An Analysis of Swimming in Remipede Crustaceans

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An analysis of swimming in remipede crustaceans

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SUMMARY

An analysis of swimming in the remipede crustacean *Speleonectes lucayensis* is presented. Animals swim freely in the water column of their cave environment. Each trunk segment has a pair of biramous, paddle-like, setose swimming appendages. The rami extend from a large protopod. Swimming is by means of oar-like metachronal beats of the appendages. In the cave habitat, two swimming patterns have been observed, normal metachronal cruising and an ametachronal mode, which may be used to gain speed. These patterns are confirmed using 16 mm footage of captive remipedes. A single leg performs a power and a recovery stroke. During the power stroke the entire leg remains straight and swings posteriorly with exopod and endopod spread apart at 40°, from an angle of 150° between body and leg to an angle of about 50°. The recovery stroke is carried out by several consecutive legs together. The protopod begins the recovery stroke while the distal parts of the leg continue the power stroke. These parts are then flexed until they curl almost into a circle and finally uncurl anteriorly until the leg is fully stretched again. Several waves of legs engaged in power and recovery strokes can be observed simultaneously. The ametachronal pattern differs from the metachronal in that many consecutive legs are in the same phase. It is described how the shift between the two patterns is accomplished. The normal metachronal cruising speed was 7.3 mm s^{-1}. During ametachronal locomotion, it increases to 12 mm s^{-1}. Locomotion of remipedes is interpreted as an adaptation to the cave environment which is poor in food and oxygen. Although the morphology of the legs of copepods and remipedes is similar, the locomotion pattern and Reynolds number range differ. Evolutionary aspects of locomotion and anatomy are discussed.

1. INTRODUCTION

Remipedes are troglobitic crustaceans restricted to submerged anchialine habitats (for a review see Yager 1991). When observed in their natural habitat, the animals are free-swimming in the water column. The usual mode is dorsal-side down. Larger remipedes exhibit considerable flexibility of the trunk and can twist and loop easily whilst swimming. Captive animals swim throughout the aquarium but also near the bottom, sometimes descending into the gravel. This has, however, never been observed in the cave habitat.

Speleonectes lucayensis and *Godzilliognomus frondosus*, are found in anchialine caves in the Bahamas. They live at salinities of 35 ppt at depths of 17–30 m and temperatures of 25–27°C. The individuals of *S. lucayensis* are considered to be sub-adults because of their smaller size and fewer trunk segments. Those examined for this study ranged in length from about 12–18 mm with 20–28 trunk segments. The largest adults of *S. lucayensis* have a length of 24 mm and 32 trunk segments. *G. frondosus* is the smallest remipede, averaging 9 mm in length and has 16 trunk segments in adults.

The remipede body consists of a short cephalothorax and an elongate trunk. The appendages of the cephalothorax are utilized for obtaining food and probably for grooming. The trunk appendages are used solely for swimming. Each trunk segment bears a pair of biramous, paddle-like, setose swimming appendages. Swimming is achieved by the metachronal oar-like beat of the trunk appendages.

2. MATERIALS AND METHODS

Living remipedes were observed by one of us (J.Y.) in their natural habitat and in captivity. Captive remipedes were placed in a small glass chamber and filmed using a Bolex 16 mm movie camera. Film analysis was made frame-by-frame with a Selecta-Frame 5 16 mm Analysis Projector; pictures were projected onto a digitizer (Podscat PT 3030) to measure the x and y co-ordinates of certain points on the animals.

Preserved remipedes were dissected and appendages examined. Scanning electron microscopy was used to examine trunk appendages.

3. LIMB MORPHOLOGY

(a) Rami and segments

The trunk appendages are directed laterally. Each (figure 1 inset) has a large protopod. A cuticular

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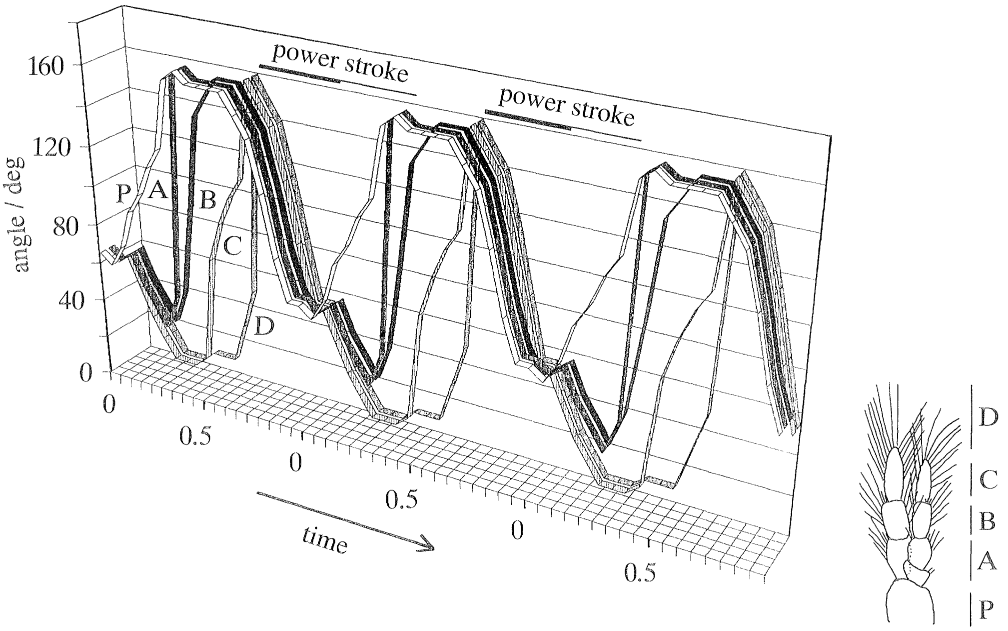

Figure 1. Angles of the leg segments or setae (see inset) of *Speleonectes lucayensis* during three normal metachronal locomotion cycles. The plotted angles are measured between the leg parts and the body. 160° end of recovery stroke, 0° end of power stroke. (From 0 to 0 = one locomotion cycle).

sternal bar connects left and right limbs but the limbs are not mechanically connected like those of copepods. No muscle has been observed in sections through the sternal bars. There is no true coxa. Because of its large array of muscles, the protopod is thicker than the rami that arise from its distal margin.

