

HOMOLOGIES BETWEEN BODY MOVEMENTS AND MUSCULAR CONTRACTIONS IN THE LOCOMOTION OF TWO DECAPODS OF DIFFERENT FAMILIES

By DOROTHY HAYMAN PAUL

*Hopkins Marine Station, Pacific Grove, CA**

SUMMARY

The movements performed by the abdomen and tailfan during tailflipping in the sand crab *Blepharipoda occidentalis* (family Albuneidae) are described from an analysis of high-speed cinematic film (Figs. 1, 2, 3 A), and compared with component movements in the swimming-by-uropod-beating behaviour of the sand crab *Emerita analoga* (Family Hippidae) (Fig. 3 B; Paul, 1971). The most striking qualitative difference is the absence of uropod retraction and protraction in *Blepharipoda*. Comparisons of electromyograms recorded from some of the principal muscles involved in these overtly very different behaviour patterns reveal that homologous muscles in the two sand crabs tend to be activated at comparable phase positions (Table 1). Tailflipping and uropod beating in the two crabs appear to be homologous, and to have been derived from ancestral macruran tailflipping.

INTRODUCTION

The neural networks that have been most thoroughly investigated mediate simple behavioural sequences, such as feeding and escaping, that are fundamental to an animal's existence, and probably phylogenetically ancient (e.g. Getting *et al.* 1980; Kaneko, Merickel & Kater, 1978; Krasne & Wine, 1977; Selverston, 1977; Silvey & Wilson, 1979; Stent *et al.* 1978). These studies have focused almost exclusively on *how* nervous systems are organized. The neural substrates of overtly simple patterns of behaviour that are products of recent evolution might carry with them legacies of ancestral organization that could reveal their phyletic origin. Comparison of the neural substrates for new and ancestral behaviour might allow one to distinguish between evolutionarily conservative and evolutionarily plastic features and thereby provide insights into *why* nervous systems are organized in the ways we observe.

An example of such a 'new' behaviour is the mode of swimming exhibited by the sand crab, *Emerita*, a member of the family Hippidae, one of two sand-crab families that appeared from macruran ancestry only in recent geologic time (Moore, 1969). The abdomen of *Emerita* remains folded upon itself while the uropods, appendages of abdominal segment 6, perform rapid sculling motions behind the body that propel the animal backward (Paul, 1971 a). A related sand crab, *Blepharipoda*, belonging to the other sand-crab family, Albuneidae, does not beat its uropods; instead, it exhibits

* Present address: Department of Biology, University of Victoria, Victoria, B.C. V8W 2Y2.

locomotory behaviour that resembles macruran tailflipping, in which the uropod movements are closely linked to those of the abdomen as a whole (this study). Furthermore, despite the characteristic sand crab shape and orientation of *Blepharipoda*'s uropods, the neuromuscular arrangement in its tailfan resembles that of macrurans, such as crayfish, almost as much as it does that of *Emerita* (Paul, 1981). Thus *Blepharipoda* may serve as an intermediate in a comparison of neural control systems serving the tailfans of *Emerita* and macrurans that are themselves too dissimilar for direct comparison (Paul, 1971*b*). Identification of homologies between tailfan muscles in the two sand crabs and morphological comparisons of the motoneurons innervating most of these muscles are reported elsewhere (Paul, 1981). In this paper the temporal organization of tailflipping in *Blepharipoda* is described and compared to that of swimming-by-uropod-beating in *Emerita*. The similarities suggest that the neural bases of these two locomotory patterns share a common evolutionary origin.

MATERIALS AND METHODS

Sand crabs, *Blepharipoda occidentalis* (Randall) and *Emerita analoga* (Stimpson), were collected at low tide from Jetty Road Beach, Moss Landing, Monterey Bay, California, and kept in running sea-water aquaria at Hopkins Marine Station.

