

'DEEP-SEA SPIDERS' THAT WALK THROUGH THE WATER

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Summary

Deep-sea isopods of the family Munnopsidae exhibit four modes of swimming: forward striding, slow backward pedalling, fast backward pedalling and escape, the first two of which use asymmetric phases of leg movement. Instead of moving the left and right limbs (pereopods, P₂–P₇) of a segment in-phase (e.g. RP₂LP₂, RP₃LP₃, RP₄LP₄), as do most aquatic insects, leg movement is more like that of fast-walking insects, where closest synchrony occurs between

diagonal limbs (e.g. RP₂LP₃, RP₃LP₄, RP₄LP₂). This is similar to the alternating tripod gait used by many animals on land to prevent them from toppling over. It therefore seems likely that this group of isopods learned to walk before they could swim.

Key words: isopod, munnopsid, deep-sea, locomotion, gait.

Introduction

Animals that walk on two-dimensional surfaces, such as the ground or on the sea-bed, and those that move in the three-dimensional world of air or open water, face different locomotory problems. It is, therefore, a surprise to find a small group of deep-sea isopods which 'walk' through the water. These are the munnopsid isopods (Isopoda, Asellota, Janiroidea; Wolff, 1962; Wilson, 1989). In common with many deep-sea janiroid isopods, all possess two or three pairs of enormously long pereopods (P₂, P₃ and P₄) and three pairs of short paddle-shaped pereopods (P₅, P₆ and P₇) (Hessler and Strömberg, 1989; Fig. 1). These ungainly animals are frequently observed from submersibles (at depths of approximately 1000–3000 m) swimming slowly through the water. They may also be encountered 'hanging' in the water with their long legs spread radially outwards to prevent rapid sinking (Fig. 1). As a result (although they are not related to pycnogonids), they have been nicknamed 'deep-sea spiders'.

Materials and methods

Initial observations and video filming were carried out during two *Johnson Sea-Link* submersible cruises working off the coast of St Croix in the Caribbean (17° 35' 39" N, 64° 47' 53" W).

Animals were either filmed *in situ*, at a depth of approximately 1000 m, or brought to the surface and filmed in a plankton crysel aboard the mother ship, R/V *Edwin Link*. The video camera used was a JVC GR-S505 S-VHS which recorded at 50 frames s⁻¹. Pereopod movements were subsequently analyzed, using frame-by-frame analysis of the video films, with the aid of an Archimedes 440 computer and

For a digital frame store. Each stored video frame was mixed with a PAL computer-generated signal, using an Electro Craft VMC-85 mixing box, and projected onto a single screen. In this manner, a computer-cursor model isopod could be superimposed on the actual position of the animal in each frame. Leg angle relative to the body could be changed on the model isopod and this angle was automatically recorded. For striding, the cursor legs were aligned with the carpal segment of the real animal, and in pedalling the ischial segment was used. Each analysed sequence shown is the clearest representative taken from 4–6 such sequences analysed for each locomotion type.

Fig. 1 illustrates the four species of munnopsid isopod used in this study. They were *Munneurycope* sp.I (five individuals), *Munneurycope* sp.II (three individuals), *Munnopsis bathyalis* (Wolff) (six individuals) and *Munnopsis longiremis* (Richardson) (five individuals). *Munneurycope* sp.I and sp.II have not been fully taxonomically described. This is currently under way at the British Museum of Natural History.

Results

Four categories of swimming were observed; backward pedalling (fast and slow), forward striding (walking) and, when startled, escape by very rapid backward swimming. This escape response is similar to that of other crustaceans. The pedalling and striding described here are apparently unique to the munnopsids.

Pereopods used for locomotion

Munneurycope sp.I has three long pairs of pereopods (P₂, P₃

and P₄, Fig. 1), and on the propodal segments of each limb are two rows of long, closely packed setae (Figs 1–3). *Munneurycope* sp.II also has three long pereopod pairs (P₂, P₃ and P₄), but these are neither setose nor used for mid-water locomotion. *Munnopsis bathyalis* and *Munnopsis longiremis* possess only two pairs of long pereopods (P₃ and P₄), which are also non-locomotory but, when spread, seem to perform a stabilising function while swimming and to prevent the animal from sinking too fast in the water (Fig. 2). This characteristic ‘hanging’ or parachuting posture is adopted by all four species to prevent sinking (Fig. 2). The slight setation on P₃ and P₄ in *M. bathyalis* (Fig. 1) may help in this respect.

Short, paddle-shaped pereopods (P₅, P₆ and P₇) are found in all four species. The paddle blade is made up of flattened propodal and carpal segments, the margins of which are packed with plumose setae (Fig. 3).

Pereopod movement and the basic ‘stepping pattern’

Figs 4 and 5 illustrate representative results obtained from the video recordings and subsequent analysis of the moving isopods. Leg phase or ‘stepping pattern’ diagrams were plotted

from these data and are shown in Fig. 6, which also illustrates, for comparative purposes, values for a fast-walking insect from Wilson (1966).

