HOMOLOGIES BETWEEN NEUROMUSCULAR SYSTEMS SERVING DIFFERENT FUNCTIONS IN TWO DECAPODS OF DIFFERENT FAMILIES

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SUMMARY

Evidence is provided for homologies between specific parts of the tailfan neuromusculatures in two sand crabs, *Emerita analoga* (family Hippidae) and *Blepharipoda occidentalis* (family Albuneidae). The gross anatomy of the tailfan, particularly of the telson, is very different in the two species, the biggest difference being the absence in *Blepharipoda* of a power-stroke muscle which in *Emerita* constitutes 50% by wet weight of the telson musculature. Homologies between motoneurones innervating telson muscles in the two crabs are established based on comparisons of their positions and central morphology. The derivation of the sand crab telson muscles and their innervation from neuromusculature in an ancestral macruran is proposed.

INTRODUCTION

Although swimming is performed in different ways by the sand crabs *Emerita* (family Hippidae) and *Blepharipoda* (family Albuneidae), the component movements have been shown to have similarities of form and phase that suggest an evolution from tailflipping in a common macruran ancestor (Paul, 1981). If the two types of swimming are homologous, then there should be homologies between the muscles and motoneurones of the tailfans in the two species, and this is examined in the current paper.

Comparison of the tailfan neuromusculature in these sand crabs is complicated because the form of the uropod's movements as well as the gross anatomies of the tailfans are quite different; and, furthermore, *Emerita* has apparently evolved two movements that are not present in *Blepharipoda*'s repertoire: the return stroke and power stroke of the uropod (Paul, 1981). However, comparison is also made easier by the relatively small number of neurones (five) that innervate the principal muscles responsible for these movements, the return-stroke and power-stroke muscles (Paul, 1971 a). The structural similarity found in this study between homologous motoneurones performing different functions in the two species suggests that morphological changes in nervous systems may be quite conservative even during diversification of neuromusculature to serve different behaviours.

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Sand crabs were collected and maintained as described elsewhere (Paul, 1981).

The articulations of the uropods were examined after the following procedure, recommended by Robert Hessler. Whole abdomens were immersed in 5% KOH and left at 55 °C for 5 days, by which time all tissue was dissolved except the exoskeleton, arthrodial membranes, and partially calcified tendons. The abdomens were then rinsed in acid-alcohol, stained in Solution 2 of Mallory's triple stain (3–4 min), transferred to 80% ethanol until appropriately destained, dehydrated in 100% ethanol, and cleared and stored in terpineol. Arthrodial membranes remain flexible and are completely transparent after this treatment, so that one can view joints and articulations 'from the inside' without the structural disturbances inherent in dissected material while manipulating appendages and body segments through their normal range of excursion.

The neuromuscular anatomy of the sixth abdominal segment and telson of *Blepharipoda* was examined mostly in ventral dissections. The innervation of particular muscles was observed repeatedly with methylene-blue staining and in some cases by recording synaptic potentials in muscle fibres with 2·7 M-KCl-filled microelectrodes following delivery of single or brief trains of electrical pulses to the nerve through a suction electrode. The neuromuscular anatomy of *Emerita* has been described in detail (Paul, 1971 a, b). All of the features important in the comparison with *Blepharipoda* have been reconfirmed in this study.

The wet weights of the muscles in the sixth abdominal segment and the telson were obtained after carefully dissecting out each muscle and blotting it to remove excess sea water. Three sets of muscles were weighed for each species. The percentage of the total weight contributed by each bilateral pair of muscles was calculated and the means and standard deviations of the three sets of percentages for each species determined.

Motoneurones were backfilled with $CoCl_2$ (Pitman, Tweedle & Cohen, 1972; Wine, Mittenthal & Kennedy, 1974). Many of these preparations were subsequently intensified with silver (Bacon & Altman, 1977). The positions and central morphologies of the filled motoneurones were examined in wholemounts, drawn with the aid of a camera lucida, and photographed. All of the motor roots discussed in this study have been backfilled in 10–30 animals with the exception of the lateral rotator nerve, which has been backfilled four times in *Blepharipoda* and three times in *Emerita*.

Articulation of the uropod (Fig. 1)

Examination of the articulation of the uropods in *Blepharipoda* and *Emerita* in undissected tailfans following the KOH treatment revealed considerable differences in skeletal structures and their arrangements in the two sand crabs. From this comparison alone one could predict the different vectors and amplitudes of uropod movement observed during swimming (Paul, 1981). Fig. 1 shows the dorsal aspect of the tailfans of *Blepharipoda* and *Emerita* (A, D) and the articulation of the right uropod viewed both from the side (C, F) and from a position within the telson from
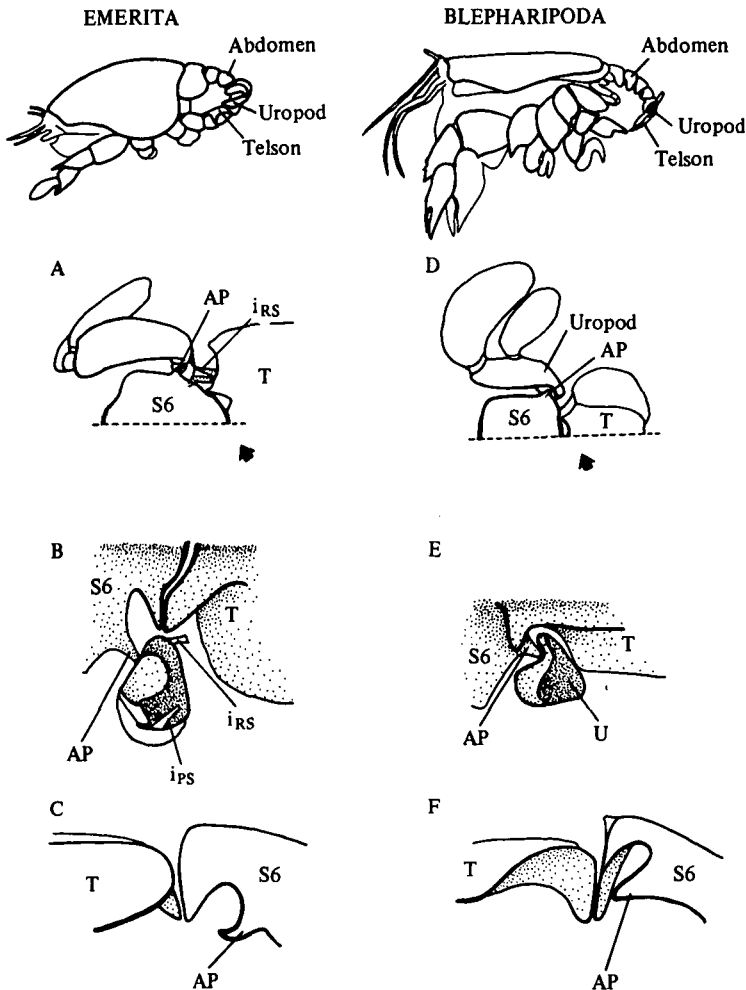
Fig. 1. Anatomy of the right uropod articulation in *Emerita*, left column (A–C), and in *Blepharipoda*, right column (D–F). (A, D) Dorsal aspect of the right half of the tailfan, anterior to the left. Only the anterior part of the telson is shown for *Emerita*. Dashed lines mark the dorsal midline. The arrows below each figure (A and D) indicate the axis along which the articulations are viewed in B and E. To go from the viewpoint of A to that of B or of D to that of E rotate the top of figure A or D 90° into the page. (B, E) articulation of the right uropod viewed from the midanterior telson; from this position the base of the uropod is seen end on. (C, F) Lateral view of the right articular process. To go from B to C (*Emerita*) or E to F *Blepharipoda* remove the uropod and rotate segment 6 and telson horizontally through 180°. AP, articular process; i_{ps} and i_{rs}, insertion of power-stroke muscle and return-stroke muscle in *Emerita*; S6, sixth abdominal segment; T, telson; U, inside uropod. Scale: 4 mm (A, D); 1·8 mm (B, C, E, F).