Blepharipoda were hand-held in the middle of an aquarium while their tailflipping was filmed from the side and from the rear on Tri-X reversal film (Kodak 7278) at 200 frames/s. The HyCam 16 mm high-speed motion-picture camera was equipped with a 1:2/55 Super Takumar lens (Redlake Corp., Santa Clara, CA). Illumination was provided by four 650 W flood-lamps; films were developed with a 1½- or 2-stop push. A 100 Hz timing light made dots along one edge of the film for accurate time calibration. In order to analyse the movements of the abdomen and tailfan, the films were projected frame-by-frame and the outlines of structures of interest traced on thin white paper. The tracings of consecutive frames were superimposed to measure the excursions of the various structures with the aid of an engineer's protractor. The data are presented as degrees of arc through which a structure moved as a function of time with one exception: the excursions of abdomen and telson filmed from the rear are in linear dimensions (see Fig. 3*a*). Three *Blepharipoda* were filmed tailflipping; their behaviour appeared identical to that of other individuals that were observed tailflipping in their home aquarium.

In order to monitor activation of muscles monopolar electrodes of 0.004 in. diameter copper wire, insulated except at the tip were inserted through small holes in the exoskeleton after coating the surrounding area with a thin layer of Eastman 910 adhesive. The electrodes were then sealed in place with Stickiwax (Adax Electronics, Eugene, OR). Two or three electrodes were implanted in each animal. The electrode wires, soldered to flexible, shielded leads, were fixed to the mid-dorsal carapace by Eastman 910 adhesive and Stickiwax. The leads were connected to the inputs of Tektronix 122 preamplifiers and the signals displayed on a Tektronix 565 Oscilloscope and photographed with a Kymograph camera.

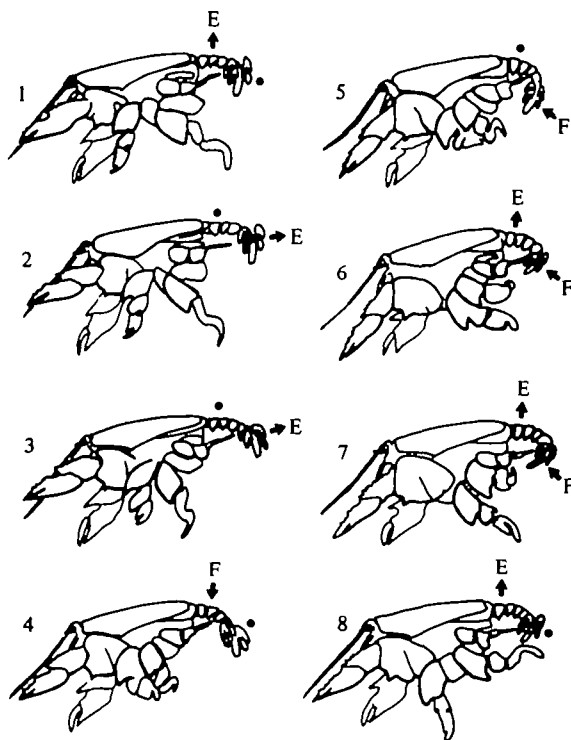


Fig. 1. *Blepharipoda* tailflip. Frames from a movie selected to illustrate the principal stages in the movements of the abdomen and tailfan. Tailflipping starts with extension of the abdomen (1) followed by extension of the tailfan (2, 3), the latter often overlapping the onset of abdomen flexion (4). Flexion of the tailfan lags flexion of the abdomen and continues while the abdomen is re-extending (5–7). E, Extension; F, flexion; black dots, transition periods when adjacent structures are not actively moving. Time between frames is not uniform: see Figs. 2 and 3A for time course of tailflips.

RESULTS

Cinematic analysis of Blepharipoda tailflip

The abdomen of *Blepharipoda* is usually somewhat flexed so that tailflipping generally begins with straightening to full extension followed by flexions and re-extensions, repeated rhythmically usually at about 2–4 Hz. I have observed episodes of rhythmic tailflipping comprising from a few to more than 20 cycles performed by unrestrained and by hand-held animals. *Blepharipoda* unrestrained in an aquarium rhythmically flap the abdomen both while digging into sand and while swimming. Small animals often swim dorsal side up, but large crabs usually swim up-side down. Progression is slow, most of the motive force apparently being provided by 'rowing' motions of the powerful, flattened second and third pereopods. These legs are specialized for burrowing backward into sand but also serve, incidentally it seems, for swimming.

