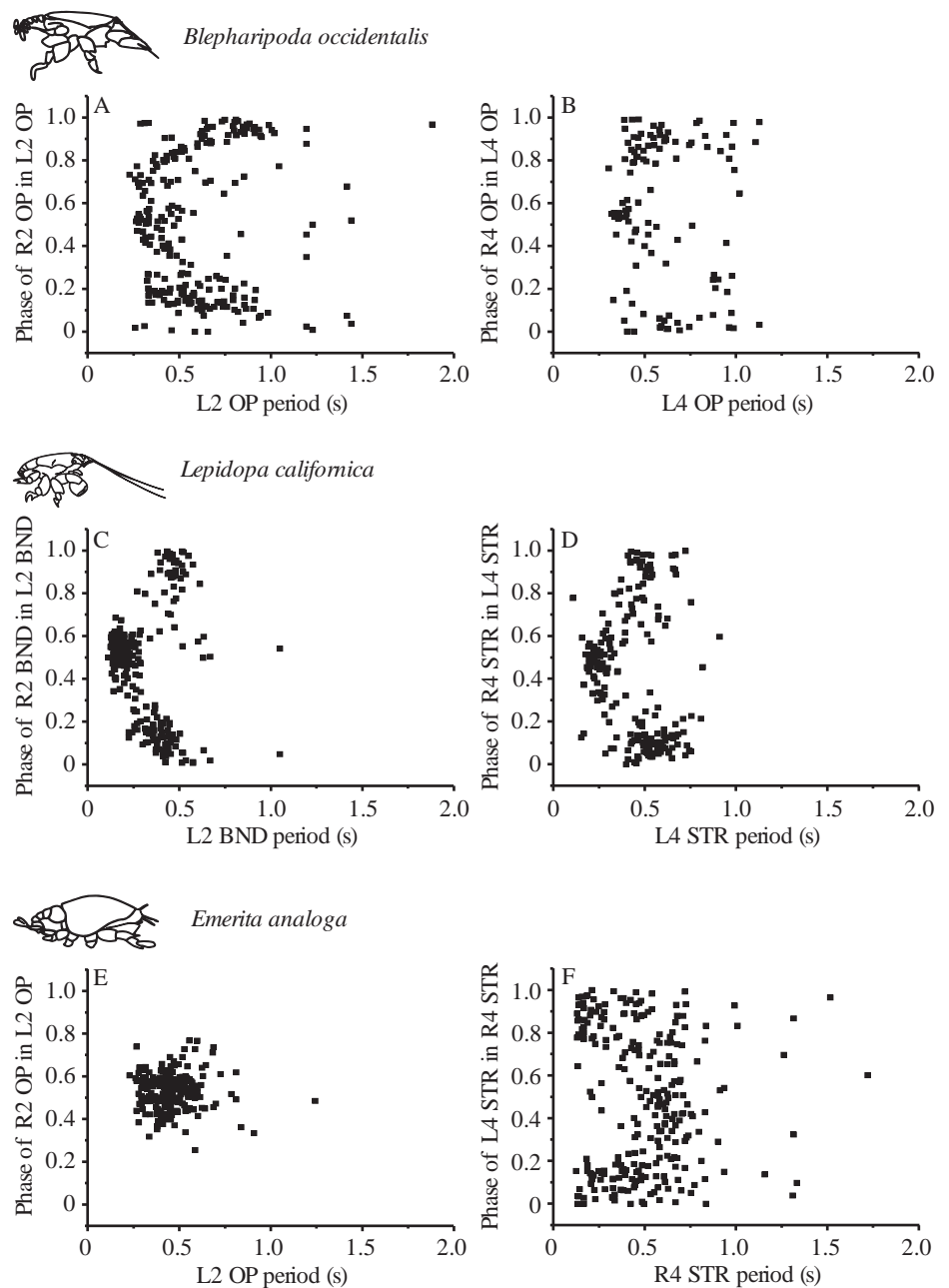

Fig. 11. Dynamics of bilateral leg coordination during digging. (A) Leg 2 opener (17 digs from three animals) and (B) leg 4 opener (OP, nine digs from one animal) in *B. occidentalis*. (C) Leg 2 bender (BND, four digs from one animal) and (D) leg 4 (seven digs from one animal) stretcher in *L. californica*. Bilateral synchrony (i.e. phase≈0 and 1) occurs at the end of digging in *B. occidentalis* and *L. californica* (see Fig. 12). (E) Leg 2 opener (20 digs from five animals) and (F) leg 4 stretcher (STR, 19 digs from four animals) in *E. analoga*. In *E. analoga*, bilateral legs 4 tend to be synchronous in periods of less than approximately 0.3 s, at the onset of digging (see Fig. 13B), but show no preferred bilateral coordination at periods greater than approximately 0.3 s (but see Faulkes and Paul, 1996*b*).