which the base of the uropod is seen end-on (B, E). A right-angle bend in the propodite of the uropod brings this terminal appendage forward in the sand crabs, along the side of the abdomen, rather than flanking the telson as in the conventional crustacean tailfan. Articulation of the uropod with the sixth segment is at a single point; a shallow socket in the anterior side of the uropod rides over an articular process which projects laterally and posteroventrally from the tergum. This articular process is slender in *Emerita*, and is further forward and projects further ventrally than its stubby counterpart in *Blepharipoda*; the latter is close to the inward-projecting flanges of the articulation between the sixth segment and telson (Fig. 1 B, C, E, F). The proximal portion of the propodite is also longer in *Emerita* than in *Blepharipoda* (Fig. 1 A, D). The effect of these skeletal differences is that the uropod in *Emerita* is displaced away from the body, to the side of segment 6, and is free to move in all three planes, most particularly in a sizeable arc along the antero-posterior axis. In contrast, the uropod in *Blepharipoda*, as in macrurans, is wedged in close to the body, beside the junction of segment 6 and the telson, where its movement is restricted, particularly along the long axis of the body; in these animals abduction and depression of the uropod are the principal movements that are made.

Muscles of the tailfan (Fig. 2)

An estimate of the relative importance of different muscles in the execution of particular movements may be obtained from comparisons of their relative masses. The relative wet weights of muscles in the tailfan of *Blepharipoda* and *Emerita* (excluding those muscles that are contained entirely within the uropod) are compared in Fig. 2. *Blepharipoda* are larger animals than *Emerita*: the mean carapace length of the *Blepharipoda* was 4.6 ± 0.5 cm ($n = 3$) and of the *Emerita* 2.1 ± 0.3 cm ($n = 3$). However, only 40% of the tailfan muscles is contained in the telson of *Blepharipoda* compared to 80% in *Emerita* (Fig. 2A).

The histograms in Fig. 2 B and C show the distribution of muscle mass among the muscles contained in segment 6 and the telson respectively; the terminology used is that suggested for *Emerita* (Paul, 1971 a), and is, at least provisionally, appropriate for the muscles in *Blepharipoda*. Homologous muscles in segment 6 are relatively the same size in the two species (Fig. 2 B), while homologous muscles in the telson differ greatly in size (Figs. 2 C, 4, 7, 10). The largest muscle in *Blepharipoda* is one of the smallest in *Emerita* (the dorsomedial muscle, DM), whereas the second

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Fig. 2. Comparison of muscle mass in the tailfans of *Blepharipoda* and *Emerita*. The outlines in A of the dorsal aspects of segment 6 and telson were drawn with the aid of a camera lucida; the wet weight of telson and segment 6 muscles combined is about the same for crabs of these sizes: carapace lengths, *Blepharipoda* 4·8 cm and *Emerita* 1·9 cm. Histograms are means ± standard deviations ($n = 3$) of percentages of total wet weight distributed between segment 6 (seg. 6) and telson (A) and between the individual muscles within segment 6(B) and within the telson (C). The flexors in segment 6 (T.Fl.) of *Emerita* insert on the ventral rib of this segment and, therefore, have no effect on the already fully flexed telson (see Fig. 10). LR, Lateral (rotator) muscle; MR, medial (rotator) muscle; T.Ex., telson extensors. The histograms in C are grouped according to the origins and insertions of the muscles; *Blepharipoda* has no homologue of *Emerita*'s PS muscle. Abbreviations: DM, dorsomedial muscle; LA, lateral muscle; ME, medial muscle; PS, power-stroke muscle; Q, small muscle of unknown function in *Blepharipoda* only; RS, return-stroke muscle; VM, ventromedial muscle.

(A)

(B) Muscles in sixth segment

(C) Muscles in telson
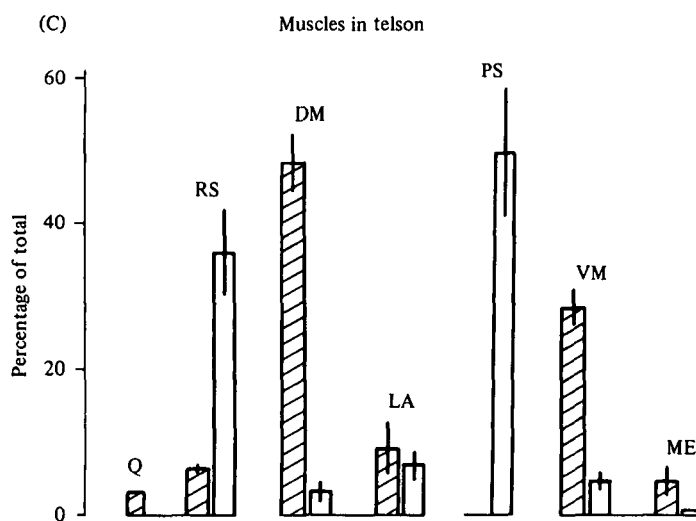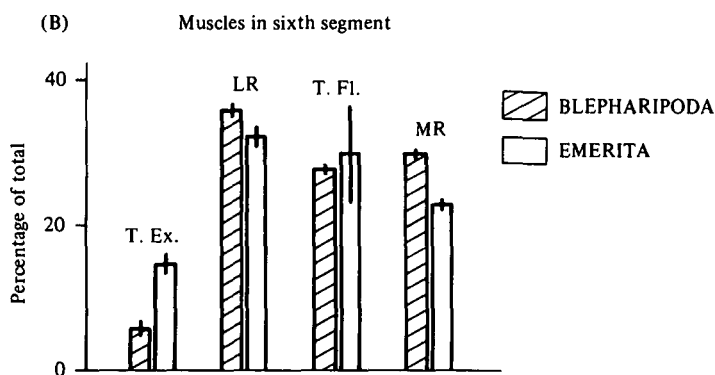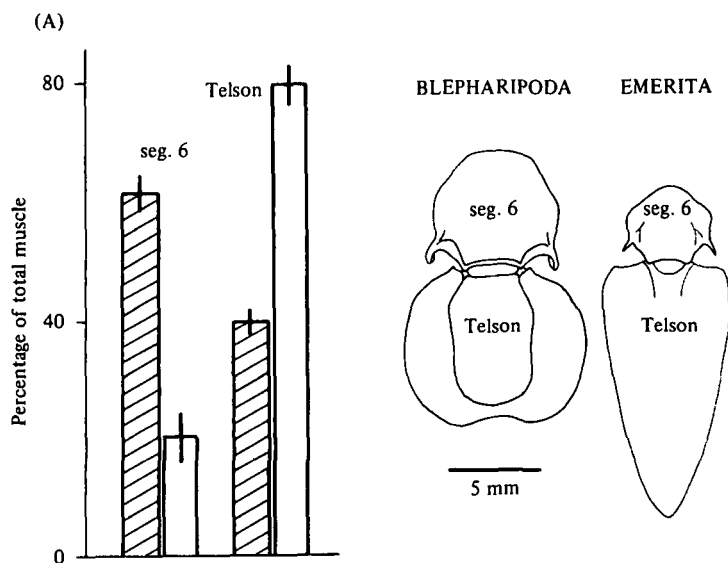
largest in *Emerita* is very small in *Blepharipoda* (the return-stroke muscle, RS) There appears to be no homologue in *Blepharipoda* for *Emerita*'s massive power-stroke muscle (PS); the functional analogue is DM (see below and Paul, 1981). Each muscle, PS in *Emerita* and DM in *Blepharipoda*, makes up about 50% of the telson muscle mass. The lateral muscles, LA, are power-stroke synergists and of relatively equal size in both animals. Thus, the muscles primarily responsible for the power phase of the uropod movement have similar weights relative to tailfan size in both species.