Tailflips of the three *Blepharipoda* filmed were similar in form and in relative timing of the component movements. The tracings in Fig. 1 are selected to show the sequential positions assumed by the abdomen and tailfan during the course of one tailflip, viewed from the side. Observe that there is a phase lag between the movements of the

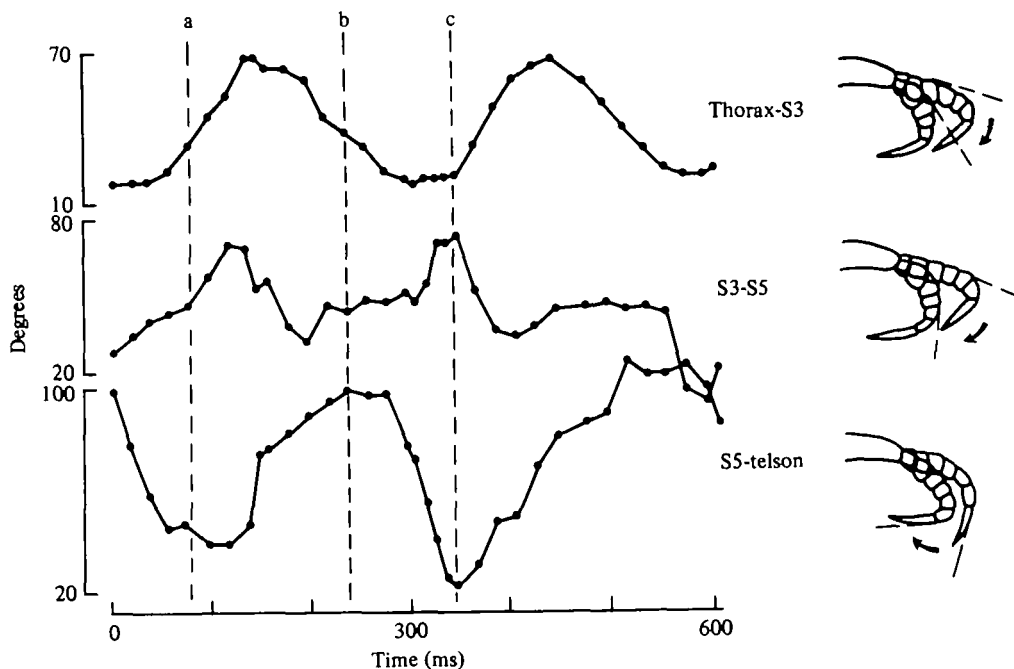


Fig. 2. Temporal analysis of two *Blepharipoda* tailflips filmed from the left. The arcs (in degrees) through which the anterior (thorax-S₃), the middle (S₃-S₅), and the terminal (S₅-telson) regions of the abdomen move are plotted against time, flexion upward. Note that flexion of the tailfan (S₅-telson) begins when the anterior abdomen is fully flexed (to the right of dashed line a) and reaches its full extent when the anterior abdomen is re-extending (dashed line b).

posterior and the anterior abdominal segments such that the tailfan (S₆ and telson) is most tightly folded when the anterior segments have completed their flexion and are beginning to re-extend (tracings 6-7, Fig. 1). The tailfan remains cupped through most of the extension phase and is itself extended, with uropods abducted (see below), just prior to the next flexion of the anterior abdomen (tracings 2 and 3, Fig. 1). The uropods move rather little out of the horizontal plane of the sixth segment; they are abducted and perhaps slightly elevated just prior to flexion of the anterior abdomen, when the tailfan is extended (see Fig. 3A), thus increasing the area of the 'tail' as it is swept downward. Toward the end of tailfan flexion and during its re-extension the uropod is depressed and adducted. Movements of the exopodite and endopodite relative to the propodite are barely discernible.

The temporal phasing of the movements is shown graphically in Figs. 2 and 3A. The power phase of each movement is plotted with a positive slope. When viewed from the side the large-amplitude flexions of the anterior and posterior segments are evident, the S₅-telson flexion beginning when the anterior abdomen is nearly fully flexed (to the right of line a, Fig. 2) and continuing during extension of the anterior segments (line b, Fig. 2). The uropods are best observed from the rear (Fig. 3A). The principal components of the tailflip sequence occur in the following order. Uropod abduction, beginning when the abdomen is extended (left, Fig. 3A), is completed during the early stages of flexion of the anterior abdomen; the latter is essential