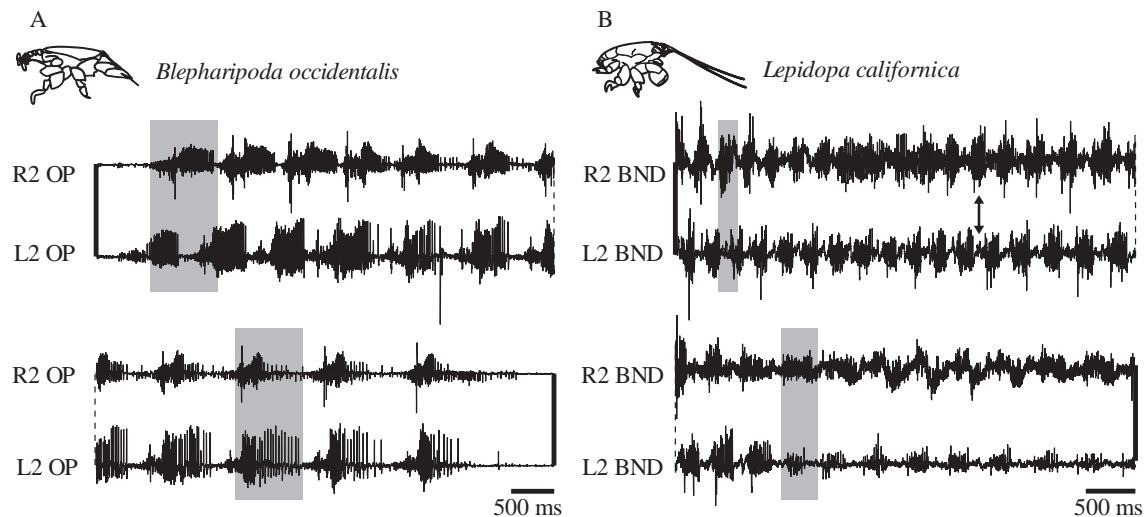
Fig. 12. EMGs showing a gait switch during digging in (A) *B. occidentalis*, recorded from opener muscles (OP) and (B) *L. californica*, recorded from bender muscles (BND). In B, the animal was suspended above the sand at the start of the recording; the double-headed arrow marks the approximate point at which digging started. Note the difference in EMG frequency in the two species. In this and Fig. 13, vertical lines link concurrent EMGs; dashed vertical lines indicate the continuation of consecutive EMG traces; shaded boxes highlight representative EMG bursts before and after the gait switch.

legs 2 and 3. Finally, legs 2 and 3 move in bilateral alternation when animals are held in sea water.