Innervation of homologous muscles

The external appearance of the terminal ganglion is very different in the two sand crabs (Figs. 3, 5). It is broad and flat in *Emerita* and almost cylindrical in *Blepharipoda*. In both crabs, three roots exit from the posterior face of the ganglion to innervate uropods, telson and, along with the second and third roots of ganglion 5, the sixth abdominal segment. (Intestinal nerves exit dorsally from the posterior part of the ganglion.) The branching and destination of these roots are shown in Fig. 3. Apart from the different dimensions, the major difference between the two crabs is the course of the axons innervating RS: in *Blepharipoda* they leave the large lateral root along with the LR motoneurones in the sixth segment; in *Emerita* they continue into the telson in close association with the PS and LA motoneurones, until near their destination.

Muscles with dorsal origins and insertions (Fig. 4)

The return-stroke (RS) muscle in the telson and the lateral muscle (LR) in the sixth segment are synergists in the return-stroke phase of the uropod movement. Their combined action is to abduct and perhaps slightly elevate the uropod in *Blepharipoda* and to retract it in *Emerita*. This difference is due to the different axes of RS contraction and different positions of their common insertion on the dorsal rim of the uropod, medial to the articular process in *Blepharipoda* and posterior to it in *Emerita* (Fig. 4).

The morphology of return-stroke (RS) motoneurones (Fig. 5)

Three neurones innervate RS in *Emerita* (Paul, 1971a). Their large somata (diameter $\geqslant$ 40 μm) are ventral and ipsilateral to the axons, two being in the posterior quadrant and the third near the middle of the ganglion (Fig. 5A, E). The neurite of the latter (Fig. 5A$_2$) forms an arch closer to the dorsal surface of the ganglion than do those of the pair of cells, so that its integrating segment and first-order branches extend through a more dorsal plane than the corresponding parts of the other two motoneurones. The finer dendritic branches of all three cells, however, appear to intermingle and terminate in the same regions, principally along the ipsilateral margin of the ganglion, but each also has a few processes that cross the midline in the dorsal neuropil (Fig. 5A). The posterior two RS motoneurones have nearly identical shapes and positions, including even the finer branches of their dendrites.

Three cells stain in cobalt-backfills of the RS nerve in *Blepharipoda* (Fig. 5). On
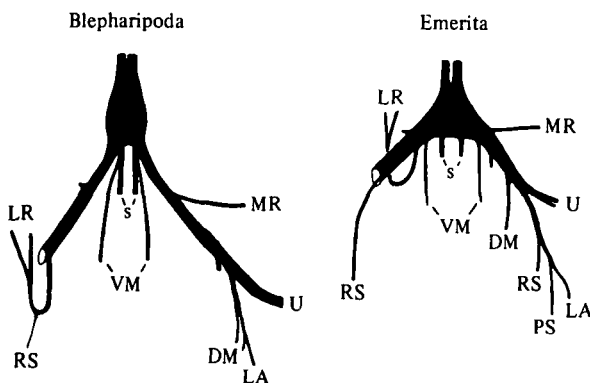
Fig. 3. The terminal ganglia, anterior toward top of page. In cross-section the ganglion is round in *Blepharipoda* and flat in *Emerita*. The schematic drawings show the course of the nerve branches innervating segment 6 and telson muscles; DM, dorsomedial muscle, LA, lateral muscle; LR, lateral 6th segment muscle; MR, medial 6th segment muscle; PS, power-stroke muscle; RS, return-stroke muscle; S, sensory nerve from posterior telson; U, uropod; VM, ventromedial muscle. Note the different courses of the RS motor axons and the absence of PS motor axons from the LA branch in *Blepharipoda*.
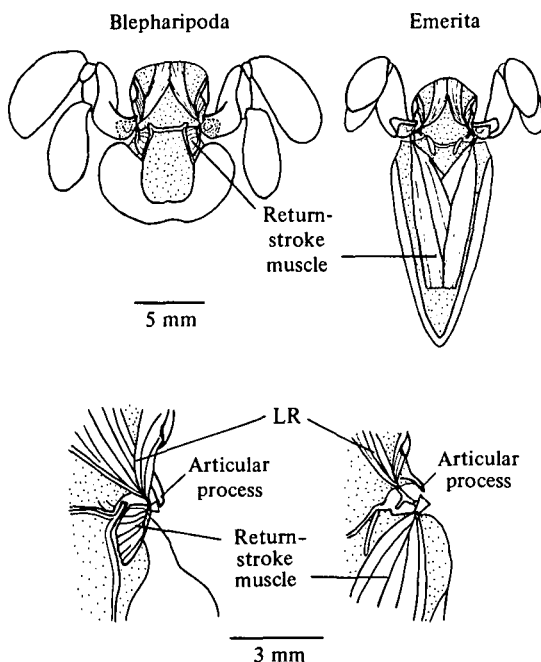