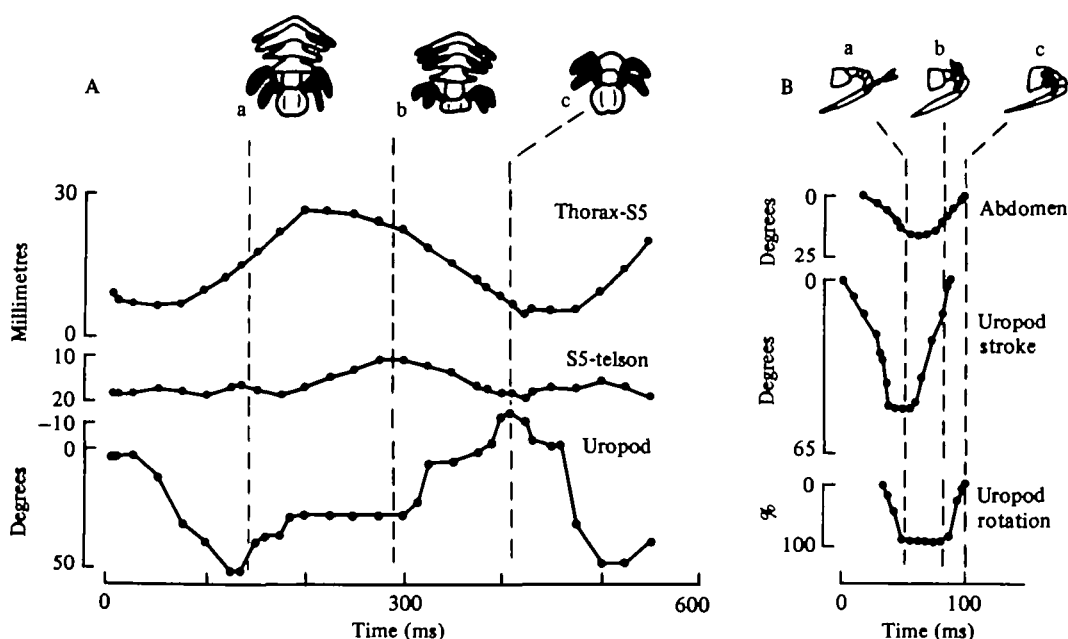


Fig. 3(A) Temporal analysis of a *Blepharipoda* tailflip viewed from the rear. Top trace is comparable to the upper two traces and the middle trace is comparable to the bottom trace in Fig. 2. The bottom trace plots the abduction of the uropod (downward) which is completed during flexion of thorax-S5; the uropod is depressed during abdominal flexion and adducted (upward) as extension is completed (line c). Dashed lines a-c correspond to the dashed lines in Fig. 2. Note that uropod abduction precedes abdomen flexion.

(B) Temporal analysis of uropod beating in *Emerita* (data from an earlier study replotted on same time base as data for *Blepharipoda*). Top trace: small extension and flexion (upward) of the anterior abdomen; middle trace: excursion of uropod, power-stroke upward; bottom trace: rotation of uropod, pronation upward. The forward-directed power stroke (tracings a-c) provides the motive force for swimming. The tracings a-c are from roughly comparable stages of the two behaviour patterns. The black structures are the uropods. At time a, *Blepharipoda*'s tailfan is extended with the uropods abducted and *Emerita*'s anterior abdomen is straightened and the uropods retracted and supinated. At time b, flexion of the entire abdomen of *Blepharipoda* is completed and depression-adduction of the uropods starting; at the comparable stage (b) in *Emerita*'s swim-stroke the power-stroke of the uropod is nearing completion and the abdomen is resuming its tightly folded posture. By time c, the tailfan (including uropods) power stroke phase is completed in both crabs and *Blepharipoda* has begun the next cycle by extending the abdomen; *Emerita* pauses between uropod strokes with the abdomen tightly folded (see Paul, 1971a).

completed by the time that tailfan (S5-telson) flexion begins (Figs. 2, 3A). Uropod adduction-depression accompanies re-extension of the tailfan, both completed by line c, Fig. 3A. The stationary phase in the trace of uropod movement may be artifactual, the result of viewing the angle between uropod and segment 6 from a changing perspective during flexion of S5-telson (Fig. 3A).

Electromyography of Blepharipoda tailflipping and Emerita swimming-by-uropod-beating

The function of muscles may be inferred from the positions of their origins and insertions (Table 1), but direct evidence of their role in a particular behaviour requires demonstration of their activation in appropriate patterns during execution of that

behaviour. Figure 4 includes representative electromyograms recorded from several of the muscles implicated in tailflipping of *Blepharipoda* (A–D) and from homologous muscles in *Emerita* during swimming by-uropod-beating (E–F).