After digging behaviour originated, it diverged within the sand crab superfamily. The albuneid species, *B. occidentalis* and *L. californica*, switch gait from bilateral alternation to synchrony as they dig. That this gait switch is exhibited by two species of different sizes, which belong to genera that do not appear to be closely related (Efford, 1969), suggests that the

trait is common to all albuneids. The function of the albuneid gait switch may be to reduce the tendency of the body to zigzag during digging, but an additional reason why *E. analoga* (and presumably other hippids) do not switch gait may be because their first pair of legs is very long. In *E. analoga*, leg 1 is rudder-shaped and aids steering during swimming by uropod beating (Paul, 1971). Legs 1 are equally long or slightly longer in the genus *Hippa*, and are remarkably long in *Mastigochirus*,
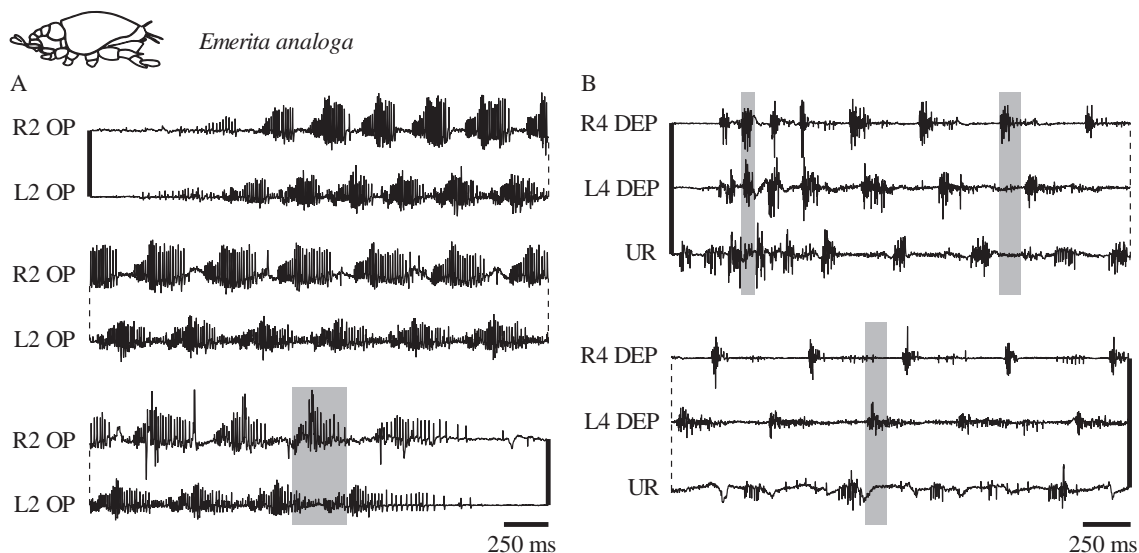

Fig. 13. EMGs showing bilateral leg coordination during digging in *E. analoga*. (A) The right and left legs 2 in *E. analoga* always alternate (see shaded box on lowest set of traces). EMGs from opener (OP) muscles in leg R2 and L2. This recording shows one complete digging sequence. (B) Legs 4 of *E. analoga* are synchronous during fast movements, but become asynchronous as the animal slows during digging. The frequency of leg 4 movements approximates the frequency of uropod beating movements, particularly early in a digging sequence. EMGs were recorded from depressor (DEP) muscles in legs R4 and L4, and from uropod (UR) power stroke (large potentials) and return stroke (small potentials) muscles in the telson.

where the dactyl is multi-segmented (approximately 20 articulations; Snodgrass, 1952; Haig, 1974). These legs would collide with each other during digging if hippids moved their bilateral pairs of legs in synchrony, as albuneids do.

The second distinction between the albuneids and *E. analoga* is the coordination of leg 4. Probably by virtue of being more tightly coordinated with movements of the uropods (Paul and Faulkes, 1995; Faulkes and Paul, 1997*b*), leg 4 in *E. analoga* is able to cycle at higher frequencies than legs 2 and 3, and to move in bilateral synchrony, even though legs 2 and 3 always move in bilateral alternation.