Fig. 4. Ventral view of muscles that insert dorsally on the uropod. Top: the return-stroke muscle in *Blepharipoda* (left) lies dorsally in the anterior-lateral corner of the telson whereas the return-stroke muscle in *Emerita* (right) occupies nearly the entire dorsal half of the elongate telson. Medial ventral part of uropod is cut away in *Blepharipoda* (broken lines). Bottom: detail of the common insertion of the return-stroke muscle and the lateral 6th segment muscle (LR), which in *Blepharipoda* is medial to and in *Emerita* is posterior to the articular process. See text for discussion. Inner surfaces of exoskeleton are stippled.
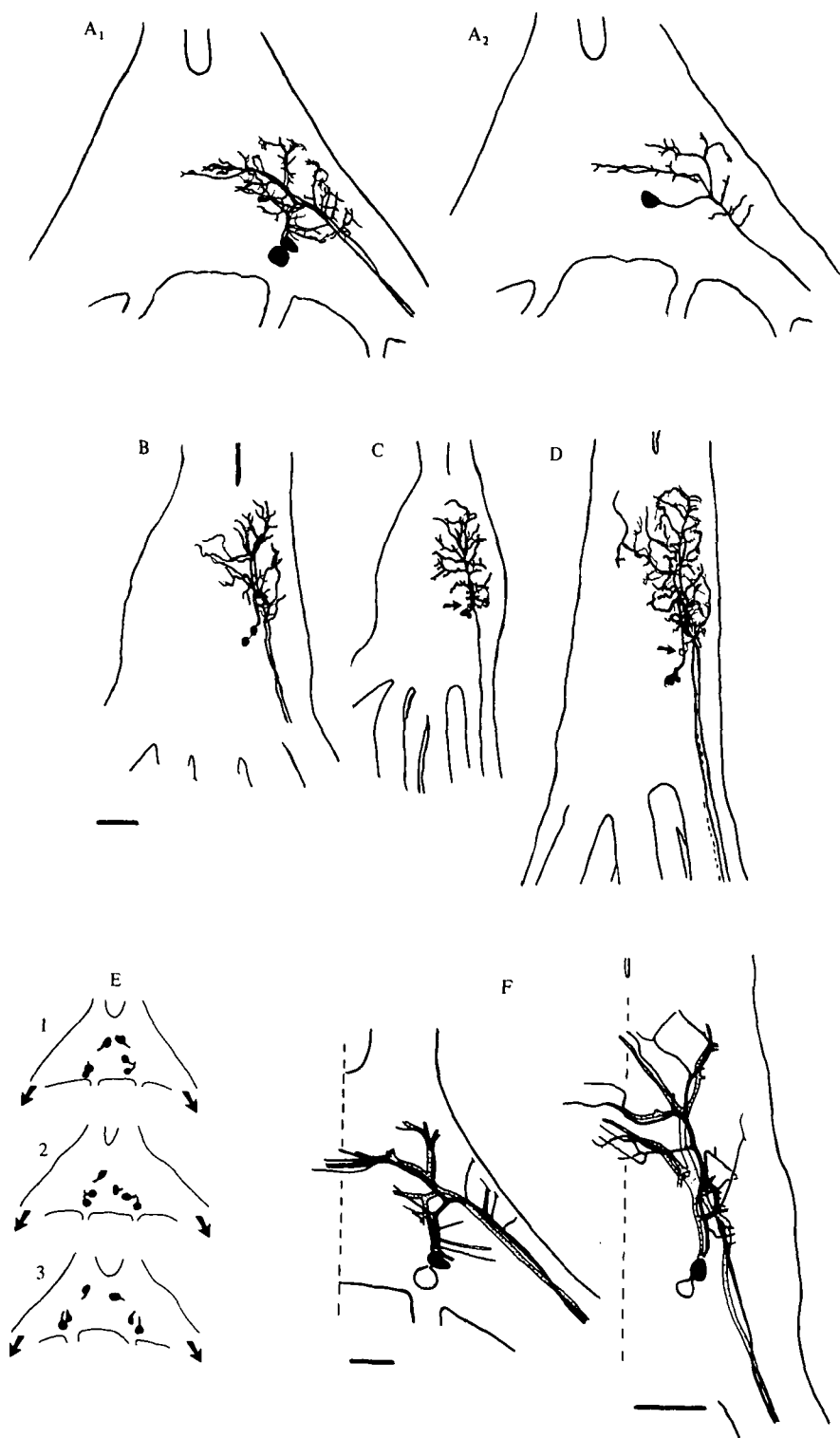
of these has not been filled completely; its axon in the root and soma are shown in Fig. 5 C, D. The other two are closely associated, synchronously branching neurones that are much smaller (soma diameters = 10–20 μm), but have a form and occupy a position in the ganglion extremely similar to the posterior pair of RS motoneurones in *Emerita* (Fig. 5 B–D, F).

In summary, the same number of RS motoneurones occurs in each crab; they occupy equivalent positions in the sixth abdominal ganglion despite the latter's very different proportions; and there is strong resemblance in shape between at least two of the three RS motoneurones in the two sand crabs. The much larger size of these neurones in *Emerita* than in *Blepharipoda* correlates well with the difference in size of the muscles they innervate (Figs. 2, 4).

Innervation of the lateral muscle in segment 6

The RS muscle is peculiar to sand crabs, being absent from macrurans (Daniel, 1931; Schmidt, 1915; unpublished observation) as well as the more distantly related penaeids (Young, 1959). How does a new muscle and its innervation evolve? The common tendon of RS and the lateral muscle, LR, in the sixth segment in both sand crabs (Fig. 4) and the close association of the innervation of these two muscles in the less specialized *Blepharipoda* (Fig. 3) suggest that RS might have been derived from sixth segment musculature, that is from part of LR in an ancestral macruran (probably equivalent to uropod remotors in modern macrura). Comparison of the central morphology of motoneurones innervating these two muscles in each crab reveals resemblances that may be indicative of ancestral affinity (Figs. 5, 6). The somata positions, neurite orientations and dendritic fields of RS and LR moto-neurones in *Emerita* are nearly identical (compare Fig. 5 A and 6 A) as are those of the RS motoneurones and the ipsilateral, posterior cluster of LR neurones in *Blepharipoda* (compare Figs. 5 B–D and 6 B, C). Note also the similarity in position and morphology of LR motoneurones in the two sand crabs. These morphological observations are consistent with the possible derivation of both sets of motoneurones from a single pool of motoneurones serving a single progenitor muscle in a common ancestor, although other explanations of these similarities are possible.

Muscles with dorsal origins and ventral insertions (Fig. 7)

These muscles are much more substantial in *Blepharipoda* than in *Emerita* (see Fig. 2C). The dorsomedial muscle (DM) has two massive heads in *Blepharipoda* with broad insertions adjacent to each other on the ventral surface of the propodite (Fig. 7). This muscle depresses the uropod and is, therefore, the major uropod