Alternating activity in extensors of segment 4 (E4) and flexors of segment 3 (F3) in *Blepharipoda* were recorded differentially on the top trace of Fig. 4A. The lower traces shows activity in the dorso-medial muscle, DM, that depresses the uropod during the flexion (power) phase of the tailflip, when the flexors are active; these DM bursts are prolonged when *Blepharipoda* tailflips vigorously (Fig. 4B). The DM bursts occur during activity of the extensor muscles in the fifth and sixth segments, E5 and E6, that extend the tailfan (Fig. 4C, D), as expected from the behaviour (Figs. 1, 3A). The two heads of DM are activated concurrently (Fig. 4C), although some preliminary data on their innervation suggest that all motoneurons may not be shared by both heads (unpublished observation). Depression of the uropods occurs throughout the entire flexion phase (anterior and posterior segments), presumably to counteract any tendency of the uropod to be deflected dorsally during the downward thrust of the abdomen, and during re-extension to reduce surface area and, therefore, resistance in the recovery phase (from prior to a to c, Fig. 3A). The medial muscle (rotator) in the sixth segment presumably contributes to this function, but its electromyographic activity has not been monitored (but see legend of Fig. 4B).

The return-stroke muscle (RS) in *Blepharipoda* is positioned so that it should elevate the uropod; it is so small and delicate, however, that it is difficult both to record electromyograms from it and to imagine that its mechanical effect on the massive appendage could be particularly noticeable. In fact, skeletal constraints severely limit uropod movements above the horizontal plane (Paul, 1981). An electrode implanted over *Blepharipoda's* RS muscle records activity prior to and also during DM bursts (Fig. 4D). The large potentials coinciding with the latter may not have emanated from RS: after recording the electromyograms, the nerve branch containing return-stroke axons was exposed for electrical stimulation with a suction electrode while continuing to record from the muscle with the electromyogram lead; short trains of pulses delivered at different frequencies to the return-stroke nerve could mimic the small amplitude activity but not the larger potentials seen in the second trace of Fig. 4D.

Blepharipoda lacks a homologue of *Emerita's* massive power-stroke muscle (Paul, 1981), one of the two principal muscles driving the uropod during swimming-by-uropod-beating (Paul, 1971, 1976). The functional analogue is the massive DM, that depresses the uropod during the power (flexion) phase of the tailflip (see above). In *Emerita* DM is much smaller than in *Blepharipoda*, relative to the other telson muscles, but its action in depressing and pronating the uropod is approximately the same (Paul, 1981) as is its electromyogram (Fig. 4). The second traces in Fig. 4E and F illustrate that the peak activity of *Emerita's* DM coincides with bursts in the power-stroke muscle, but that it becomes active somewhat earlier, during RS activity. This is similar to the pattern recorded from DM and RS in *Blepharipoda*. This early activation of DM in *Emerita* may help stabilize the uropod in its extended positions, since the insertion of the powerful RS is lateral to the pivotal point of the appendage (see Figs. 1A, 4, Paul, 1981). Like its more massive homologue in *Blepharipoda*