Striding, which was only ever observed in *Munneurycope* sp.I, is forward locomotion using pereopods P₂, P₃ and P₄, the setae of which spread open and fold closed during the power and recovery strokes, respectively (Fig. 4; Wilson *et al.* 1989). The pereopods also fold and open at the propodus/carpus joint (Figs 3, 4). Fig. 4 shows a series of traced video images from a striding sequence for *Munneurycope* sp.I, demonstrating the apparently ungainly nature of this swimming pattern. Substantial muscles are only found in the ischium and basis of this leg; hence, opening and folding of both the limb and the setae are automatic.

The short pereopods P₅, P₆ and P₇ are used for backward pedalling. *M. bathyalis* and *M. longiremis* were most often observed using all six short pereopods. *Munneurycope* sp.II also locomotes by backward pedalling, but only P₅ and P₆ are utilised. During the power and recovery strokes, the limb flips opens and folds closed at the propodus/carpus and the carpus/merus joints (Fig. 3). Muscles are present in all paddle

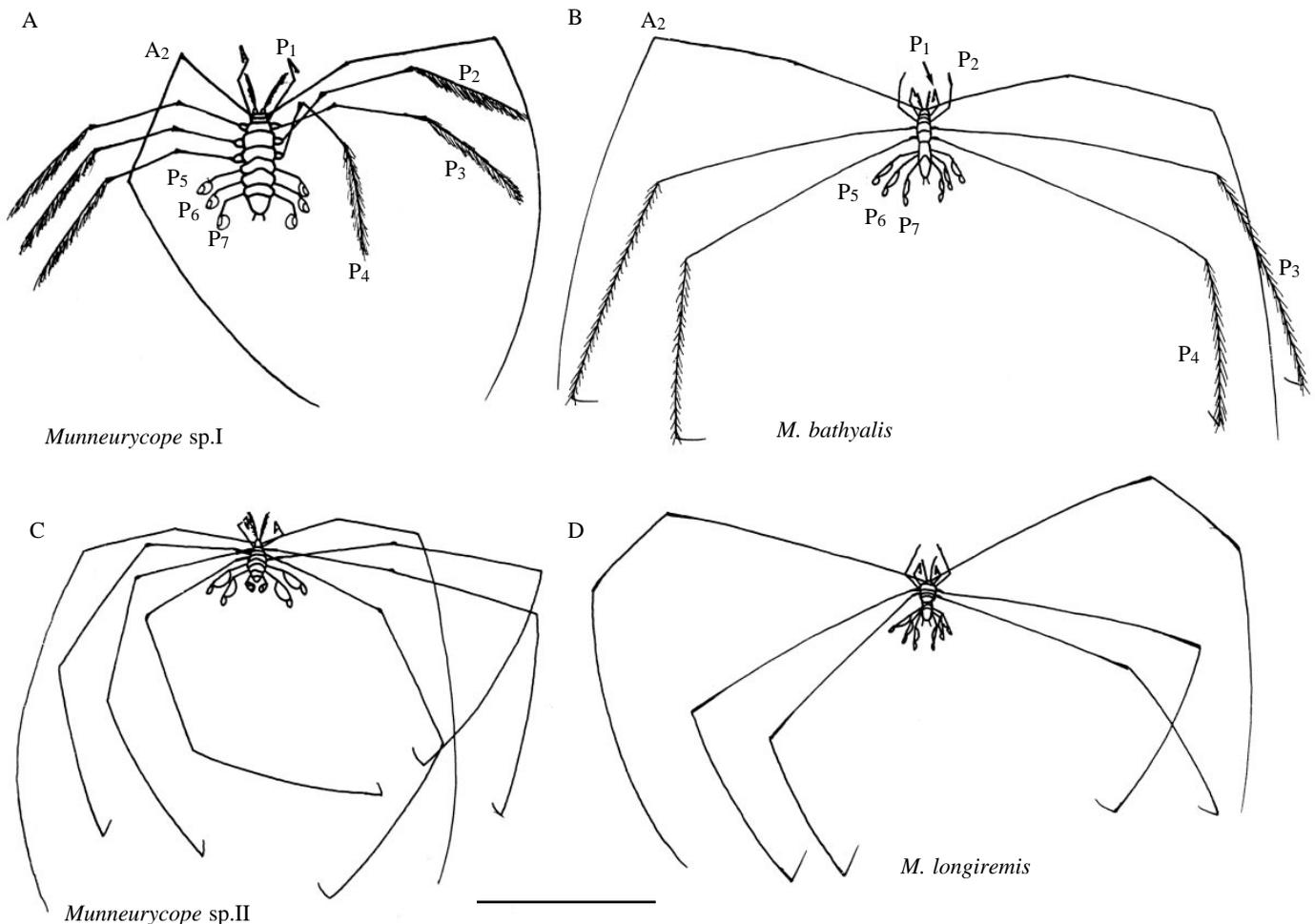


Fig. 1. The four species of munnopsid isopod used in this study. (A–D) Semi-diagrammatic representations of the body form of (A) *Munneurycope* sp.I (species not fully described), (B) *Munnopsis bathyalis* (Wolff), (C) *Munneurycope* sp.II (species not fully described) and (D) *Munnopsis longiremis* (Richardson). P₁–P₇, pereopods; A₂, antenna. Scale bar, 35 mm.