In *Speleonectes lucayensis*, the rami extend from the anterodistal portion of the protopod. A flexible cuticular or arthrodial membrane (figure 2*b*) extends from the posterior distal margin of the protopod over much of the posterior side of the first segments of endo- and exopod in *S. lucayensis*. This membrane extends nearly the full length of the posterior side of the first exopod segment of *G. frondosus*. In SEM pictures, the anterior side of the protopod appears smooth and stiff, the posterior side shows a slightly-folded structure which is even more expressed in the joint areas. The axis of swing of the articulation lies posteriorly, corresponding to what Manton (1977) described as an evolutionary old hinge joint (see illustration figure 2*b*). The stiff anterior parts stabilize the leg (figure 2*a*). The posterior parts are more flexible and compressible. During preparation for SEM, they shrink slightly (more in discussion).

The four-segmented endopod (see inset to figure 1) is the ventral ramus. The endopod is slightly shorter than the exopod. Segment 1 is small and approximately rectangular in shape, and overlaps the first segment of the exopod anteriorly. The three distal segments are more elongate, the distal being the longest. Long plumose setae are borne along the entire margin of the distal segment and on the inner margin of the other segments.

The three-segmented exopod is the dorsal ramus. The terminal segment is similar in shape to that of the endopod but longer, and bears many plumose setae along the entire margin. The two proximal segments frequently bear several small serrate or comb setae on the distolateral margins. The small serrate setae are found both dorsolaterally and distomedially on both segments.

All remipede trunk limbs have the same basic morphology. The segments of both rami are flattened and paddle-like. There is little variation in limb shape from anterior to posterior but the posterior-most limbs may lack the full complement of segments. For example, the terminal limb may have a two-segmented endopod and a single long exopod segment. Additional segments appear to form by a pinching of the terminal segment. The main differences between the numerous trunk limbs are in size and the number of setae. Appendage size increases slightly until about mid-animal and then decreases posteriorly. In *G. frondosus*, the largest are limbs 7–9, while in sub-adult *S. lucayensis* (with 19 legs), the largest are 6–8.

The long setae on the trunk appendages are all plumose; the fine setules form a broad fan. Almost every seta is as long as, or longer than, the width of the segment on which it is found. This setal fan triples the surface area of the appendage. In *S. lucayensis*, the anterior socket of all setae, including small dentate setae, bears a cuticular fringe. This is thought to have a proprioceptor function, although not confirmed by microscopy. At the tip of endopod and exopod distal segments in *S. lucayensis*, there are two terminal setae between which is rounded, padlike cuticle. From 4–6 nerves, each with an enlarged bulbous ending, can be observed in this area. Terminal segments of *G. frondosus* bear one seta and lack the intersetal pad.

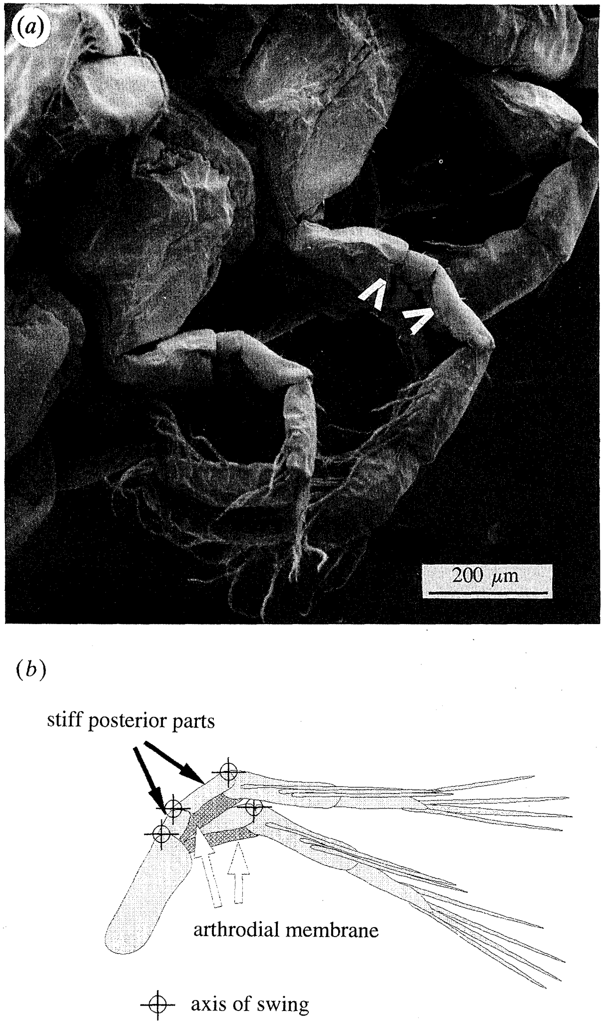

Figure 2. (*a*) Leg of *Speleonectes lucayensis*, SEM. Arrows indicate large expanses of arthrodial membrane. (*b*) Leg, showing axes of swing.

4. FUNCTIONAL ANALYSIS OF SWIMMING

(*a*) *Generalized swimming movement*

Most large species of remipedes swim continually in the water column in what we term a normal cruising swimming pattern. They typically swim dorsal-side down, extending their long first antennae forward dorsally. When they swim in a normal cruise, the appendages beat in a metachronal pattern. The smallest remipede, *Godzilliognomus frondosus*, has a different type of swimming habit. Rather than cruising through the water column, it seems to hang suspended, seldom moving very far. It maintains position by a special metachronal swimming: the angle of swing of the legs during movement is reduced from 150° to less than 45°, and the beat frequency is lower. Copious lipid droplets throughout its body give additional lift for hovering.