Evolutionary origins for digging

While the evidence suggests that digging is a monophyletic feature in sand crabs, it is less obvious how digging originated. It is unlikely that a complex biological feature such as digging is an entirely new type of behaviour with no important relationship to behaviour patterns in other decapod crustaceans, and the similarity of leg motor neurones in digging and some walking species (Faulkes and Paul, 1997*a*) supports this contention. Candidate antecedent behaviour patterns in a non-digging sand crab ancestor include waving (Pasztor and Clarac, 1983), swimming (Hartnoll, 1970; Spirito, 1972) and walking (reviewed in Evoy and Ayers, 1982; Clarac, 1984).

Waving (Pasztor and Clarac, 1983) is an unlikely homologue to digging for several reasons. First, the forward and backward leg movements during waving are strictly metachronal and unilateral, which digging leg movements are not. Second, only the thoracic–coxal joint is moved during waving, whereas all joints are moved during digging. Third, waving occurs when legs are unloaded, whereas the legs are loaded during digging. Fourth, waving is slow and digging is not.

A few brachyuran crabs can swim with their thoracic legs (Hartnoll, 1970; Spirito, 1972), and *B. occidentalis* (Paul, 1981*a*) and *L. californica* (Z. Faulkes and D. H. Paul, personal observations) also swim using a combination of rowing movements of the legs and tailflipping. It might be argued that digging evolved from swimming, but considering that most adult decapods swim by swimmeret beating or tailflipping (Hessler, 1981; Sillar and Heitler, 1985; Wilson and Paul, 1987) and that no other known anomuran swims by leg rowing, it is more likely that the use of the legs in swimming albuneids is a secondary adaptation derived from digging, and not the reverse.

Digging is most likely to have evolved from walking, and the data on interleg coordination during swimming and digging are generally compatible with such a hypothesis. First, in the albuneids, the ipsilateral leg coordination in sea water is generally similar to a walking gait; that legs 2 and 4 tend to move forward together is reminiscent of an alternating tripod gait. Alternating tetrapod or tripod gaits (where each leg has a phase of approximately 0.5 with its ipsilateral neighbour) have been described in several walking species (e.g. Barnes, 1975; Clarac, 1984; Evoy and Ayers, 1982; Herreid and Full, 1986; Z. Faulkes and D. H. Paul, personal observations of *M. quadrispina*). Although the phase of legs 2 and 3 is not approximately 0.5, as it would be in a true alternating tetrapod or alternating tripod gait,

stepping patterns in walking decapods are also frequently metachronal (e.g. Sleinis and Silvey, 1980) or intermediate between alternating tripod and metachronal, particularly when individuals are moving freely (Barnes, 1975; Macmillan, 1975; Jamon and Clarac, 1995). A second similarity between digging and walking is that the coupling of ipsilateral limbs is stronger than bilateral coupling in sand crabs, as appears to be generally true in arthropods (Cruse, 1990; Jamon and Clarac, 1995). This is shown by the changes in coordination of the bilateral legs in the transition from swimming to digging (i.e. the albuneid gait switch and the loss of bilateral synchrony in legs 4 in *E. analoga*), whereas the phase of the ipsilateral legs remains approximately the same. Third, the bilateral legs of sand crabs usually alternate, as occurs in most other arthropods during walking (Cruse, 1990; Jamon and Clarac, 1995; Müller and Cruse, 1991). There are cases where the bilateral legs move synchronously: the albuneids switch gait when digging, and legs 4 in *E. analoga* move synchronously at high frequencies. In freely walking crayfish, legs 4 also switch between bilateral alternation and bilateral synchrony (Jamon and Clarac, 1995) but, in contrast to the single gait switch in sand crabs, there can be reversals between the two modes during a single walking sequence.

Backward walking is the obvious candidate homologue of digging simply because the body is displaced backwards in both types of behaviour. The putative evolutionary relationship between backward digging and walking may be more complicated than a simple transformation of backward walking into digging, however. Sand crabs only dig backwards, but walking decapods use different patterns of interjoint coordination to move in different directions (Ayers and Clarac, 1978). For an animal heading in one direction, the movements of walking legs tend to be more similar than are the movements of sand crab digging legs (e.g. leg 4 compared with legs 2 and 3), which suggests that the motor patterns of different digging legs could have different evolutionary origins. Hypotheses concerning the possible homology of digging and walking are examined elsewhere (Faulkes, 1996; Faulkes and Paul, 1995, 1997*b*; Z. Faulkes and D. H. Paul, in preparation).