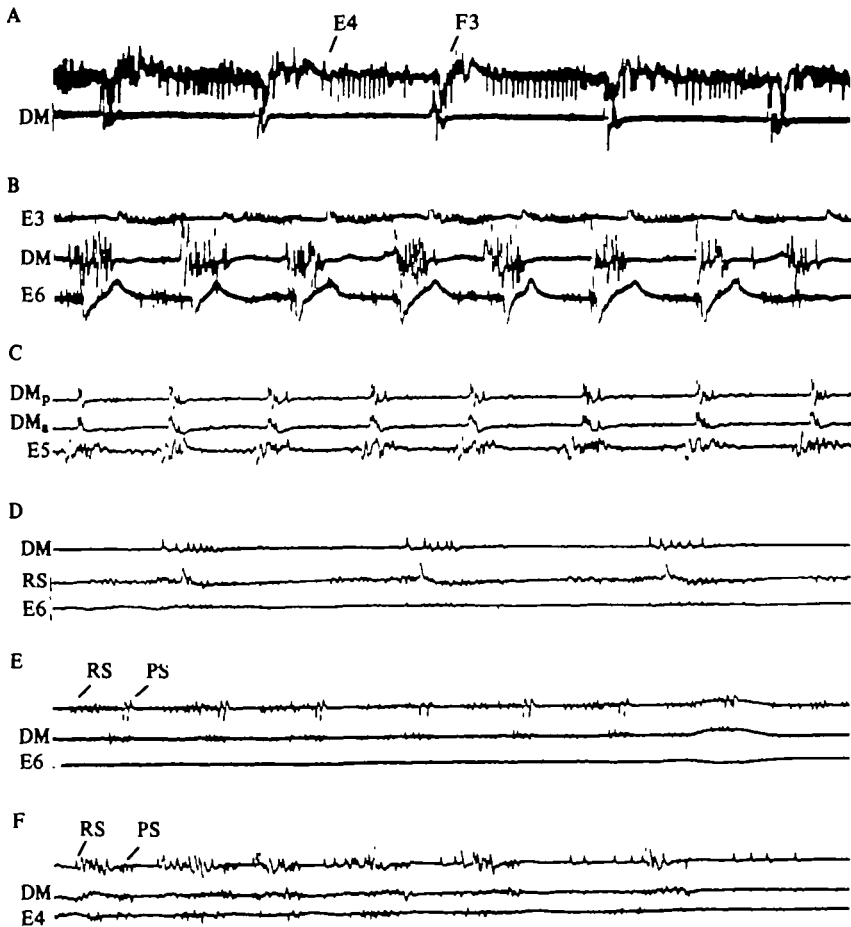


Fig. 4. Electromyograms of some muscles active during tailflipping of *Blepharipoda* (4 individuals, A–D) and swimming of *Emerita* (2 individuals, E and F). (A) Top trace: differential recordings from extensors in segment 4 (E4) and flexors in segment 3 (F3). Bottom trace: Dorsomedial muscle, posterior head (DM) bursts occur during the flexor bursts as predicted from analysis of the movements (time a, b, Fig. 3A). (B) Extensor bursts in segment 6 (E6, bottom trace) lag extensor bursts in segment 3 (E3, top trace) (see Fig. 2). The large potentials in the E6 trace coincident with DM activity are probably from the medial rotator muscles (MR) which arise near the dorsal midline of segment 6, close against E6. MR appears to be a synergist of DM (Table 1; Paul, 1981). It is not possible to tell from this record whether DM bursts overlap E6 activity. (C) Electromyograms from the posterior head (top trace) and anterior head (middle trace) of DM are concurrent and occur during activity of extensors in segment 5 (E5, bottom trace) (b–c, Fig. 3A). (D). The beginning of activity in the return-stroke muscle, RS (uropod elevator, Paul, 1981) alternates with DM bursts (compare with *Emerita*'s RS and PS bursting in E, F). (E, F). Top traces: Differential recordings from return-stroke, RS (retractor) and power-stroke, PS (protractor) muscles (see Paul, 1971, 1976, for detailed analysis of this motor pattern). Middle traces: DM's activity begins before and continues during PS bursts (in F there was some cross talk from RS muscle). The PS muscle, along with DM, is the functional analogue of *Blepharipoda*'s DM muscle. (E) Bottom trace: No activity has been recorded from extensors in segment 6 (E6) during swimming, as expected since the telson does not extend (Fig. 3B). (F) Bottom trace: Extensors in segment 4 (E4) become active concurrently with RS (Fig. 3B). Time scale: A, C–F, 0.5 s; B, 1 s.

Table 1. *Components of Blepharipoda tailflip and Emerita swim cycle*

(The principal muscles involved in each movement are given in parentheses. The movements are listed in order of decreasing prominence.)

<i>Blepharipoda</i>	<i>Emerita</i>
	Recovery phase
Abdomen extension	Uropod retraction (RS) and supination (LR)
Uropod abduction and slight elevation (LR, RS)	Anterior abdomen extension, slight
	Power phase
Abdomen flexion	Uropod protraction (PS, VM) anterior abdomen flexion, slight
Telson flexion (VM)	Uropod pronation and depression (DM, VM, MR)
Uropod depression and adduction (DM, MR)	

Abbreviations of muscles: DM, dorsomedial; MR, medial rotator; LR, lateral rotator; PS, power-stroke; RS, return-stroke; VM, ventromedial (see Paul, 1981).