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Fig. 5. Drawings made with the aid of a camera lucida of intensified, cobalt-backfills of RS motoneurones *Emerita* (A, E) and in *Blepharipoda* (B–D), anterior toward top. A_1 and A_2 are the same preparation: the motoneurone with medial soma (A_2) was drawn separately so that the pair of cells with posterior somata (A_1) could be more easily compared with the pair of *Blepharipoda* motoneurones (B–D, F). Arrows in C and D point to the soma of the third RS motoneurone in *Blepharipoda*. See text. (E) Bilateral backfills of RS motoneurones in three *Emerita*, showing positions of somata and orientations of initial segments of the neurites. (F) Schematic comparison of the right pair of RS motoneurones in *Emerita* (left) and *Blepharipoda* (right) to show the similarity in order of their primary, secondary, and tertiary branching; broken line indicates midline. 100 μm scale lines (A–D, same scale).
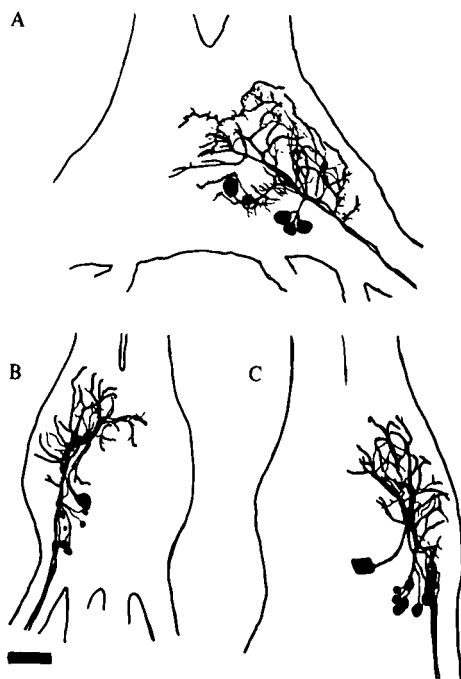
Fig. 6. Camera lucida drawings of cobalt-backfills of motoneurones innervating the LR in *Emerita* (A) and *Blepharipoda* (B, C). In C the whole branch of the first root from the ganglion 6 containing both LR and RS axons was immersed in $CoCl_2$ (see Fig. 3) so that the posterior cluster of somata include those of the RS motoneurones (compare with Fig. 5). Scale: 100 μm.
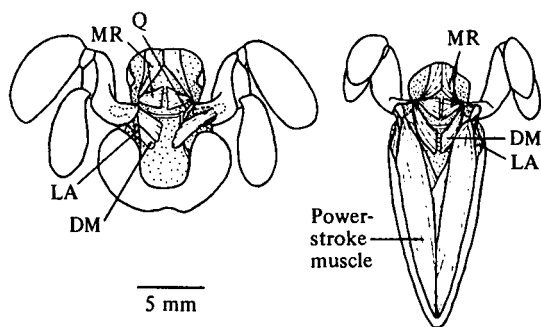

Fig. 7. Ventral view of muscles with dorsal origins that insert ventrally on the uropod. These are, in the telson: DM, dorsomedial muscle; LA, lateral muscle; and in *Emerita*, the power-stroke muscle. In segment 6: MR, medial muscle. The anterior head of the left DM in *Blepharipoda* has been removed to expose the full extent of the posterior head. Areas of ventral surface of uropods enclosed by dotted lines demark DM's insertions.

'power-stroke' muscle in the telson of *Blepharipoda*. DM in *Emerita* is rather small and inserts via a discrete tendon on the medial ventral edge of the uropod, close to the insertion of two sensory strands (Paul, 1971*b*, 1972, 1976). (The medial muscle in the sixth segment, MR, also inserts here (Fig. 7) as does VM (see below).)

The insertion of the lateral muscle, LA, is medial to the articular process in *Blepharipoda* and lateral to it in *Emerita*, so that LA would be expected to adduct as well as depress the uropod in *Blepharipoda*, but abduct and protract the uropod in *Emerita* (Fig. 7). From an evolutionary perspective it may be more accurate to include LA with those muscles that have ventral (or posterior) origins (PS, VM, ME, see next sections) because the entire group may have evolved from telson musculature innervated by the sixth root of ganglion 6 in a macruran ancestor, an hypothesis suggested by the arrangement of muscles in the crayfish (unpublished observations).

Motoneurones of the lateral and dorsomedial muscles (Fig. 8)

In *Emerita* LA and DM are innervated by widely separated branches of the large lateral root of the terminal ganglion, whereas in *Blepharipoda* the motoneurones of these muscles separate from the same branch only in close proximity to their destinations (Fig. 3). Preliminary data on positions and morphologies of these groups of moto-neurones are in partial agreement with the suggestion that motoneurones innervating homologous muscles in different species resemble each other morphologically and in their position within the central nervous system. That is, in both sand crabs the somata and integrating segments of LA motoneurones lie anterior in the ganglion; in both, long neurites extend across the midline, proliferating and terminating in anterior contralateral neuropil (Fig. 8A, B). In contrast to the similar location and branching pattern of the neurites, the positions of the somata of LA motoneurones are rather different, being anterior to the integrating segment in *Emerita* and lateral to it in *Blepharipoda*. Does this difference reflect adoption of different ways of packing homologous cells into differently proportioned ganglia during the divergent evolution of the two sand crabs or are these motoneurones not homologous to each other? Might the similarity of their dendritic morphologies be the result of convergent evolution, stemming perhaps from similarly organized functional connexions? Analysis of the properties and roles of these motoneurones may provide answers to these questions.

The axons of DM motoneurones in *Emerita* are contained in a large ventral branch of the lateral root that includes the dendrites of four non-spiking stretch receptive cells and also a number of small axons associated with the muscular strand (Paul, 1971*a*, *b*; 1972). Backfills of this nerve that exclude the nonspiking sensory cells reveal two clusters of neurones, one posterior and one central, in the ipsilateral posterior quadrant of the ganglion. The dispositions of these cells in *Emerita* is similar to those of the additional cells revealed in *Blepharipoda* when the nerve branch containing both LA and DM motoneurones is backfilled (compare C and D, Fig. 8).
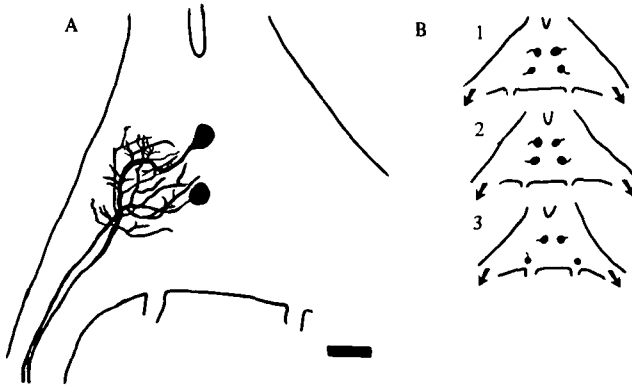
Fig. 9. Power-stroke (PS) motoneurones in *Emerita*. (A) Camera lucida drawing of intensified cobalt-backfill, scale: 100 μm. (B) Bilateral backfills of PS motoneurones in three *Emerita*, showing positions of somata and orientations of proximal neurites.

Power-stroke motoneurones in Emerita *(Fig. 9)*

The power-stroke muscle (PS) arises far posterior in the elongate telson of *Emerita* (Fig. 7; see also Fig. 2C) and is innervated by one excitatory and one inhibitory motoneurone (Paul, 1971a). Both of these are large cells with somata (diameter ≥ 40 μm) near the midline; the proximal portion of their integrating segments are transversely orientated and the branching of their neurites rather sparse (Fig. 9). Their axons exit through the large, lateral root and are adjacent to axons innervating LA until the nerve bifurcates near these muscles in the telson (Fig. 3).

