

Water Uptake via Two Pairs of Specialized Legs in *Ligia exotica* (Crustacea, Isopoda)

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Abstract. When individuals of *Ligia exotica* were exposed to dry environments, their weight decreased within 3 h to 90% of the initial weight. When the animals were subsequently presented with wet paper, pereopods VI and VII were firmly apposed and moved around until their tips were stationary for some seconds. Subsequently the pleopods became soaked in water and the body weight recovered. Morphological observations revealed hollow structures on the surface of the dactylus and propodus of pereopods VI and VII, and a series of thin cuticular protrusions, oriented in several parallel lines, from the propodite to the ischiopodite of pereopod VI and on the basipodite of pereopod VII. The width between the parallel lines varied little, but the total width of the regular lines increased linearly with increasing body size. When isolated caudal pereopods were immersed, beginning at the distal end, in water, water flowed along pereopod VI as far as the proximal end of the ischiopodite, but water flow along pereopod VII occurred only in conjunction with the basipodite. This means that water uptake with the legs requires both pereopods VI and VII and can be achieved only when these legs are closely apposed.

Introduction

Isopods are a group of peracaridan crustaceans with representatives in almost any conceivable habitat, from the Arctic and Antarctic to the tropics, the deep sea to high mountains, lakes and streams to caves and deserts. On the

basis of the diversity of environments, the Oniscidea, variously known as slaters, woodlice, sow bugs, and pill bugs, are the most successful of terrestrial crustaceans today (Carefoot and Taylor, 1995). As a consequence of their terrestrial way of life, oniscids developed certain adaptations to reduce water loss in order to survive in their xeric environs (Edney, 1977). Yet they are considerably less well adapted to live on land than are other terrestrial arthropods such as insects and spiders. To minimize evaporation of water from their bodies, many terrestrial species of isopods frequent cool and humid areas, seek shelter beneath stones and bark, and often are nocturnal like some of the desert species (Edney, 1951).

Isopods of the semiterrestrial oniscid species *Ligia exotica*, which live on the seashore among pilings, beach fortifications, jetties, and rocks, usually not more than a few meters from the water's edge, lead a rather different life from that of wholly terrestrial isopods such as pill bugs. *L. exotica* has keen eyesight (Hariyama *et al.*, 2001; Keskinen *et al.*, 2002) and is active during the day as well as at night, when it can be seen clambering around on boulders and rocky platforms even in the brightest sunlight. At the same time, however, *L. exotica* shows poor resistance to desiccation and cannot live without water (Tsai *et al.*, 1998). It was shown by Hoese (1981) that *Ligia* spp. possess a multifunctional water-conducting system, used in connection with respiration and thermoregulation, which helps to replenish water lost through desiccation by direct uptake from standing water. Hoese (1982) also showed that isopods of the family Ligiidae use both pereopods VI and VII (walking legs) as a unit to take water up from a droplet or puddle by allowing the water to move upward by capillary action along grooves formed between the apposed legs. Despite

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these excellent observations, some questions remain about the precise mechanisms by which these animals achieve the necessary capillary action during water uptake and how they have been able to thrive in their restricted land habitat. The present paper focuses on the specific roles that the caudal pereopods with their specialized morphological features play in the uptake of water from wet surfaces in *L. exotica*.

Materials and Methods

Animals

Adult specimens of *Ligia exotica* Roux (1828) were collected at random from the boulders of the littoral of Lake Hamanako (34°45'N, 137°35'E), a brackish lake in Shizuoka Prefecture, on the Pacific Ocean side of Japan. The animals were maintained in the laboratory in plastic tanks (42 × 32 × 18 cm) containing shallow amounts of filtered seawater and a block of cement.

Change of body weight under dry and wet conditions

Specimens of about 2.5 cm in body length (*i.e.*, body excluding antennae and uropods) were moved individually from the plastic tank to an arena consisting of a plastic box 20 × 12.5 × 11 cm, and kept without water and food for 3.5 h (a time that is known to be critical for the continued survival of *L. exotica* specimens when water is unavailable). After this desiccation period, a piece of filter paper wetted by distilled water or filtered seawater and covering the bottom of a small plastic case (6.4 × 3.5 × 0.5 cm) was placed in the arena. Dry paper alone was given to a control group. Each animal was weighed once an hour after transfer from the plastic tank to the plastic arena. All experiments were performed under conditions of 23–26 °C and 46%–67% humidity.

Water-uptake behavior

To observe water-uptake behavior in *L. exotica*, each individual of about 2.5 cm in body length was placed in the plastic arena and kept there without water and food for 2 h (long enough to increase the motivation of the isopod to absorb water if allowed access to it). After this period, a piece of wet paper (see above) was placed in the arena. The distilled water or filtered seawater used to soak the paper was colored red with a water-soluble food dye (Tsukemoto Corporation) to facilitate the observation of water flow up the specimens' legs and body. Water-uptake behavior was observed for 30 min and recorded on digital videotape (Sony DCR-TRV30), followed by checking which regions of the animal were stained red.