Sensory input

During walking, sensory inputs from the proximal joints (Klärner and Barnes, 1986; Sillar *et al.* 1986, 1987) and the tip of the leg (Müller and Clarac, 1990*a*,*b*) are important cues mediating the timing of stepping. Because the legs of sand crabs move through a substratum, however, it seems unlikely that sensory signals from the leg tip are used as cues to mediate the precise timing of digging leg movements, since there is no moment when dactyl afferents would receive a distinct, phasic signal. It is more probable that tactile input from the many leg hairs acts as a 'primer,' facilitating activity in the nervous system generally. In *E. analoga*, touching the legs, particularly the tips of leg 4, often initiates digging, and electrical stimulation of the distal leg nerve *in vitro* augments tonic activity in the terminal abdomen ganglion for relatively long periods (D. H. Paul, unpublished observations).

Sensory input could be important in coordinating aspects of

digging leg movements, such as the transition from power to return stroke of legs 2 and 3 (similar cases are reviewed in Pearson, 1993). In leg 2, a possible homologue to the thoracic–coxal chordatonal organ (TCCO) in crayfish (Skorupski *et al.* 1992) is an especially good candidate, because the TCCO responds to leg promotion, which is the movement in which the sand crab leg experiences the most drag. During 'fictive walking' in crayfish, the TCCO mediates an assistance reflex in promotor motor neurones (Skorupski *et al.* 1992). The much greater variability of the movements of leg 4 in all three sand crab species suggests that the movements of this leg are more heavily dependent on sensory feedback than the movements of legs 2 and 3, although it is unclear what the relevant sensory input for leg 4 may be.

The gait switch of *B. occidentalis* and *L. californica* may be triggered by load on the legs, since these species do not move their legs in bilateral synchrony when held in sea water or at the start of a digging sequence. Rapid phase transitions similar to the albuneid gait switch have been observed in other situations (e.g. tetrapod gaits, Alexander, 1989; human finger movements, Kelso, 1984; Kelso and Scholz, 1985; spiders switching from walking to swimming, Barnes and Barth, 1991). Unlike the albuneid gait switch, most of these occur as movement frequency increases. Nevertheless, the load on the legs will be greater during digging than when they are moving in sea water, so the motor output to the legs should be more strongly activated despite the lower frequency of leg movements. In crayfish, an increased load on the legs (by adding weight to the back of the animal) makes the legs less likely to move in bilateral synchrony, not more likely (Clarac and Barnes, 1985), but load on the digging legs of sand crabs, particularly legs 2 and 3, impedes promotion of the thorax–coxa joint, whereas load on the back of a palinuran makes depression of the coxa–basis joint (lifting the body) more difficult. A better analogue to the situation of the sand crab would be to increase the resistance on a treadmill on which a macruran decapod was walking backwards. To our knowledge, that experiment has not been performed in any studies of decapods walking on treadmills (e.g. Barnes, 1977; Chasserat and Clarac, 1983; Clarac, 1984; Clarac and Barnes, 1985; Clarac and Chasserat, 1983).

References

Alexander, R. McN. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.

Ayers, J. and Clarac, F. (1978). Neuromuscular strategies underlying different behavioral acts in a multifunctional crustacean leg joint. *J. comp. Physiol.* A **128**, 81–94.

Ayers, J. L. and Davis, W. J. (1977). Neuronal control of locomotion in the lobster, *Homarus americanus*. I. Motor programs for forward and backward walking. *J. comp. Physiol.* A **115**, 1–27.