When approached by a diver, the animal is able to 'jump' about 10 cm through the water. To achieve this escape motion, it shifts from a metachronal swimming pattern to one in which it beats almost all appendages at once. Copepod escape movements consist of many rapidly-following single-leg beats; each cycle propels the animal only a few body lengths forward (Strickler 1977; Petipa 1981; Kohlhage 1991). So, the long 'jumping distance' of 10 cm during the escape reaction of *Godzilliognomus frondosus* cannot be achieved by a single beat of the appendages. A restrained animal also beats all legs up to five times without a pause, followed by the described metachronal hovering. Larger remipedes can change their metachronal cruise and accelerate their motion. However, this is accomplished by simultaneous movement of up to 10 pairs of legs.

(*b*) *Metachronal swimming*

The locomotion cycle of a swimming leg of *Speleonectes lucayensis* lasts about 0.8 s (about 20 frames), divided into a power stroke of about 0.4 s and a recovery stroke of about 0.4 s. Waves of power-stroking legs are propagated forwards because the next anterior leg to a power-stroking leg starts its power stroke slightly later. In a large remipede, there may be 2–3 power-stroking leg waves visible at any one time.

There are five flexion points per limb, and the angles between them and the long axis of the trunk are measured as plotted in figure 1. This shows the change of orientation towards the body and towards the direction of movement during the locomotion cycle. Shown, is the posterior angle between the leg and the long axis of the body. The value of this angle increases when the leg is moved forwards, and decreases when it is moved backwards.

For the purpose of this analysis, the leg parts are: the protopod (P), segments 1 and 2 of the endopod and segment 1 of the exopod (A); segment 3 of the endopod and segment 2 of the exopod (B); the terminal segments of exo- and endopod (C), and the setae (D).

Figure 3 shows the movement of a single leg during normal metachronal locomotion. Movement in relation to the body is indicated by arrows.

Exopod and endopod are spread apart at the beginning of the power stroke and the angle between them is about 40°. The spreading is caused by a combination of muscle action and water resistance. The overlap of the first segment of the endopod with the exopod may also be involved. During the posteriorly-directed power stroke, the entire limb remains straight from about 150° to about 50°, between the body and the leg. At that point, the limb flexes at the first point of flexion. After an acceleration of 80 ms the angle velocity is 0.75 ms^{-1} and remains constant for 120 ms. When the protopod slowly begins the anteriorly-directed recovery stroke, the terminal segments of the rami still continue posteriorly with their power stroke until they are parallel to the trunk (value *ca.* 0°, figure 3). The distal portions of each limb bend until they reach the leg posterior to them. All water between the rami of two consecutive legs is pressed out and may increase the propulsion drag. At this point, the rami are still spread so that they are now positioned lateral to the rami of the legs posterior to them. During this phase,

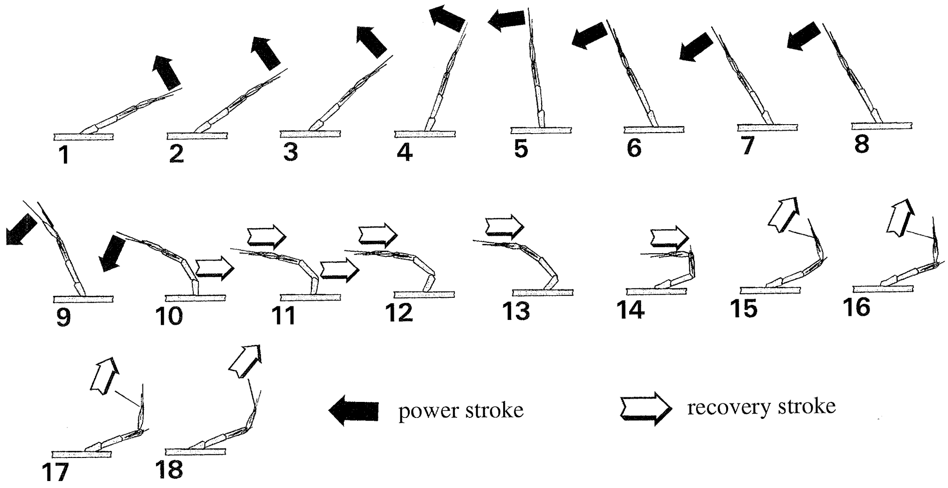

Figure 3. Movement pattern of a single leg during normal metachronal locomotion, lateral, from a film sequence. The time interval between pictures is 0.042 s. Leg about 1 mm long. Movements of leg parts indicated by arrows.

the rami form a wall-like structure at each side of the animal and the protopods connect it like the rungs of a ladder.

During the recovery stroke, the protopod moves anteriorly and the limb portions (A–D) move successively until the limb is once again straight at an angle of about 150° to the trunk. During the recovery stroke, the limbs can be flexed until they almost curl into a circle. The various flexion points uncurl anteriorly until they reach the same angle as the protopod. What has been described above as a wall of rami is disentangled by moving forward, and the rami are pulled out in a curve. This reduces drag on the appendages when they move forward. Also, the overall area becomes smaller because the angle between the rami decreases from about 40°, when completely spread apart, to nearly 0° at the end of the recovery stroke.

Figure 4 illustrates the interference of the legs. During the power stroke, the legs are separate. At the end of it, the tips of the legs come into contact with the next behind, and the water between them is squeezed out. In the films, no tilting of the limbs was observed, because the protopod is flat rather than cylindrical, and the articulation between body and protopod is long. Thus, only back-and-forth movement is possible. This is the same as in copepods, but different from the leg movement of Mysidacea and many other Crustacea.