Scanning electron microscopy

Three size classes of animals were used: *ca.* 1.5 cm, *ca.* 2 cm, and *ca.* 3 cm. Whole animals were pre-fixed overnight in 2% glutaraldehyde and 2% paraformaldehyde buffered with 0.1 mol l⁻¹ sodium cacodylate buffer adjusted to pH 7.2. The specimens were then rinsed several times in 0.1 mol l⁻¹ sodium cacodylate buffer solution, post-fixed for 2 h in 1% OsO₄ in phosphate buffered saline (0.13 mol l⁻¹, pH 7.4) at room temperature, dehydrated through a graded series of ethanol solutions, and rinsed in 100% *t*-butyl alcohol three times at 37 °C. Then the specimens were freeze-dried (JEOL, JFD-300) for several hours at 2 °C (Inoue and Osatake, 1988). Dried specimens were coated with OsO₄ (Meiwa, Plasma multicoater PMC-5000) and observed with a scanning electron microscope (Hitachi, S-800).

Observation of water flow using isolated pereopods

Pereopods VI and VII were autotomized by controlling their free movements with the help of a pair of fine forceps. Each pereopod was then attached to a glass electrode that penetrated the autotomized end. The other side of the electrode was held in an electrically controlled manipulator (Narishige SM-21), so that the pereopod could be stationed in its natural vertical position. The pereopod was then immersed from the tip. The water was colored with red water-soluble food dye (Tsukemoto Corporation) to facilitate observation of its flow with the help of a horizontally mounted stereomicroscope. The action was recorded on digital videotape (Sony DCR-TRV30) or with a digital camera (Nikon Coolpix 990).

Results

Behavioral observations

Ligia exotica has seven pairs of pereopods on the ventral side of the pereon (thorax), five pairs of pleopods on the pleon (abdomen), and one pair of uropods at the end of the body (Fig. 1). Individual animals can run very fast using their pereopods, each consisting of an unguis and six podites. Podites are here given numbers from 1 (the most distal) to 6, which correspond to the scientific terms of dactylopodite, propodite, carpopodite, meropodite, ischiopodite, and basipodite, respectively. The pleopods are part of the respiratory system and not used for locomotion.

When isopods were first placed in the arena, they typically walked around and explored it for several minutes before they suddenly stopped, crouched with all legs drawn into the body, and then usually rested at the edge of the arena unless disturbed. During this phase, in which the ventral side of the animal was pressed to the surface of the plastic case, the pleopods adhered to each other and did not ventilate. The body weight of each animal was determined

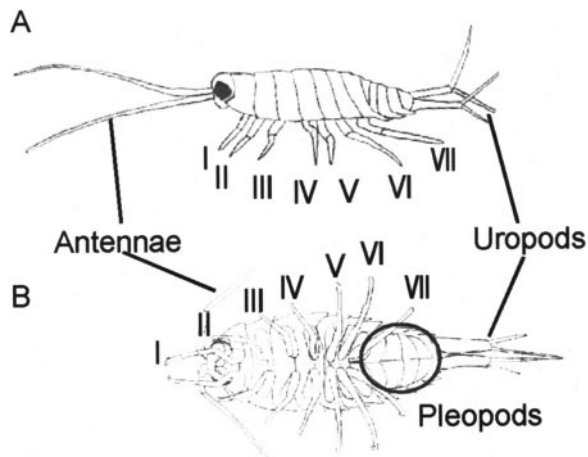


Figure 1. Lateral (A) and ventral (B) views of *Ligia exotica* to show arrangement of legs and region of the pleopods (circle).

every hour and was seen to decrease linearly, reaching about 90% of the initial weight after 3 h (Fig. 2A). After 3.5 h of desiccation, a piece of paper soaked in water was placed in

the arena. All animals then resumed walking and started to touch the wet paper. Increase in body weight was recorded from the moment the wet paper was provided. There was no obvious behavioral difference whether the paper had been soaked in distilled water or seawater. However, the rate of body-weight recovery in connection with seawater was higher than with distilled water. When dry paper was placed in the arena with the desiccated animals, a few resumed walking behaviors for a while and pressed their bodies against the bottom surface of the plastic case, but most remained motionless in spite of being disturbed. All of these desiccated animals continued to lose body mass, and some died within 5 h.