Blepharipoda does not have a PS muscle and the homologue of this muscle does not appear to be the posterior head of *Blepharipoda*'s DM (Paul, 1979b). (1) The origins do not match. DM arises dorsally from the anterior-medial surface of the telson (in both crabs), whereas the origin of PS is far posterior in the telson of *Emerita*. (2) The two heads of *Blepharipoda*'s DM share their innervation in part (unpublished observation), whereas the innervations of *Emerita*'s DM and PS are completely separate (Paul, 1971a; unpublished observation). (3) Cobalt backfilling of the roots innervating telson muscles in *Blepharipoda* has revealed no motoneurones that resemble the two PS motoneurones in *Emerita*. (4) One of the many heads of flexor muscles in the telson of crayfish and spiny lobster is located in a position analogous to that of PS (unpublished observation), although the insertions are different. The innervation of the musculature in the crayfish telson has not been fully investigated (see Larimer & Kennedy, 1969), but cobalt backfills of root 6, which innervates nearly all the musculature in the telson, reveal that some of the motoneurones have large somata near the midline (M. Bastiani, personal communication; J. J. Wine, personal communication). No counterparts for all of these motoneurones send axons out of the corresponding (VM) nerve in either sand crab. If *Emerita*'s power-stroke muscle has evolved from part of the telson musculature of ancestral macrurans that was innervated by root 6, then the two PS motoneurones, with their large somata near the midline, could be homologues of crayfish root 6 motoneurones that have redirected their axons out of a different root (see discussion).
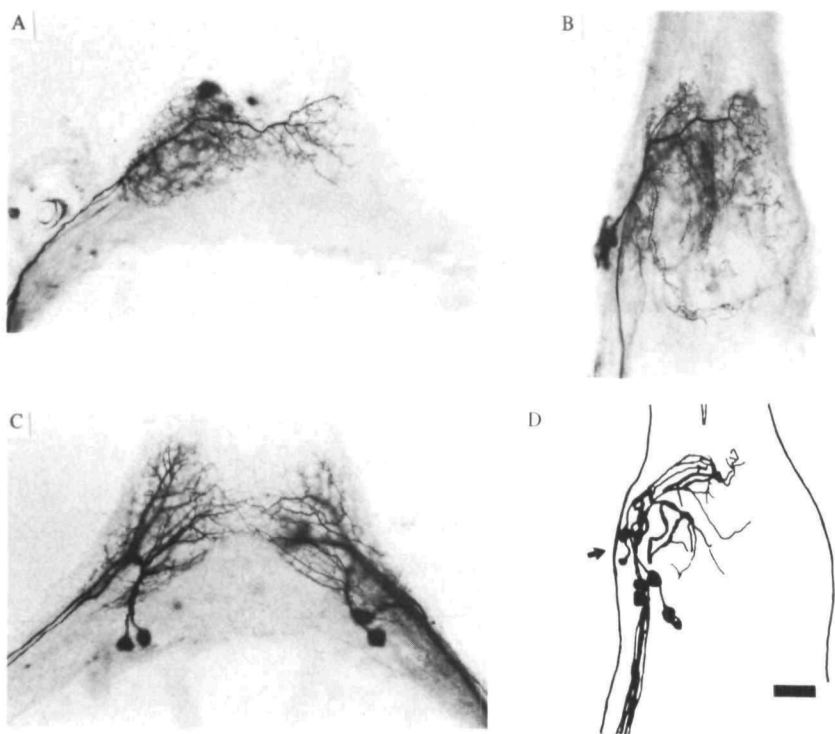
Fig. 8. Intensified, cobalt-backfills of motoneurones innervating LA in *Emerita* (A) and *Blepharipoda* (B) and DM in *Emerita*, bilateral fill (C) and *Blepharipoda* (D). In D the LA motoneurones were also filled, arrow. See text for discussion. Scale: 100 μm.
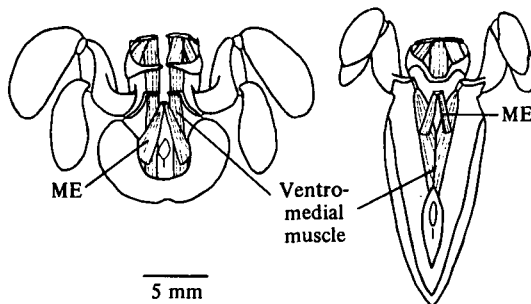
Fig. 10. Ventral view of muscles with ventral origins and ventral insertions. The ventro-medial muscle, is a telson flexor in *Blepharipoda* (left) and a uropod pronator-protractor in *Emerita* (right). ME, the medial muscles, cup the telson in *Blepharipoda*; their function in *Emerita* is unknown. Note the different insertions of the flexors in segment 6 in the two sand crabs.

Muscles with ventral origins and insertions (Fig. 10)

In *Blepharipoda* the two muscles with ventral origins and insertions are the terminal components of the flexor musculature that spans the length of the abdomen (Fig. 10). The ventromedial muscle, VM, inserts on the posterior side of a partial skeletal rib at the juncture of segment 6 and telson; the flexors in the sixth segment insert on the anterior side of this rib. The smaller medial muscles, ME, insert on the midline of the anterior telson on a small calcified area in the ventral arthrodial membrane. Both muscles arise in the posterior telson, primarily from the ventral arthrodial membrane; deeper fibres of VM arise from the posterior dorsal surface of the telson. The VM flex the telson – in conjunction with the flexors of the 6th segment; the ME cup the telson by deflecting ventrally its flexible margins.

In *Emerita*, both VM and ME arise entirely from the middle region of the ventral arthrodial membrane (Fig. 10). The ME insert on the midline in a manner similar to their homologues in *Blepharipoda*, but their function is obscure since the telson is rigid. Each VM inserts on a uropod, its tendon attaching to the medial extension of the ventral side of the propodite, directly ventral to the DM tendon (see above). The long axis of this muscle is parallel to that of PS (Figs. 7, 10), but since its insertion on the uropod is medial to the point of articulation it tends to adduct and pronate as well as protract the appendage.

Although the VM muscles perform different functions in the two sand crabs, their homology to each other and to part of the telson flexion musculature in crayfish and spiny lobster (unpublished observation) is clear from their positions relative to other anatomical features, their morphology, and their innervation. Each is innervated by the most posterior motor nerve (excluding intestinal nerves) of the terminal abdominal ganglion; and the positions and morphologies of the motoneurones are similar in the two sand crabs (below) and resemble the sixth root motoneurones in crayfish (M. Bastiani, personal communication; J. J. Wine, personal communication).