The normal cruising speed recorded for *S. lucayensis* was about 7.3 mm s^{-1}. Speeds ranged from about 6–10 mm s^{-1}. Speed oscillates, depending on which legs are in the power stroke. All legs beat with the same frequency and normally with the same elongation. Because the largest legs are in the middle region, more velocity is achieved when they make their power stroke (figure 5).

(*c*) *Free swimming and wall effects*

In their natural habitat, the animals cannot be found diving into gravel, nor swimming in contact with a wall. In the small film vessel, animals come into contact with the walls, so it can be assessed whether they can use the wall effect positively by comparing the speed achieved close to a substratum with that achieved in free water. Cyclopoid copepods can use this wall effect and increase their speed (Kohlhage, in preparation).

When the animal swims with the ventral side facing

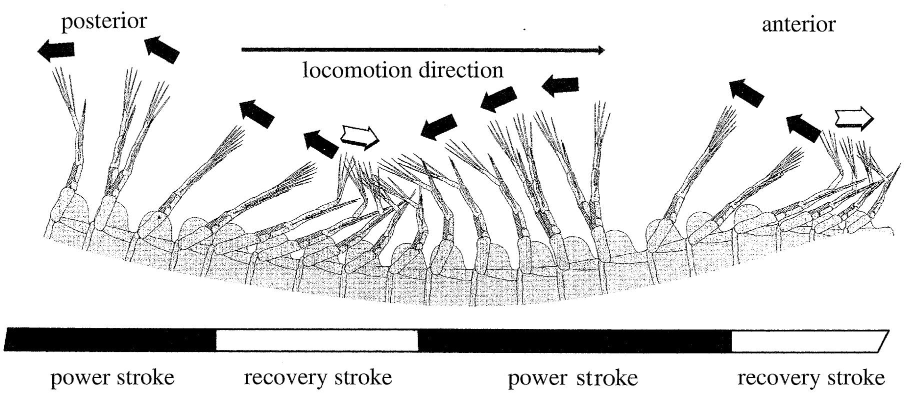

Figure 4. Outline of two waves of locomotion, showing interference of legs during recovery stroke. Movements of legs are indicated by arrows, as in figure 3.

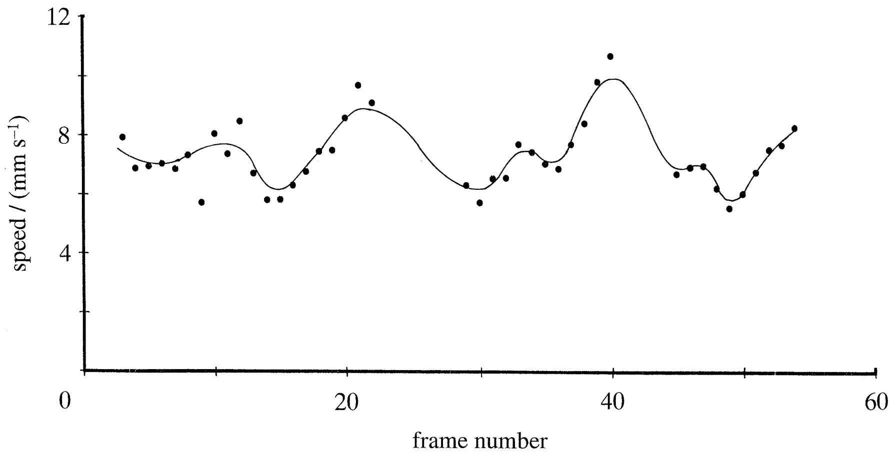

Figure 5. Cruising speed of *Speleonectes lucayensis*. Speed is greatest when the longer middle legs make a power stroke.

the glass vessel, the endopod can come into contact with the bottom when the rami are spread apart during the power stroke. It then slides over the surface and, at the end of the power stroke, it loses contact with the bottom during the whole recovery stroke. The legs appear to move up and down ('walking'), but actually the rami are only spread, and it is not like walking. The beat frequency does not change. It is normal swimming with contact with the bottom, but the velocity is slower. The average velocity during normal cruise along the bottom is 6.7 mm s^{-1} when the animal has its ventral side down and the legs glide over the bottom. An even lower value is measured when the animal swims dorsal-side down. The velocity then is about 6.5 mm s^{-1}. In this position, the legs never come into contact with the bottom, so the speed is slowed by the wall effect between body and wall. When swimming ventral-side down, there is the same higher resistance of the body, but also a slightly stronger propulsion of the legs. Adding positive and negative effects, the negative ones predominate, and speed is reduced.

(*d*) *Ametachronal swimming*

The ametachronal pattern differs from the typical metachronal pattern in that many consecutive legs are in the same phase, either all making the power stroke or all performing the recovery stroke. Leg movement does not differ from that adopted during normal cruising. The difference lies in the number of limbs beating simultaneously.

Figure 6 outlines the two patterns of swimming: metachronal and ametachronal, for *Speleonectes lucayensis*. The time between each picture is 0.083 s. Many types of swimming can be seen: normal metachronal, ametachronal swimming, and the switch from ametachronal to metachronal after the velocity change of an escape reaction.

Frames 1–5 show normal metachronal swimming. In frame 1, two metachronal areas can be observed: power and recovery. One zone of power stroking runs out at the head area until frame 5; the other power stroking zone is moving slowly anteriorly. At frame 7, the metachronal change of the recovery area can be seen; at 9, there are seven legs involved in an ametachronal power stroke. At the same time, the anterior- and posterior-most limbs are still in their metachronal phase. It is the middle, larger, legs that become ametachronal in this frame. The ametachronal pattern can also occur in the anterior- and posterior-most limbs. Frames 7–13 show ametachronal swimming in the midsection of the animal. In frames 15–19, the change from ametachronal to metachronal beat can be observed. However, this change is not complete because another ametachronal pattern begins at frame 21. Frames 21–33 show another ametachronal swimming pattern. From frames 35–43, the change from ametachronal to metachronal beat can be seen (the beginning of the metachronal movement is indicated by an arrow in frame 35). In frame 43, the legs moving posteriorly at the start of the normal metachronal beat hit the legs which are still at the end of their ametachronal recovery stroke and push them backwards. All legs then return to their normal metachronal pattern.