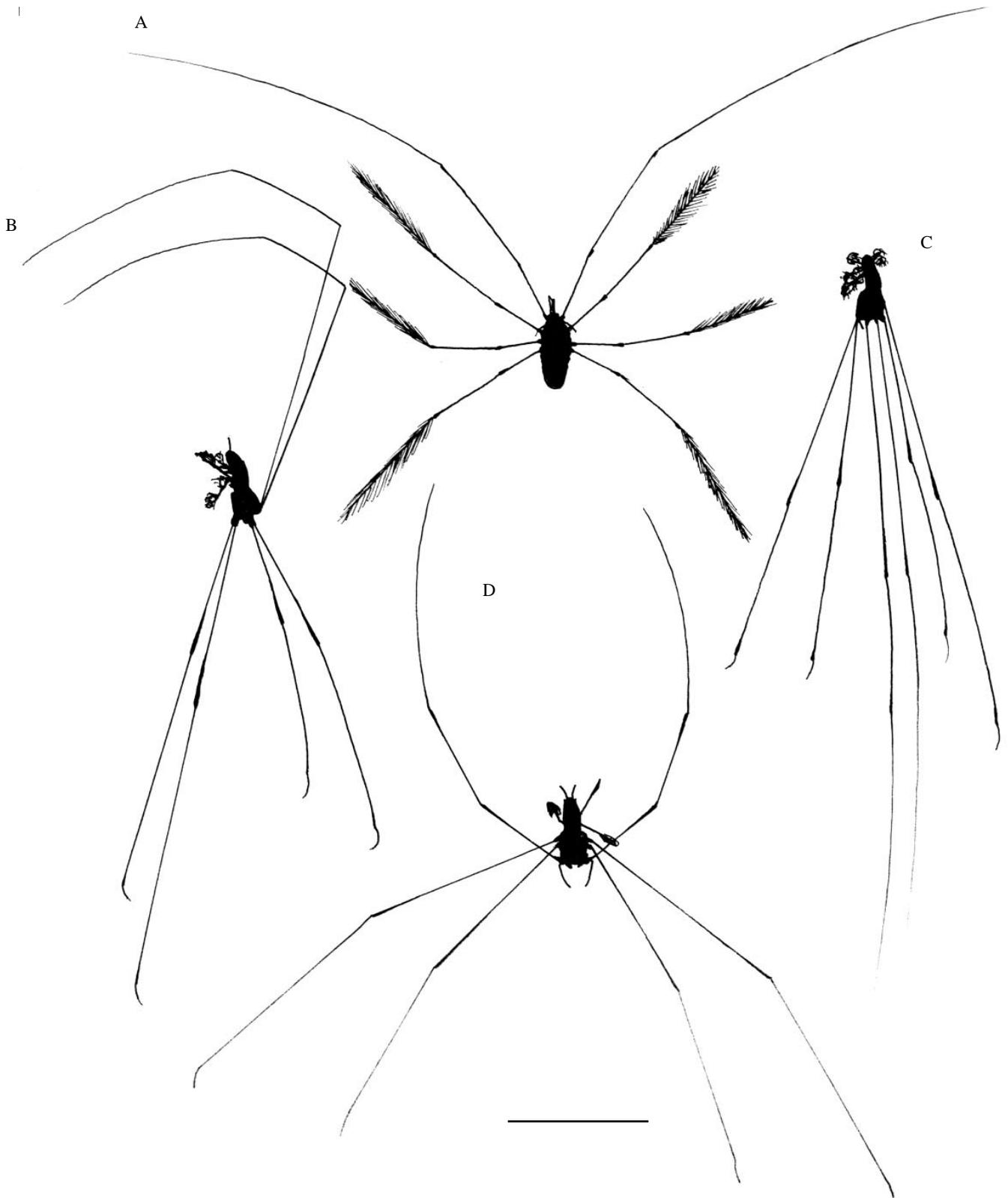


Fig. 2. (A–D) Drawings of isopods, observed and recorded on video tape from the submersible *Johnson Sea-Link II*. (A) *Munneurycope* sp.I in characteristic ‘hanging’ or parachuting pose. (B,D) *M. longiremis*, viewed laterally and dorsally during slow backward pedalling. These postures are also seen in *Munneurycope* sp.II and *M. bathyalis* during slow backward pedalling. Note the spread of the long pereopods for stabilisation and that the antennae are thrown back over the head, presumably to act as anterior sensory structures during backward locomotion. (C) Fast backward pedalling or escape in *M. longiremis*. The long pereopods and antennae are swept behind the animal during these more rapid forms of locomotion. This type of position was also adopted by the other three isopods during the escape response and by *Munneurycope* sp.II and *M. bathyalis* for fast backward pedalling. Scale bar, 25 mm.