Emerita's DM is active during extensor activity (Fig. 4, compare C and F). The fourth segment extensor activity in *Emerita* may stiffen the abdomen during the forceful uropod stroke, since the abdomen does not actually unfold (Fig. 3 B).

Comparison of Blepharipoda tailflip and swim cycle of Emerita

Emerita's swimming-by-uropod-beating has been described in detail earlier (Paul, 1971a, 1976). The following summary covers those features of this behaviour that are pertinent to the comparison with *Blepharipoda's* tailflipping. At rest, the uropods of *Emerita* are protracted along the sides of the tightly folded abdomen. Contractions of the return-stroke and power-stroke muscles are responsible for the uropod stroke and, therefore provide the motive force for swimming (Fig. 4 E, F; Paul, 1971a, 1976). Swimming starts with retraction of the uropods out of the horizontal plane of segment 6 (the return stroke) so that they extend rearward (Fig. 3 B, a). Toward the end of the return stroke, the uropod supinates and is abducted, the rami unfold, and during vigorous swimming the anterior segments of the abdomen straighten very slightly (compare a and c, 3 B; Paul, 1971a). This small extension of the anterior abdomen elevates the retracted uropods behind the crab. During the power phase, three overlapping movements begin in rapid succession: uropod protraction (power stroke); anterior abdomen flexion: uropod pronation-adduction.

The stages of the tailflip of *Blepharipoda* and one swim cycle of *Emerita* are juxtaposed in Table 1. Abdominal extensions and flexions are presumed to be homologous in the two sand crabs [neural control systems and effectors are homologous, i.e. have common evolutionary origin (Ghiselin, 1966)]. These movements are so slight in *Emerita* that their time course is difficult to follow accurately (Paul, 1971a). The small flexion in *Emerita* appears to be relatively later in the power phase of the behaviour than the thorax-S₅ flexion in *Blepharipoda*, but the flexions between individual segments in the latter are not synchronous the length of the abdomen (see Fig. 2). The frames traced at time 'a' in Fig. 3 A and B catch the position of the

tailfan of each sand crab at the beginning of its power phase. The similar phasing of the other movements listed in Table 1 may reflect their homology since these movements are at least in part the result of activation, observed electromyographically (see above), of muscles that are homologous to each other (Paul, 1981); i.e. homology is suggested between similarly timed movements that are identified with the same muscles in the two sand crabs. Thus uropod abduction and slight elevation in *Blepharipoda* and uropod retraction (return stroke) and supination in *Emerita* are similarly phased in the two locomotory sequences (Fig. 3). *Emerita's* rapid protraction (power stroke) of the uropod (Fig. 3 B) has no counterpart in *Blepharipoda's* behaviour and *Blepharipoda* lacks a homologue of the power-stroke muscle (Paul, 1981). But the uropod power-stroke in *Emerita* (middle trace, position a-b, Fig. 3 B) may be homologous to the telson flexion part of the tailfan flexion in *Blepharipoda* (S5-telson trace, position a-b, Figs. 2, 3 A), since the muscles involved in these two movements appear to be derivatives of the same group of ancestral telson flexor muscles (Paul, 1981). The complex movement of the uropod that occurs at the culmination of each locomotory pattern, adduction-depression-pronation (c in Fig. 3 A, B; Table 1), is apparently brought about by a combination of two muscles in *Blepharipoda* and three muscles in *Emerita*: medial (rotator) muscles in the sixth segment and dorsomedial muscles in the anterior telson of each crab, and in *Emerita* the ventromedial muscles contribute to this movement as well as to the preceding protraction (power-stroke) of the uropod.

DISCUSSION

Blepharipoda and *Emerita* live in dissimilar environments and require quite different locomotory capabilities. *Blepharipoda* are subtidal scavengers, whereas *Emerita* are intertidal filter feeders. Both burrow backward into sand until only the antennae and eye stalks protrude at the surface.

Swimming is clearly not a forte of *Blepharipoda*. Nevertheless, their tailflipping behaviour may have important survival value, for these relatively sedentary crabs are vulnerable to displacement by turbulent water and by other animals. At such times tailflipping would provide a means of moving about locally over short distances until a suitable place was found to burrow.