Barnes, W. J. P. (1975). Leg co-ordination during walking in the crab, *Uca pugnax. J. comp. Physiol.* **95**, 237–256.

Barnes, W. J. P. (1977). Proprioceptive influences on motor output during walking in the crayfish. *J. Physiol., Paris* **73**, 543–564.

Barnes, W. J. P. and Barth, F. G. (1991). Sensory control of locomotor mode in semi-aquatic spiders. In *Locomotor Neural Mechanisms in Arthropods and Vertebrates* (ed. D. M. Armstrong and B. M. H. Bush), pp. 105–106. Manchester: Manchester University Press.

Bowerman, R. F. and Larimer, J. L. (1974). Command fibres in the circumoesophageal connectives of crayfish. II. Phasic fibres. *J. exp. Biol.* **60**, 119–134.

Bowman, T. E. and Abele, L. G. (1982). Classification of the recent Crustacea. In *The Biology of Crustacea*, vol. 1, *Systematics, the Fossil Record and Biogeography* (ed. L. G. Abele; ed.-in-chief D. H. Bliss), pp. 1–27. New York: Academic Press.

Burrows, M. and Hoyle, G. (1973). The mechanism of rapid running in the ghost crab *Ocypode ceratophthalma. J. exp. Biol.* **58**, 327–349.

Chasserat, C. and Clarac, F. (1983). Quantitative analysis of walking in a decapod crustacean, the rock lobster *Jasus lalandii*. II. Spatial and temporal regulation of stepping in driven walking. *J. exp. Biol.* **107**, 219–243.

Clarac, F. (1977). Motor coordination in crustacean limbs. In *Identified Neurons and Behavior of Arthropods* (ed. G. Hoyle), pp. 167–186. New York: Plenum Press.

Clarac, F. (1984). Spatial and temporal co-ordination during walking in Crustacea. *Trends Neurosci.* **7**, 293–298.

Clarac, F. and Barnes, W. J. P. (1985). Peripheral influences on the coordination of the legs during walking in decapod crustaceans. In *Coordination of Motor Behaviour* (ed. B. M. H. Bush and F. Clarac), pp. 249–269. Cambridge: Cambridge University Press.

Clarac, F. and Chasserat, C. (1983). Quantitative analysis of walking in a decapod crustacean, the rock lobster *Jasus lalandii*. I. Comparative study of free and driven walking. *J. exp. Biol.* **107**, 189–217.

Clarac, F., Libersat, F., Pflüger, H. J. and Rathmayer, W. (1987). Motor pattern analysis in the shore crab (*Carcinus maenas*) walking freely in water and on land. *J. exp. Biol.* **133**, 395–414.

Cruse, H. (1990). What mechanisms coordinate leg movement in walking arthropods? *Trends Neurosci.* **13**, 15–21.

Daumer, K., Jander, R. and Waterman, T. H. (1963). Orientation of the ghost-crab *Ocypode* in polarized light. *Z. vergl. Physiol.* **47**, 56–76.

Efford, I. E. (1969). *Leucolepidopa sunda* gen. nov., sp. nov. (Decapoda: Albuneidae), a new Indo-Pacific sand crab. *Breviora* **318**, 1–9.

Eshkol, N. (1980). *50 Lessons by Dr. Moshe Feldenkrais*. Tel-Aviv: The Movement Notation Society.

Evoy, W. H. and Ayers, J. (1982). Locomotion and control of limb movements. In *The Biology of Crustacea*, vol. 4, *Neural Integration and Behavior* (ed. D. C. Sandeman and H. L. Atwood; ed.-in-chief D. H. Bliss), pp. 61–105. New York: Academic Press.

Evoy, W. H. and Fourtner, C. R. (1973). Crustacean walking. In *Control of Posture and Locomotion (Advances in Behavioural*

Biology, vol. 7) (ed. R. B. Stein, K. G. Pearson, R. S. Smith and J. B. Redford), pp. 477–493. New York: Plenum Press.