How is the metachronal pattern altered so that the many legs can all be in the same phase? Figure 6 shows an animal switching from metachronal to ametachronal beat. The limbs change at the end of the recovery stroke or at the very beginning of the power stroke. To allow many consecutive legs to enter the same phase, the recovery stroke may be accelerated while the power stroke is slowed. Thus, all legs involved are synchronized and ready for the same movement: the power stroke. The change back to normal metachronal movement occurs at the end of the ametachronal recovery stroke and is accomplished by either shortening the recovery stroke or by beginning the power stroke early. In either case, the posterior legs are still in the ametachronal recovery position and are too far anteriorly. The more anterior power-stroking legs come into contact with the posterior legs and push them back. This reduces the efficiency of the power stroke, which can be seen in figure 6, frame 43.

The velocity of the animal increases during ametachronal locomotion, and was found to be up to 12 mm s^{-1} in *S. lucayensis*, but this speed is achieved for less than one second.

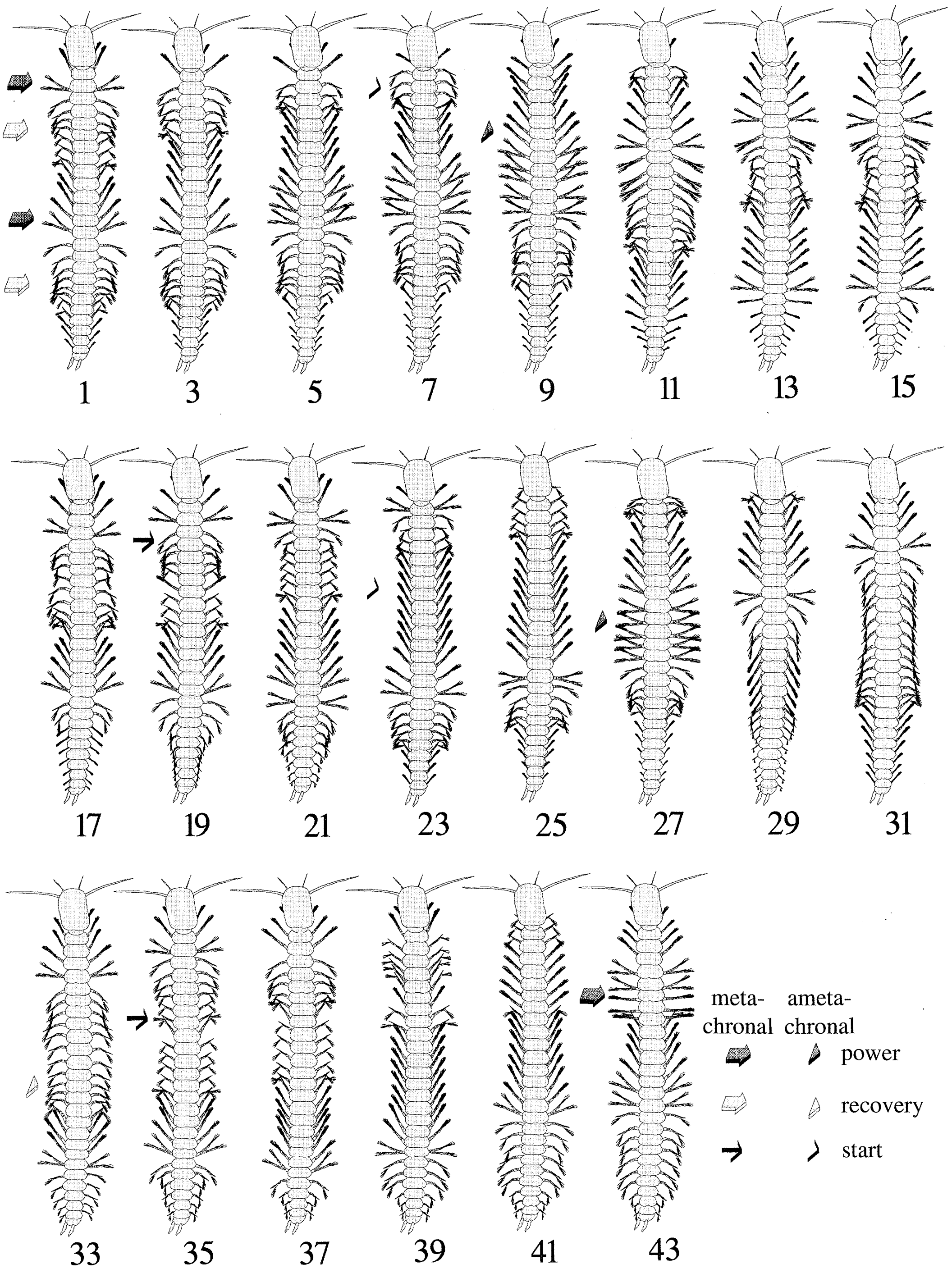

Figure 6. Leg movements of a swimming *Speleonectes lucayensis*. Time interval between sketches: 0.083 s. Arrows indicate power stroke and recovery stroke of metachronal and ametachronal locomotion patterns. Detailed description in text.

Remipedes can undergo various contortions of the body in the water column. There is no indication that limbs opposite to each other beat asynchronously, when the animal turns or loops. Such movements seem to be due to the action of trunk muscles.