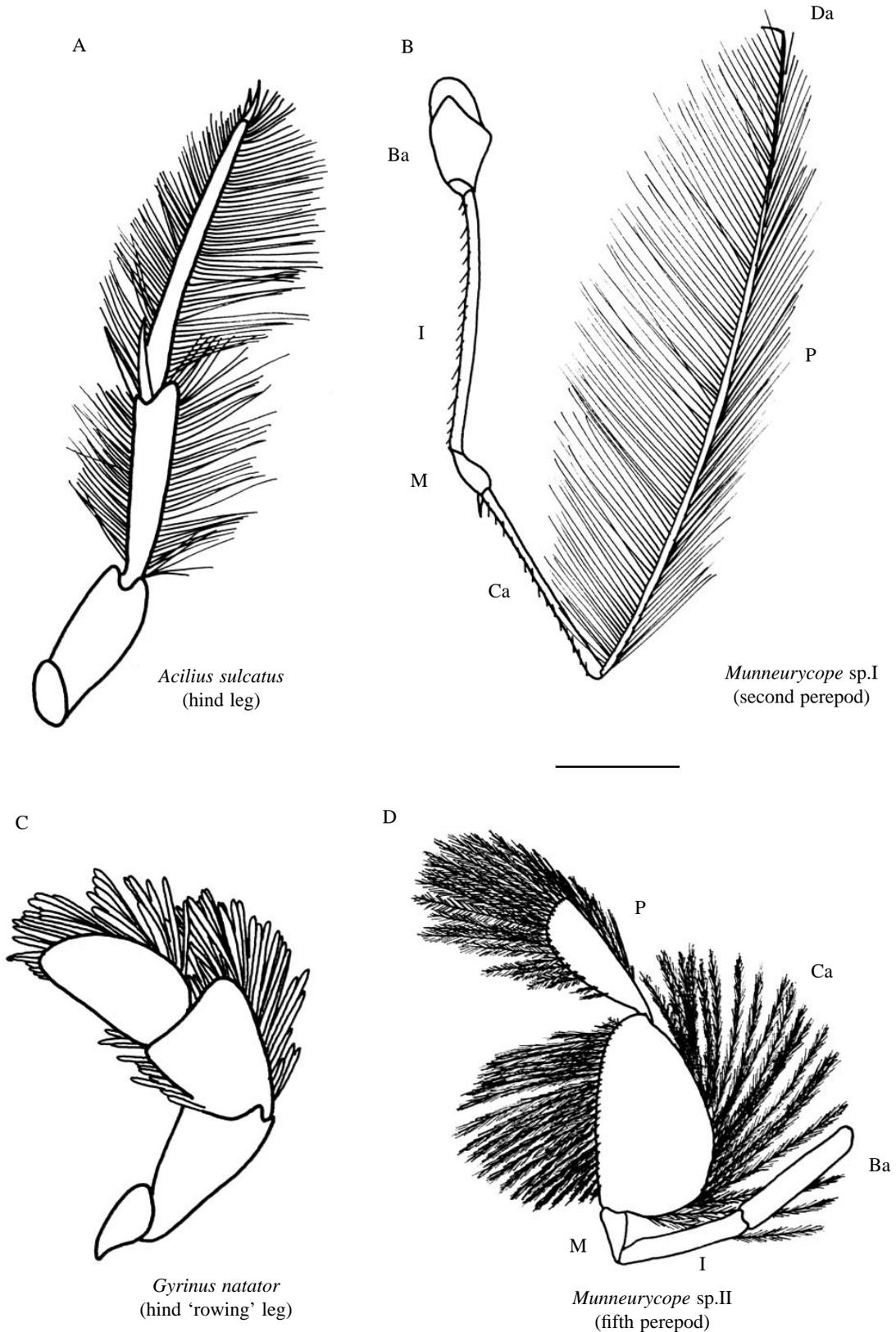


Fig. 3. The shape of various natatory limbs. (A) Hind leg of the water beetle *Acilius sulcatus*. Scale bar, 3 mm. (B) Second pereopod of *Munneurycope* sp.I with setae on the propodal segment. The various pereopod segments are labelled as follows: Da, dactylus; P, propodus; Ca, carpus; M, merus; I, ischium; Ba, basis. Scale bar, 4 mm. (C) 'Rowing' hind leg of the water beetle *Gyrius natator*. Scale bar, 2 mm. (D) Short paddle-shaped pereopod (P_5) from *Munneurycope* sp.II. The flattened propodus and carpus are fringed with plumose setae. Segments are identified as in B. Scale bar, 1.5 mm. A and D are drawn from Nachtigall (1980).

segments; hence, blade angle and opening and closing of the blade may be under their control. *Munneurycope* sp.I was never seen to pedal, although there are no reasons to suppose that it could not do so. However, P₇ in *Munneurycope* sp.II and P₅, P₆ and P₇ in *Munneurycope* sp.I are notably smaller and less setose than pereopods known to be used frequently for pedalling (Fig. 3).

During periods of slow pedalling, the extremely long antennae are spread and extended back over the body. In this position, they presumably act as the 'anterior' sensory structures as the animal moves backwards (Fig. 2B,D). The long pereopods P₂, P₃ and P₄ are spread wide during slow backward pedalling, acting as stabilisers and perhaps performing a sensory function (Fig. 1). During fast pedalling,

the antennae and long legs fold to streamline the animal for faster movement (Fig. 2C).