FAULKES, Z. (1996). Sand crab digging: the neuroethology and evolution of a 'new' behaviour. PhD dissertation, Department of Biology, University of Victoria, Victoria, Canada.

FAULKES, Z. AND PAUL, D. H. (1995). Sand crab digging: an evolutionary mosaic of disparate ancestral locomotor modules? In *Nervous Systems and Behaviour. Proceedings of the Fourth International Congress of Neuroethology* (ed. M. Burrows, T. Matheson, P. L. Newland and H. Schuppe), pp. 483. Stuttgart: Georg Thieme Verlag.

FAULKES, Z. AND PAUL, D. H. (1997a). A map of the distal leg motor neurons in four decapod crustacean species. *Brain Behav. Evol.* (in press).

FAULKES, Z. AND PAUL, D. H. (1997b). Coordination between the legs and tail during digging and swimming in sand crabs. *J. comp. Physiol.* A (in press).

FAULKES, Z., PAUL, D. H. AND PELLIS, S. M. (1991). Digging by the sand crab *Blepharipoda occidentalis. Soc. Neurosci. Abstr.* **17**, 1245.

HAIG, J. (1974). A review of the Australian crabs of family Hippidae (Crustacea, Decapoda, Anomura). *Mem. Queensland Mus.* **17**, 175–189.

HAIG, J. AND ABBOTT, D. P. (1980). Macrura and Anomura: The ghost shrimps, hermit crabs and allies. In *Intertidal Invertebrates of California* (ed. R. H. Morris, D. P. Abbott and E. C. Haderlie), pp. 577–593. Stanford: Stanford University Press.

HARTNOLL, R. G. (1970). Swimming in the dromiid crab (*Homola barbata*). *Anim. Behav.* **18**, 588–591.

HERREID, C. F. AND FULL, R. J. (1986). Locomotion of hermit crabs (*Coenobita compressus*) on beach and treadmill. *J. exp. Biol.* **120**, 283–296.

HESSLER, R. R. (1981). Evolution of arthropod locomotion: a crustacean model. In *Locomotion and Energetics in Arthopods* (ed. C. F. Herreid and C. R. Fourtner), pp. 9–30. New York: Plenum Press.

JAMON, M. AND CLARAC, F. (1995). Locomotor patterns in freely moving crayfish (*Procambarus clarkii*). *J. exp. Biol.* **198**, 683–700.

KELSO, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *Am. J. Physiol.* **246** , R1000–R1004.

KELSO, J. A. S. AND SCHOLZ, J. P. (1985). Cooperative phenomena in biological motion. In *Complex Systems – Operational Approaches in Neurobiology, Physics and Computers* (ed. H. Haken), pp. 124–149. Berlin: Springer-Verlag.

KLÄRNER, D. AND BARNES, W. J. P. (1986). The cuticular stress detector (CSD2) of the crayfish. II. Activity during walking and influences on leg coordination. *J. exp. Biol.* **122**, 161–175.

LARIMER, J. L. (1976). Command interneurons and locomotor behavior in crustaceans. In *Neural Control of Locomotion* (ed. R. M. Herman, S. Grillner, P. S. G. Stein and D. G. Stuart), pp. 293–326. New York: Plenum Press.

MACMILLAN, D. L. (1975). A physiological analysis of walking in the American lobster (*Homarus americanus*). *Phil. Trans. R. Soc. Lond.* **270**, 1–59.

MÜLLER, U. AND CLARAC, F. (1990a). Dactyl sensory influences on rock lobster locomotion. I. Intrasegmental and intersegmental leg reflexes during standing and walking. *J. exp. Biol.* **148**, 89–112.

MÜLLER, U. AND CLARAC, F. (1990b). Dactyl sensory influences on rock lobster locomotion. II. Role in interleg coordination. *J. exp. Biol.* **148**, 113–128.

MÜLLER, U. AND CRUSE, H. (1991). The contralateral coordination of walking legs in the crayfish *Astacus leptodactylus. Biol. Cybernetics* **64**, 429–436.