Strong swimming, on the other hand, is the sine qua non of *Emerita's* life in the intertidal zone of exposed sandy beaches. In order to filter-feed with their antennules, *Emerita* must remain in the wash zone, just below the surface, and to do so they emerge periodically from the sand and swim up or down the beach (McGinitie, 1938).

The similarities revealed in this study between the component movements and the muscular contractions in the locomotion of the two crabs can be interpreted most parsimoniously as the result of divergent evolution from a tailflipping behaviour in an ancestral macruran. The existence of tailflipping burrowers, like *Blepharipoda*, indicates that a new mode of swimming was neither the selective factor for the evolution of the sand-crab type of tailfan, nor concomitant with it. The 'inversion' of the uropods, characteristic of sand crabs, probably offered an advantage in increased efficiency of backward burrowing into sand. However, it also set the stage for new skeletal changes, as well as muscular and neural modifications, that eventually freed

movements of the uropods in *Emerita* from those of the abdomen as a whole. *Emerita*'s novel use of the uropods, therefore, appears to be an example of 'a behaviour that developed following the evolution of new structures [the sand-crab tailfan] under new selective pressures' (taking up residence in subtidal sand) (Mayr, 1974). Only then could swimming-by-uropod-beating have developed, presumably in response to pressures to move into the intertidal zone to take up residence as filter feeders.

I thank C. Pittendrigh, Director, and S. Thompson for providing facilities at Hopkins Marine Station for this work and L. A. Miller, B. Mulloney and M. Paul for reading drafts of the manuscript. Publication costs paid by NSF grant BNS78-10516 (to B. Mulloney).

REFERENCES

- GETTING, P. A., LENNARD, P. R. & HUME, R. I. (1980). Central pattern generator mediating swimming in *Tritonia*. I. Identification and synaptic interactions. *J. Neurophysiol.* **44**, 151-164.
- GHISELIN, M. T. (1966). An application of the theory of definitions to systematic principles. *Syst. Zool.* **15**, 127-130.
- KANEKO, C. R., MERICKEL, M. & KATER, S. B. (1978). Centrally programmed feeding in *Helisoma*: identification and characteristics of an electrically coupled premotor neuron network. *Brain Res.* **146**, 1-21.
- KRASNE, F. B. & WINE, J. J. (1977). Control of crayfish escape behaviour. In *Identified Neurons and Behaviour of Arthropods* (ed. G. Hoyle), pp. 275-305. New York: Plenum Press.
- MAYR, E. (1974). Behaviour programs and evolutionary strategies. *Am. Scient.* **62**, 650-659.
- MCGINITIE, G. E. (1938). Movements and mating habits of the sand crab, *Emerita analoga*. *Am. Mid. Nat.* **19**, 471-481.
- MOORE, R. C. (ed.) (1969). *Treatise on Invertebrate Paleontology*, Vol. 2, part R, Arthropoda 4.
- PAUL, D. H. (1971a). Swimming behaviour of *Emerita analoga* (Crustacea, Anomura). I. Analysis of the uropod stroke. *Z. vergl. Physiol.* **75**, 233-258.
- PAUL, D. H. (1971b). Swimming behaviour of *Emerita analoga* (Crustacea, Anomura). II. Morphology and physiology of the uropod neuromuscular system. *Z. vergl. Physiol.* **75**, 259-285.
- PAUL, D. H. (1976). Role of proprioceptive feedback from nonspiking mechanosensory cells in the sand crab, *Emerita analoga*. *J. exp. Biol.* **65**, 243-258.
- PAUL, D. H. (1981). Homologies between neuromuscular systems serving different functions in two decapods of different families. *J. exp. Biol.* **94**, 169-187.
- SILVERSTON, A. E. (1977). Mechanisms for the production of rhythmic behaviours in crustaceans. In *Identified Neurons and Behaviour of Arthropods* (ed. G. Hoyle), pp. 209-225. New York: Plenum Press.
- SILVEY, G. E. & WILSON, I. S. (1979). Structure and function of the lateral giant neurone of the primitive crustacean *Anaspides tasmaniae*. *J. exp. Biol.* **78**, 121-136.
- STENT, G. S., KRISTAN, W. B., FRIESEN, W. O., ORT, C. H., POON, M. & CALABRESE, R. L. (1978). Neuronal generation of the leech swimming movement. *Science, N.Y.* **200**, 1348-1357.