Escape is also a backward movement, and each of the four species used all of their short paddle-shaped pereopods in strong synchronous sweeps during escape. The limb movements during the power and recovery strokes are the same as in backward pedalling whereas, as in fast pedalling, the antennae and long legs fold to streamline the animal. Fast backward pedalling and escape are never sustained for long and are clearly energetically expensive.

Different gaits

On close examination, and as detailed below, several aspects of striding and pedalling locomotion resemble the terrestrial

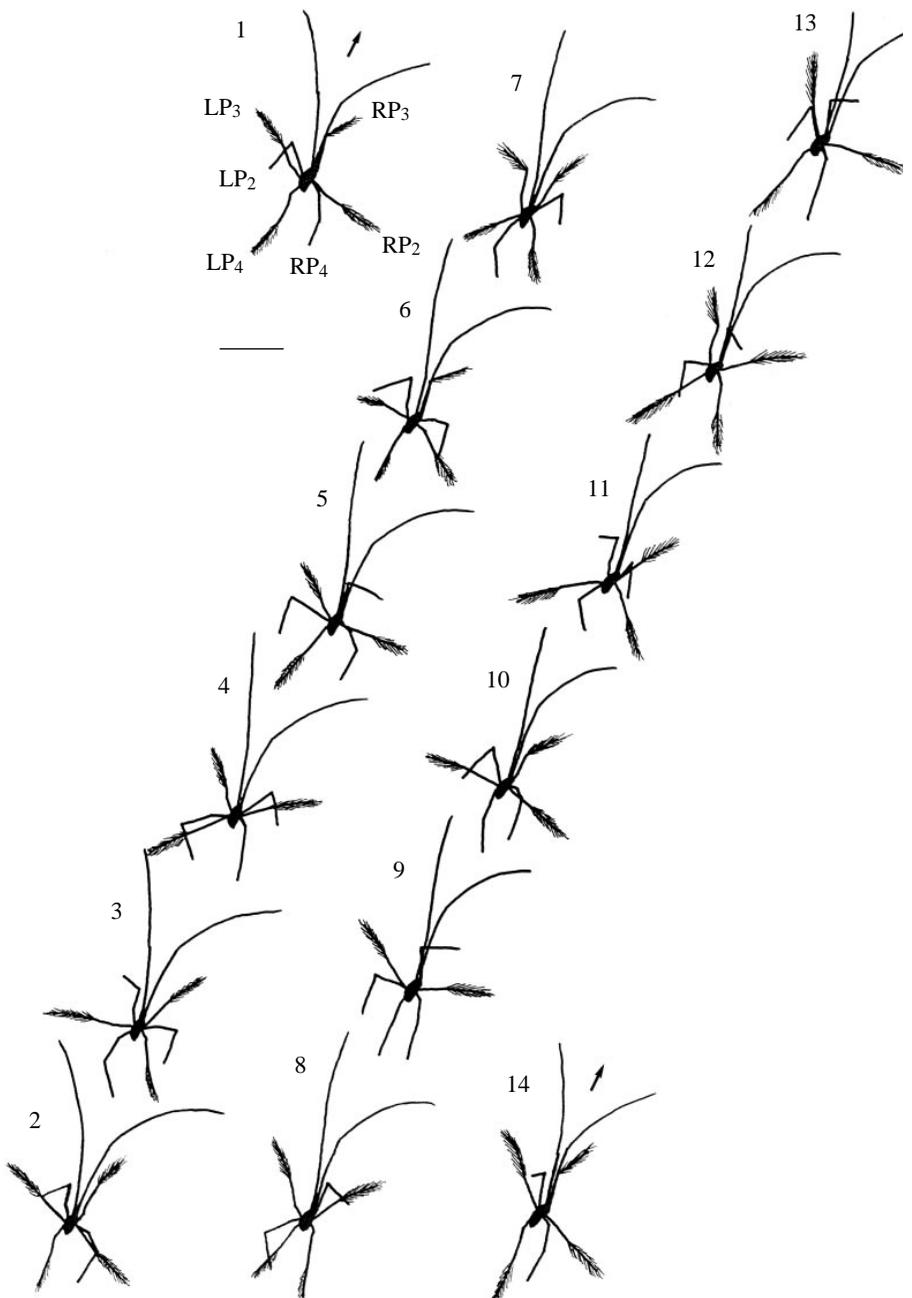


Fig. 4. A series of traced images taken from video frames (0.5 s apart) covering a single striding sequence in *Munneurycope* sp.I (frames numbered 1–14). This number of frames covers approximately one full cycle of movement for each leg. In frame 1, the six long pereopods responsible for propulsion are labelled for the right (R) and left (L) sides. Pereopods involved in the power stroke are shown with the setae spread and those in the recovery stroke have the setae folded. The arrow indicates the direction of motion. Scale bar, 3 cm. Forward speed is approximately 4 cm s^{-1} .