5. DISCUSSION

(*a*) *Protopodal arthrodial membrane*

In his paper on the origin of copepod limbs, Ito (1989) included a detailed comparison of remipede and cephalocarid trunk-limb morphology. For remipedes, he described a posterior bulbous structure that originates on the protopod and bears a lobe-like structure. Ito attached much significance to these two structures. The bulbous structure, he identified as a positional homologue of the short, proximal exopod segment of cephalocarids. The lobe-like structure, he considered a positional homologue of the cephalocarid pseudopod. Our analysis of limb morphology disputes Ito's findings. We think that what he describes is a large articulation membrane. The lobe-like structure is part of this membrane: it is a thin sheet of chitin which does not have the distinct margin found in trunk segments. The shape is consistently lobe-like, but the margins are irregular. The 'bulbous structure' Ito describes is indeed a cuticular extension of the posterior portion of the protopod. However, careful analysis reveals that it extends onto the first segment of both the endopod and the exopod. In *Godzilliognomus frondosus*, the membrane extends distally almost to the apex at the distal margin of the first segment of the exopod. We think that the arthrodial membrane serves as an articulation membrane for the rami with the protopod. It may prevent over-extension of the rami during the power stroke. Our studies show that the membrane is not another true segment of the exopod as Ito suggests.

(*b*) *Locomotion*

Like copepods, remipedes have biramous trunk limbs which they move in a metachronal pattern. However, our analysis of remipede motion and morphology also indicates many differences between them. Copepod legs do not flex but remain straight during both the power and recovery strokes (Storch 1929; Strickler 1975; Kohlhage 1983). This is not so in remipedes which flex the distal parts of their limbs during the power stroke and thus generate additional propulsion forwards. This also results in distal parts of consecutive legs becoming piled very close together. As the segments of the rami are very thin, they do not offer much resistance to the water during the recovery stroke. By comparing film pictures with SEM photos, it can be verified that the exopod of an anterior limb lies dorsal of the exopod of the next posterior leg; the endopod lies ventrally of the endopod of the leg posterior to it. Thus, the recovering distal parts of the legs form a thin plate parallel to the body on each side of the animal.

During the power stroke, the rami are widely spread. They fold together comparatively late, at the beginning of the recovery stroke. Therefore, at the very end of the power stroke, the water between the flexed distal parts of the leg and those of the more posterior legs is pressed out. In copepods, this has not been found: here, the rami are spread at the beginning and folded together at the end of the power stroke (Kohlhage 1983). The recovery stroke is totally different. In copepods, all legs are carried forward simultaneously. Power and recovery stroke follow each other immediately. However, between the recovery stroke and the next power stroke there can be a long pause. In remipedes, there can also be a pause at the beginning of the power stroke when switching from metachronal to ametachronal movement. This observation could strengthen Ito's hypothesis that copepods evolved from a remipede-like ancestor, because copepod movement could have evolved from this ametachronal remipede movement.

(*c*) *Locomotion efficiency*

Remipedes with their lateral trunk limbs swim much better in open water than in contact with a solid surface. Matters are quite different in cyclopoid and many harpacticoid copepods. With their ventrally-inserting limbs, they can perform what has been called swim-creeping (Kohlhage, in preparation). This is more effective than free swimming, because the limbs do not glide on the solid surface. When *Speleonectes lucayensis* swims with its ventral side facing a solid surface, the legs glide along it and the velocity is slower than in free swimming. The animal is slowed down by the so-called wall effect, i.e. a moving body has more resistance if it moves close to a wall than when moving freely in the water. On the other hand, power-stroking legs near a wall have a bigger resistance and cause a bigger drag than in free water. This is compensated for by greater body resistance. The velocity of an animal swimming with its dorsal side facing a wall is lower than when it swims with its ventral side facing the wall. The highest velocity is during free swimming in open water.

Lauterbach (1978) discussed the possibility that the ancient crustacean type had ventrally-inserting legs like copepods, but that they were much more numerous. Laterally-inserting legs are an evolutionary novelty. They are still numerous and of an ancient type in remipedes. This could be an adaptation for minimizing energy consumption during free swimming. Also, the overlapping first segment of the endopod could be such an adaptation. In copepods, the left and right leg are mechanically connected by a coupler and remain stiff and straight during both power and recovery stroke. The articulations only allow spreading and folding of the rami but no flexion. In remipedes, the leg is more mobile and the overlapping of the first segment of the endopod could help in synchronizing exo- and endopod, and in supporting spreading during the power and folding during the recovery stroke. This could happen if the endopod reacts slightly faster or is stronger than the exopod.

When the swimming speed and flexion time of *Speleonecies lucayensis*, a typical large remipede, is compared with other animals, especially copepods (table 1), remipedes swim relatively slowly. So, they need less energy for the same distance than if they swam at higher speeds. On the other hand, this makes them swim with comparatively low Reynolds numbers. In figure 7, the movement pattern of different appendages is presented. Movement at very low Reynolds numbers is shown at the top; at higher numbers at the bottom. It can be seen, that the movement pattern changes continuously with increasing Reynolds numbers. The cilium flexes during the recovery stroke and is carried back close to the animal's body, but during the power stroke it is stiff and straight. In remipedes, an additional spreading apart of exo- and endopod takes place during the power stroke to increase the hydrodynamically-effective area. Reduction of this area during recovery is achieved by folding of exo- and endopod and by their flexion. In nauplii, spreading of the rami is even more important and flexion during recovery is reduced. Finally, in adult copepods, the swimming appendages do not flex at all. The difference in drag is

Table 1. *Maximum swimming speed of selected small organisms in relation to their body length*

(bl: body length. Authors: (a) Kils (1979); (b) Vogel (1985); (c) this article; (d) Kohlhage (1991); (e) Sleigh & Blake (1977).)