The positions and morphology of VM motoneurones of *Emerita* and *Blepharipoda* are compared in Fig. 11. The six motoneurones in *Emerita* (Paul, 1971a, 1979a) can be divided into four groups based on position of somata and orientation of principal neurites (A–D, 11A–C). The somata of the pair of 'a' motoneurones are generally far posterior in the ganglion, close to the root through which the axons exit, and their
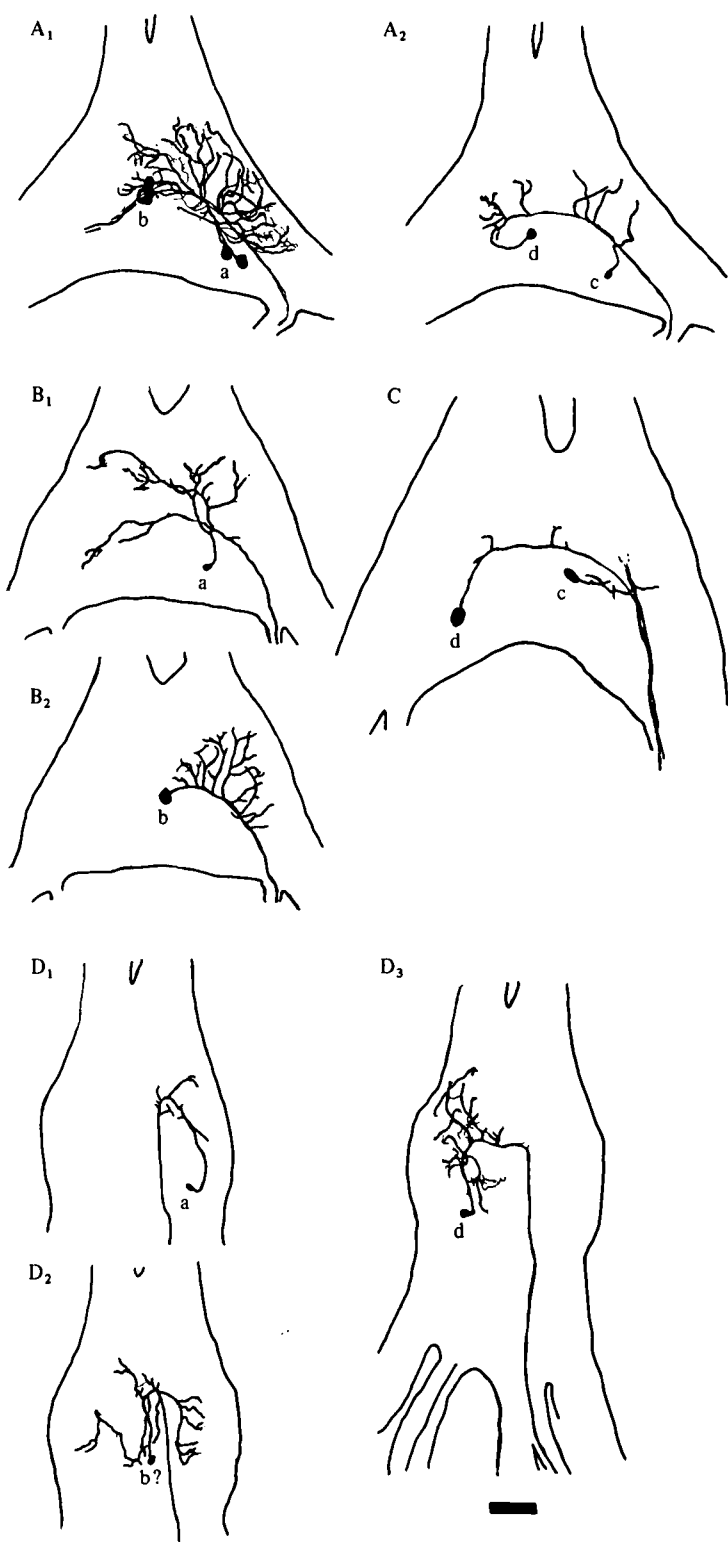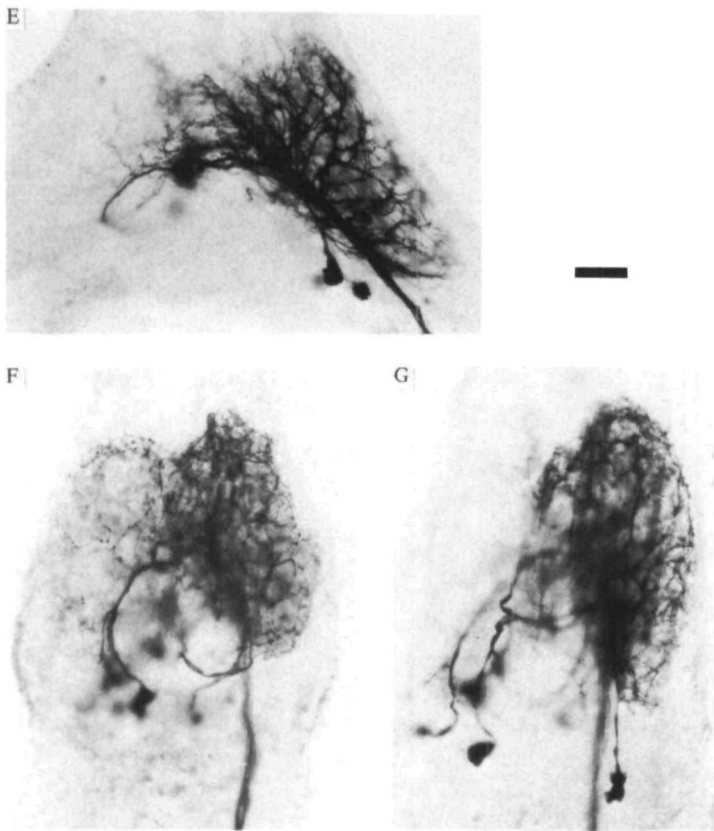
Fig. 11. Photographs and camera lucida drawings of intensified, cobalt-backfills of VM motoneurones in four *Emerita* (A–C, E) and three *Blepharipoda* (D, F, G). There are six cells in *Emerita* and at least eight cells in *Blepharipoda*. See text for discussion of cell groups (*a–d*). Scale: 100 μm.

eurites tend to be closely intertwined (A₁, B₁, E, Fig. 11); although the soma of the single 'c' neurone is often in the same region, its neurite is separate from those of the 'a' motoneurones and is distinctively shaped (Fig. 11 A₂, C). The somata of the two motoneurones in group 'b', often slightly larger than the others, lie on or just across the midline from their axons (Fig. 11, A₁, B₂). The dendritic fields of these five neurones, groups a–c, overlap extensively over most of the ipsilateral neuropil and extend to or across the midline in the anterior part of the ganglion (Fig. 11 E). The soma and proximal part of the integrating segment of the remaining cell, 'd', is contralateral to its axon (Fig. 11 A₂, C, E).

VM in *Blepharipoda* is innervated by at least eight cells that are grouped similarly to *Emerita*'s VM motoneurones (Fig. 11 D, F, G). The camera lucida drawings include only those processes that could be traced unambiguously to the somata shown, each of these motoneurones clearly having a much larger dendritic tree (Fig. 11 E–G). Although these morphological data do not allow suggestions for specific homologies between individual cells, the VM motoneurones of the two crabs are very similar to each other in position and morphology (Fig. 11 E, F). In fact, homologues of each of the six VM motoneurones in *Emerita* may not occur in *Blepharipoda*, since the muscles may be derivatives of different heads of flexion musculature in the telson, which is complex in crayfish and spiny lobster and probably was also in ancestral macrurans.

DISCUSSION

Sand-crab tailfans

The uropods of sand crabs are unlike those of other Crustacea. The propodite makes a right-angle bend so that the appendage extends forward rather than rearward from its articulation with the sixth segment as it does in other crustaceans with tailfans. *Blepharipoda*, however, uses the tailfan as an extension of the abdomen, in much the same way as do macrurans, and is able only to extend (abduct) the uropod in the horizontal plane and depress it in the vertical plane (Paul, 1981). The inventions of *Emerita* that made possible its unique swimming behaviour were the return-stroke and power-stroke movements of the uropod. In order to have evolved uropod beating, at least two additional changes had to occur in the macruran-type tailfan besides the altered shape of the uropod itself: skeletal changes to permit the large excursions of the uropod in the longitudinal axis, and the subversion, or invention, of neuromuscular systems to perform these new movements.