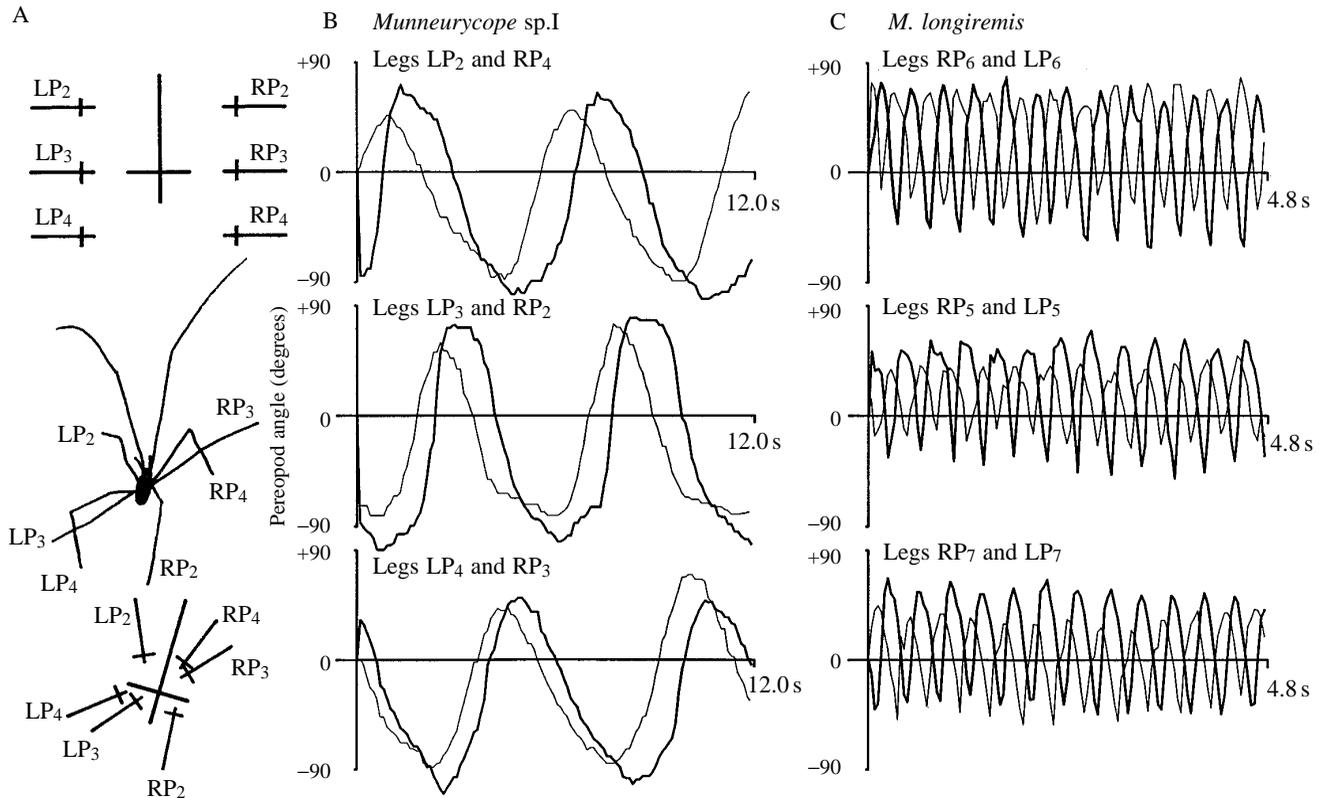


Fig. 5. Representative results from the computer analysis of video film of isopod movement. (A) Representation of the computer cursor used for analysis of both striding and pedalling, showing a central 'body' and six 'legs'. Below this is a tracing of *Munneurycope* sp.I during striding (see Fig. 4) and below this the cursor setting for this frame. (B) Plots of pereopod angle, relative to the body, for approximately two cycles during striding in *Munneurycope* sp.I. The cursor legs were placed on the carpal leg segment. In each graph, the most synchronous legs are plotted together. Power strokes are positive to negative on the graphs. Thin line, left pereopods; heavy line, right pereopods. (C) Slow pedalling in *M. longiremis*. In pedalling species, the computer leg cursor is placed on the ischium. Here, pereopods in the same segment are plotted together on each graph to emphasise that they function in antiphase. Thin line, left pereopods; heavy line, right pereopods. Slow pedalling in *M. bathyalis* was also analysed in this way, and the form of locomotion is nearly identical to that in *M. longiremis*.

'alternating tripod' gait of insects (Hughes, 1958). Metachronal sequences on the left and right sides of the animal are coupled in a similar way for both backward pedalling (fast and slow) and forward striding (Fig. 6). Instead of using bilaterally paired pereopods together, as do many aquatic insects (Nachtigall, 1980; Hughes, 1958), diagonal legs are used in the closest synchrony.

Where six legs are used, there is substantial overlap in the cycle of adjacent ipsilateral pereopods (Fig. 6). Also, as there are three pairs of pereopods involved, contralateral legs from non-adjacent segments (e.g. RP₇-LP₅) are used together. Synchrony of contralateral pereopods is close rather than absolute (Figs 5, 6). The most synchronous movements were found between pereopod pairs LP₂-RP₄, LP₃-RP₂ and LP₄-RP₃ for striding and RP₇-LP₅, RP₆-LP₇ and RP₅-LP₆ for pedalling. LP₄-RP₂, LP₃-RP₄ and LP₂-RP₃ and LP₇-RP₅, LP₆-RP₇ and LP₅-RP₆ synchrony also occurs during striding. In *Munneurycope* sp.II, which uses only P₅ and P₆, there is synchronous use of diagonal pereopods, as legs of the same segment simply beat in opposite phase, RP₅-LP₆ and RP₆-LP₅ (Fig. 6).