	velocity $(\mathrm{km\,h}^{1})$	body length (mm)	velocity $([\mathrm{bl\,h}^{-1}] \times 10^{-6})$	Author
paddle swimmer				
Euphausia superba	1.8	50	0.036	a
Dytiscus marginalis	1.8	30	0.06	b
Speleonectes lucayensis	0.028	20	0.0018	c
Gammarus locusta	0.9	17	0.053	b
Hyale nilssoni	0.73	6.2	0.12	b
Acanthocyclops robustus				
adults	0.25	0.7	0.34	d
nauplius	0.13	0.3	0.43	d
Cyclops vicinus				
nauplius	0.16	0.27	0.59	d
cilia swimmer				
Pleurobrachia	0.27	15	0.018	e
Convoluta	0.002	2	0.001	e
Spirostomum	0.0036	1	0.0036	e
Paramecium	0.0036	0.21	0.017	e
Tetrahymena	0.0017	0.07	0.025	e
Uronema	0.0041	0.025	0.17	e

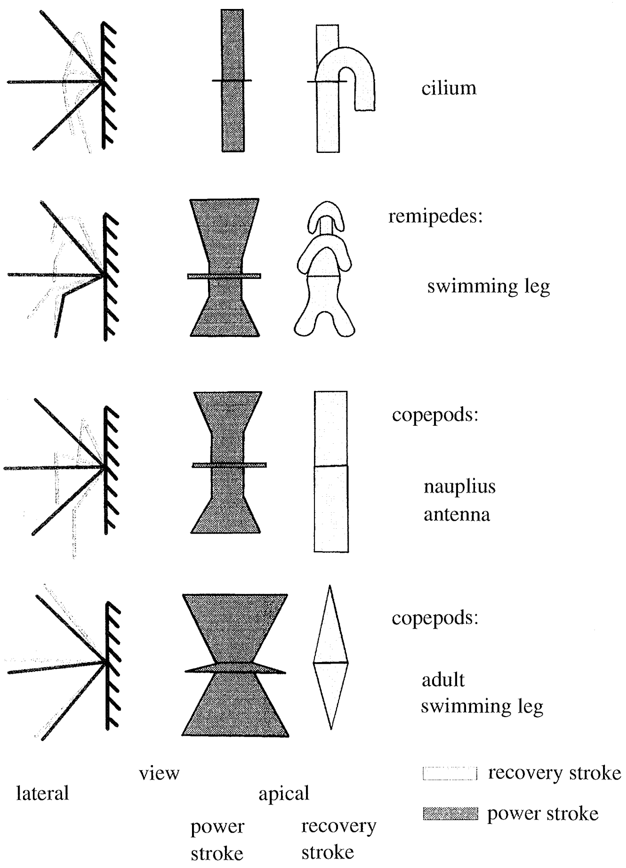

Figure 7. Characteristics of movement of types of appendages. Pattern of movement changes with increase in Reynolds numbers. See explanation in text. (Nauplius refers to those of cyclopoid and harpacticoid copepods.)

only achieved by folding of the rami of left and right leg and by an additional approaching of the tips of these legs medially during the recovery stroke and a complete spreading of the legs and rami during the power stroke. The movement pattern of the remipede leg is more like that of the second antenna of a cyclopoid nauplius and quite different from that of an adult copepod.

(*d*) *Steering ability*

For a cave-living animal, good steering abilities seem to be necessary. *S. lucayensis* can curve its body in nearly any direction – left, right, up and down – and can twist around the long axis. The animal is so flexible that it can reach its tail with its head. It can use all these abilities simultaneously, and can be observed making a narrow right curve up, and twisting around at the same time. Steering is not controlled by unequal movement of the legs, which always beat simultaneously on each side. On the other hand, forward movement caused by the legs is not assisted by undulation of the body. Changing direction and propelling the animal are separate activities and do not interfere with one another.

(*e*) *Energy saving*

The legs of dead remipedes and copepods are not in the same position as those of live or anaesthetized animals. The legs of dead copepods remain in the fully-flexed position assumed after a power stroke. In remipedes, they also take up the position assumed at the end of a power stroke, with the protopod of the legs extending at an angle of 90° from, and the distal parts of the legs lying parallel to, the body. This must be caused by contracted muscles.

Small remipedes like *Godzilliognomus* save energy by hovering, *Speleonectes lucayensis* by free swimming with a relative constant low velocity and using the laterally-inserting flexible legs. During power stroke, they produce drag as an individual leg but they recover folded and in a pile with others to reduce resistance. Compared with copepods, all this seems to be an adaptation to life in the water column in special cave environments, which are poor in food and oxygen and have few predators.