PASZTOR, V. M. AND CLARAC, F. (1983). An analysis of waving behaviour: an alternative motor programme for the thoracic appendages of decapod Crustacea. *J. exp. Biol.* **102**, 59–77.

PAUL, D. H. (1971). Swimming behavior of the sand crab, *Emerita analoga* (Crustacea, Anomura). I. Analysis of the uropod stroke. *Z. vergl. Physiol.* **75**, 233–258.

PAUL, D. H. (1981a). Homologies between body movements and muscular contractions in the locomotion of two decapods of different families. *J. exp. Biol.* **94**, 159–168.

PAUL, D. H. (1981b). Homologies between neuromuscular systems serving different functions in two decapods of different families. *J. exp. Biol.* **94**, 169–187.

PAUL, D. H. (1991). Pedigrees of neurobehavioral circuits: tracing the evolution of novel behaviors by comparing motor patterns, muscles and neurons in members of related taxa. *Brain Behav. Evol.* **38**, 226–239.

PAUL, D. H. AND FAULKES, Z. (1995). Coupling of different locomotor rhythms in sand crabs. In *Nervous Systems and Behaviour. Proceedings of the Fourth International Congress of Neuroethology* (ed. M. Burrows, T. Matheson, P. L. Newland and H. Schuppe), pp. 464. Stuttgart: Georg Thieme Verlag.

PEARSON, K. G. (1993). Common principles of motor control in vertebrates and invertebrates. *A. Rev. Neurosci.* **16**, 265–197.

POND, C. M. (1975). The role of the 'walking legs' in aquatic and terrestrial locomotion of the crayfish *Austropotamobius pallipes* (Lereboullet). *J. exp. Biol.* **62**, 447–454.

SCHRAM, F. R. (1986). *Crustacea.* New York: Oxford University Press.

SCHRAM, F. R., FELDMAN, R. M. AND COPELAND, M. J. (1978). The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. *J. Paleontol.* **52**, 1375–1387.

SILLAR, K. T., CLARAC, F. AND BUSH, B. M. H. (1987). Intersegmental coordination of central neural oscillators for rhythmic movements of the walking legs in crayfish, *Pacifastacus leniusculus. J. exp. Biol.* **131**, 245–264.

SILLAR, K. T. AND HEITLER, W. J. (1985). The neural basis of escape swimming behaviour in the squat lobster *Galathea strigosa.* I. Absence of cord giant axons and anatomy of motor neurones involved in swimming. *J. exp. Biol.* **117**, 251–269.

SILLAR, K. T., SKORUPSKI, P., ELSON, R. C. AND BUSH, B. M. H. (1986). Two identified afferent neurones entrain a central locomotor rhythm generator. *Nature* **323**, 440–443.

SKORUPSKI, P., RAWAT, B. M. AND BUSH, B. M. H. (1992). Heterogeneity and central modulation of feedback reflexes in crayfish motor pool. *J. Neurophysiol.* **67**, 648–679.

SLEINIS, S. AND SILVEY, G. E. (1980). Locomotion in a forward walking crab. *J. comp. Physiol.* **136**, 301–312.

SNODGRASS, R. E. (1952). The sand crab *Emerita talpoida* (Say) and some of its relatives. *Smithson. misc. Collns* **117**, 1–34.

SPIRITO, C. P. (1972). An analysis of swimming behavior in the portunid crab *Callinectes sapidus. Mar. Behav. Physiol.* **1**, 261–276.

TRUEMAN, E. R. (1970). The mechanism of burrowing of the mole crab, *Emerita. J. exp. Biol.* **53**, 701–710.

WILSON, L. J. AND PAUL, D. H. (1987). Tailflipping of *Munida quadrispina* (Galatheidae): conservation of behavior and underlying musculature with loss of anterior contralateral flexor motoneurons and motor giant. *J. comp. Physiol.* A **161**, 881–890.