Mechanical constraints inherent in the uropod articulation and spatial constraints inherent in the flattened, folded abdomen were probably the major determinants leading to expansion of the telson and its musculature in *Emerita*. Movement of the uropod through a large arc necessitated elongation of the retraction and protraction muscles since their insertions had to remain close to the pivotal point of the appendage where leverage is poor. The dorso-ventral flattening of the folded abdomen in sand crabs precluded vertical orientations of the muscles such as is typical for most arthropod appendages that perform large movements, e.g. the leg muscles in the thorax or the protractor and retractor muscles of macruran swimmerets. In addition, the force of the power muscles needs to be applied predominantly in the vertical ne of the articulation, not medial to it. This excludes muscles of the sixth segment

because the articular process projects laterally (Fig. 1). The telson, on the other hand, could not only elongate but broaden so that muscles could insert on both sides of the pivotal point, resulting in the unusual mobility of the uropod.

Homology of muscles

Is it possible to identify in less-specialized tailfans muscles that might be homologous to *Emerita*'s massive RS and PS? RS is apparently a sand crab invention; it is absent from macrurans (Daniel, 1931; Schmidt, 1915; unpublished observation) as well as from penaeids (Young, 1959). PS is peculiar to *Emerita* (Hippidae). Derivation of RS from LR musculature (probably corresponding to crayfish's remotor musculature) in the sixth segment of an ancestral macruran appears to be the most likely origin of this sand crab muscle. In both sand crabs RS and LR share one insertion on the uropod. Moreover, the close affinity of these two muscles is suggested by their innervation: in *Blepharipoda*, a less-specialized animal than *Emerita*, the return-stroke muscle is innervated by a branch of the LR nerve (Fig. 3); and furthermore, in both sand crabs, not only are the somata of the RS motoneurones located among those of the LR neurones but the dendritic morphologies of all these motoneurones are very similar (Fig. 5, 6). These features are most simply explained as reflecting derivation of both neuromuscular systems from a single muscle and pool of motoneurones in an ancestral macruran (see Neuronal Homology, below). Greater conservatism in motoneurones than in either peripheral structures or central connexions has been described for several other neuromuscular systems (Bent & Chapple, 1977; Chapple, 1977b; Kaars, 1979; Kahan, 1971; Mittenthal & Wine, 1978; Wiersma & Ripley, 1952). Whatever the derivation of RS, its appearance in sand crabs was probably concomitant with the altered morphology of the uropod that presumably evolved in association with the habit of burrowing backward into sand (Paul, 1981). Passive depression of the uropods must occur during this behaviour and should be opposed in part by contraction of RS.

In the crayfish telson there are two candidates for possible homology with *Emerita*'s massive PS, for which *Blepharipoda* has no homologue. Both of the crayfish muscles appear to be innervated by root-6 motoneurones (Larimer & Kennedy, 1969; unpublished observation). However, the PS axons do not exit through the homologue of root 6, the VM nerve. In arthropods even more distantly related than sand crabs and macrurans the root through which an axon exits often appears to be the same, although most of the neurones studied have been in the middle ganglia and innervate muscles that have roughly equivalent functions in the different species (Table 5, Mittenthal & Wine, 1978). Serially homologous leg motoneurones in locusts also exit by the same root even when their physiological properties are different (Wilson, 1979a, b). But developmental studies have demonstrated considerable variability in the course axons take to make more or less invariant connexions, which suggests that the route taken by nerve fibres is less critical than the destination (Cowan, 1979). And since *Emerita* has apparently evolved a 'new' muscle and considerably rearranged the telson anatomy, it seems plausible that motor axons could have become rerouted in order to take the most economical path to their targets during development.

Muscles in the crayfish telson include a number of more or less distinct heads that insert on the stout, transverse, membrane-like tendon between segment 6 and telson (unpublished observation). The telson flexor, VM, in *Blepharipoda* probably corresponds to one of the more medial of these; the homology of *Emerita*'s VM with part of the macruran telson flexor systems was not obvious without the intermediate comparative step provided by *Blepharipoda*, since functionally it belongs to the uropod and not to the axial musculature. Whether the ventromedial muscles of the two sand crabs represent derivatives of the same or of different muscles innervated by root 6 in a macruran-like ancestor can not be distinguished without a better understanding than we have at present of the functional relationships and innervation of the various telson muscles in macrurans.

The considerable difference in ventral musculature in the telsons of the two sand crabs suggest that their families separated from a macruran-like, sand crab ancestor, already possessing RS, before the musculature in the telson had become very modified. *Emerita* rerouted parts of the ventral muscular system to serve the appendage whereas *Blepharipoda* reduced the mass but retained the flexor function of these muscles.

Neuronal homologies

Homologies have been described between neurones with qualitatively similar functions in different species (e.g. Bent & Chapple, 1977; Chapple, 1977*a*, *b*; Dickinson, 1979; Kaars, 1979; Kahan, 1971; Keyser & Lent, 1977; Mittenthal & Wine, 1978; Silvey & Wilson, 1979). In these cases morphological similarities by themselves often appear predictive of neuronal homology, although evidence for homology is the more compelling the more information is available concerning a whole constellation of additional features, such as synaptic properties, membrane characteristics, input resistance, ontogeny (see Rowe & Stone, 1977; Tyner, 1975). One might anticipate greater difficulty in distinguishing on the basis of morphology alone homologous neurones in related animals who differ in musculature or behaviour because experimental as well as descriptive data suggest that function and many aspects of neurone morphology are interdependent variables (Hoy & Moiseff, 1979; Kennedy & Davis, 1977; Kimmel, Schabtach & Kimmel, 1977; Murphy *et al.* 1975). However, in these cases, also, similarity in cell shape, in location within the central nervous system, and particularly in location of soma appear to be strong criteria for homology. Wilson & Hoyle (1979; Wilson, 1979*a*, *b*) have reported retention of 'primeval' morphologies, i.e. same position and shape of major neurites (compared with their serial homologues) of locust metathoracic leg motoneurones which have altered their functional properties. Another example is the homologous Tritocerebral Commissure Giant interneurone in a locust, a cricket, and a mantid that bear strong anatomical resemblances to each other, particularly in location of cell body, of dendritic arborizations, and of output branches (Bacon, 1980).

In the sand crabs, in addition to functional changes of some of the motoneurones themselves, the very different shapes of the terminal ganglia, into which presumably approximately the same number of cells are packed, might impose shape 'distortions' that are not directly related to either ancestry or function, thereby making more

difficult the application of morphological criteria of homology. Although this may occasionally occur, it appears not to be a general problem. Rather, the results of this comparison of motoneurones in *Emerita* and *Blepharipoda* encourage attempts to identify homologies between single neurones in members of related taxa with divergent behaviour. Whether or not the swimming patterns of the two sand crabs are homologous to each other and to macruran tailflipping, many of the individual motoneurones certainly are. Future analyses of the physiological properties of these cells in sand crabs and their putative homologues in a macruran, such as crayfish, should reveal how tailfan motoneurones have changed during the evolution of *Emerita*'s new mode of swimming. Comparison of these homologous motoneurones may suggest which features of neuronal structure and function are plastic and which relatively immutable through evolutionary diversification of behaviour.

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