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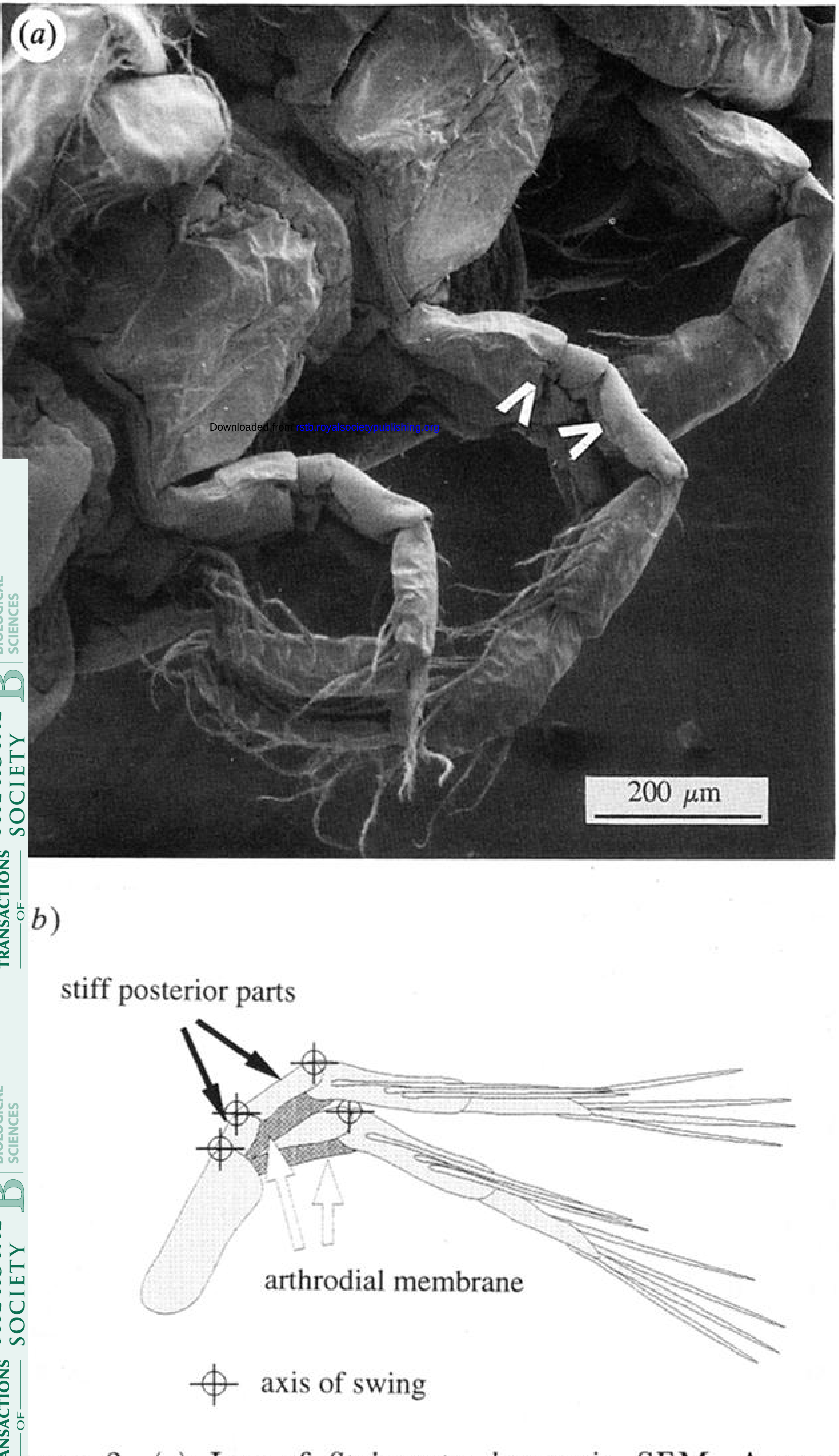
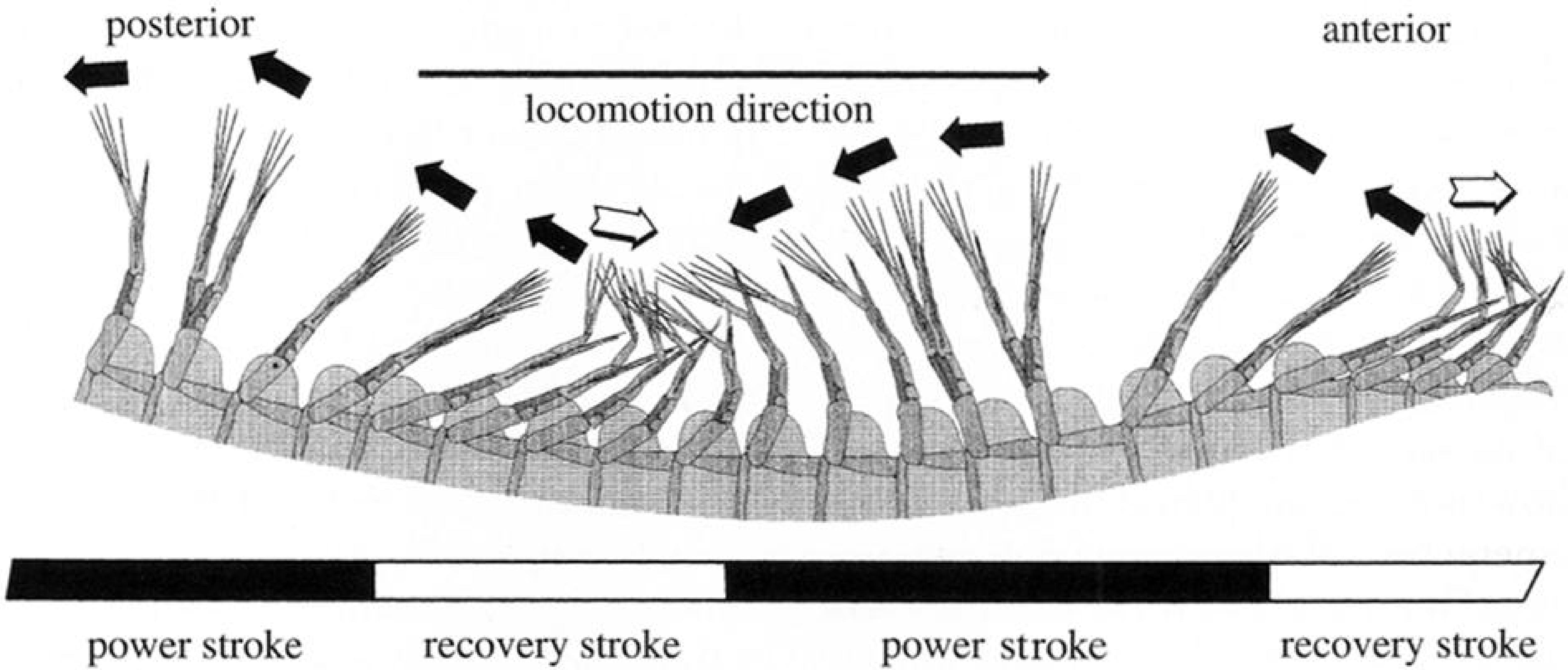


gure 2. (*a*) Leg of *Speleonectes lucayensis*, SEM. Arrows dicate large expanses of arthrodial membrane. (*b*) Leg, owing axes of swing.



gure 4. Outline of two waves of locomotion, showing interference of legs during recovery stroke. Movements of legs are indicated by arrows, as in figure 3.