With the exception of escape, no changes in gait were recorded. In common with many aquatic and some terrestrial animals, the length of the recovery stroke, and to some extent the power stroke, is shortened at higher speeds (Clarac and Barnes, 1985; Hartnoll, 1970). Compared with slow backward pedalling, the overall leg cycle time is almost halved in fast backward pedalling, so it is included as a different form of locomotion on the basis of the change in body posture accompanying it (Fig. 2C). Slightly faster striding was occasionally observed. There are, however, inertial and drag limitations to increasing speed with such long, highly setose limbs. As only four legs are used for pedalling by *Munneurycope* sp.II, this is also considered to be a different gait.

On each side of the body, a metachronal sequence of leg movement passes rostrally to caudally in both pedalling (P₅-P₆-P₇) and striding (P₂-P₃-P₄). As pedalling is 'caudal end-first', the metachronal wave in this case begins with the 'hind' leg (Fig. 6). The gaits used are slow enough for the direction of metachrony to be directly inferred from the phase diagrams (see Fig. 6) and to be verified with direct

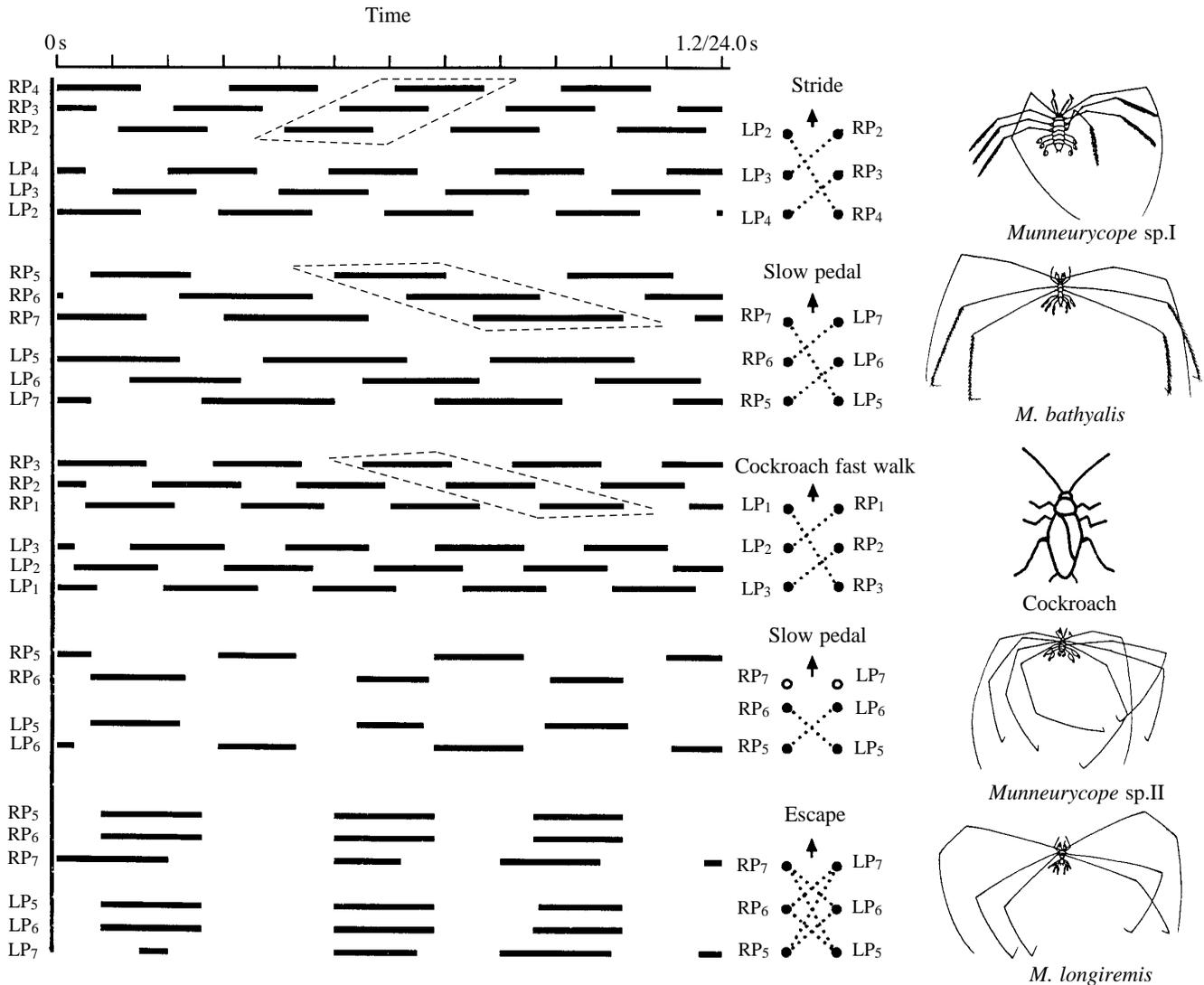


Fig. 6. Leg phase ('stepping pattern') diagrams of various animals. Black bars on the phase diagrams represent the power strokes and the gaps indicate recovery strokes. The full time scale is 24.0s for *Munneurycope* sp.I and 1.2s for all other species. Metachronal waves generally travelled posterior to anterior (relative to the direction of movement), except in *Munneurycope* sp.I. The metachronal sequence is indicated by the dashed enclosures. Next to each phase diagram, the legs used in closest synchrony are indicated by the dotted lines joining the large dots that represent the legs. The direction of movement is indicated by the arrows. Metachrony in the cockroach is apparently reversed because of the fast rate of stepping (data from Wilson, 1966). Note how similar the 'stepping' pattern is (with a reversal of metachrony in *Munneurycope* sp.I) between striding in *Munneurycope* sp.I, pedalling and the fast walk of the cockroach.

observations of animals as they start to move (Wilson, 1966; Delcomyn, 1985).

It is remarkable that both forward striding and fast and slow backward pedalling have essentially the same stepping pattern, as there is a 20-fold difference in pereopod cycling rate between the rather frantic backward pedalling and the slow ungainly forward stride (Fig. 6).

Discussion

Comparisons with other locomotory mechanisms

There is remarkable convergence in the design of the long natatory pereopods of *Munneurycope* sp.I and the swimming

legs of the water beetle *Acilius sulcatus*. Both are long and fringed with setae (Fig. 3; Nachtigall, 1980). It is also interesting to note that, in *Munneurycope* sp.I, *Acilius sulcatus* and other swimming arthropods with this limb type, the form that the leg takes when its setae are spread resembles an elongated paddle (Fig. 3; Nachtigall, 1974). This shape, clearly efficient for swimming, was favoured by both the Pacific islanders and the ancient Egyptians for the blades of canoe paddles (Heyerdahl, 1978).

The short, flattened paddling pereopods (P5, P6 and P7) exhibit structural convergence with the flattened natatory limbs of *Gyrinid* water beetles (Fig. 3; Nachtigall, 1980). However, the setae fringing the segments of isopod pereopods are

plumose, while those on the edge of *Gyrinid* swimming paddles are flattened (Fig. 3). Both adaptations, however, will provide extra thrust by opening out, or turning flat, on the power stroke and streamline during the recovery stroke by folding or turning narrow-side on (Nachtigall, 1985).

The swimming action of *Munneurycope* sp.II, which uses only P₅ and P₆, is similar, in terms of limb phases used, to the movement of the water beetle *Hydrophilus piceus* (Hughes, 1958). Both use four legs, with the closest synchrony found between diagonal pairs (Fig. 6). This is similar to the terrestrial trotting gait of, for example, a horse (Muybridge, 1957; Hughes, 1958). Where six limbs are used for walking in terrestrial animals, the legs are frequently set down as 'alternating tripods' (or a pattern close to this) in order to prevent the animal from toppling over (Hildebrand, 1976; Cocatre-Ziglen and Delcomyn, 1993; Delcomyn, 1985). For the same reason, diagonal legs are used by four-legged animals for trotting or during fast walking. Falling over is not a problem encountered by swimming aquatic animals, so the use of trotting or walking by munnopsids, or any aquatic arthropod, seems strange.

Origin of the walking gait

Where six or fewer legs are used, a stability problem may be faced by benthic aquatic animals (Clarac and Barnes, 1985; Evoy and Ayers, 1982). Shallower-dwelling isopods than those examined in this study are known to walk both backwards and forwards on the sea bed, using their long pereopods (Hessler and Strömberg, 1989). The style of walking in these animals is not fully described, however, and often involves more than six pereopods. As a result, considerations such as stability or the use of particular legs are less important. Asynchronous backward pedalling of some form is also described in members of the janiroid family Desmosomatidae (Hessler and Strömberg, 1989). However, many of these isopods apparently prefer to use their paddle-like pereopods for digging. We have observed *M. longiremis* standing on the sea bottom, and it has been suggested that their long pereopods are used for walking (Gage and Tyler, 1991). However, there is very little musculature associated with these pereopods, and any water current, even at the relatively slow speeds typically found in deep water, would make walking with such long legs very difficult. The shallow-water isopods known to be good walkers fall within the superfamily Janiroidea and are therefore related to the munnopsids (Hessler and Strömberg, 1989). It seems possible that the leg phase used by munnopsids in all types of swimming is derived from the walking habit of some common ancestor. The site where walking developed, whether in the deep sea, on shallower sea beds or, indeed, on land, is not known (see Hessler and Wilson, 1983).

Smooth forward or backward propulsion, in order to conserve energy, is more important to aquatic swimmers than not falling over. This is generally achieved by using the two limbs of a segment simultaneously so that the body is not subject to a turning force (Nachtigall, 1974). Any possible turning moment resulting from asynchronous leg use in

pedalling munnopsids is counteracted by their long legs, which act as drag-stabilisers. In *Munneurycope* sp.I, however, the unevenness of leg movement during striding results in a small amount of zig-zag motion as the animal swims, adding to the peculiarity of this form of locomotion.

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