How did the desiccated animals absorb water when the wet paper was presented? When the small plastic case containing red-colored distilled water or seawater was introduced to the animals after 2 h of desiccation—a time known to result in sufficient motivation to absorb water—all animals resumed walking in the arena. Some animals happened to move onto the wet paper by chance; others moved onto it when their antennae touched the wet paper. Pereio-

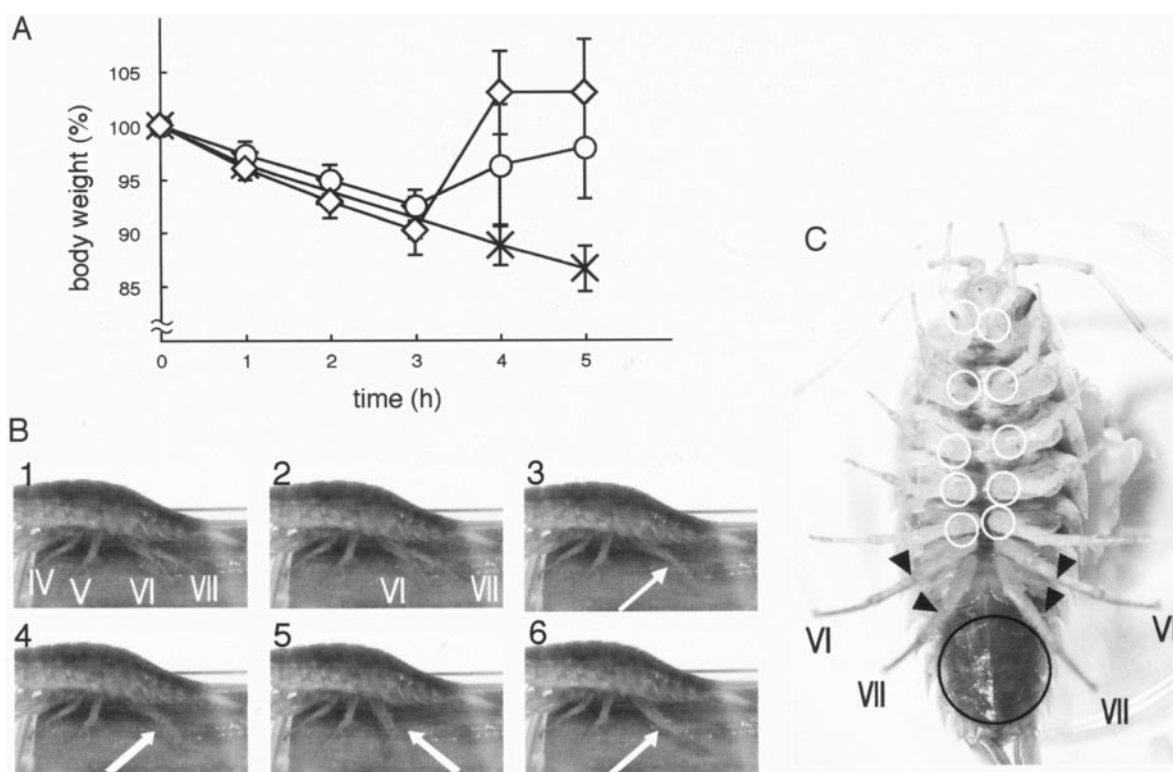


Figure 2. Change of body weight and water-intake behavior in *Ligia exotica*. (A) Body weight changes (as % initial weight) under dry conditions (0–3 h) and after access to distilled water (circle) or seawater (diamond). The number of animals in each experiment was 4 for seawater, 4 for distilled water, and 4 for the desiccation experiment. (B) Characteristic movements of VI-th and VII-th pereopods VI and VII on paper soaked with water colored red: the legs are first brought together (1–3), then moved around as a unit (4–5), before being brought to rest (6). (C) Ventral view after water uptake. The pleopods are stained red (black circle). White circles indicate relatively weak staining on pereopods I to V; black arrowheads indicate intense red staining on the surfaces of pereopods VI and VII.

pod VI was then aligned with pereiopod VII by rubbing the two against each other a few times (Fig. 2B: 1, 2, 3). After this activity, the pereiopods were apposed firmly and moved around from place to place on the wet paper as if in search of the most appropriate spot. The tips of these paired pereiopods were then kept stationary on the surface of the wet paper for several seconds (Fig. 2B: 4, 5, 6). Some animals repeated this sequence of movements of the pereiopods several times. After these pereiopodal movements, some parts of the pereiopods stained red (Fig. 2C). From pereiopods I to V, pale red spots were observed across a small area of the 4th podite (Fig. 2C, white circles), which sometimes touched the surface of the paper. Pereiopods VI and VII were deeply stained in the area where they had been closely apposed (Fig. 2C, arrowheads). Throughout this behavior on the wet paper, the animals never crouched, but kept their bodies in a raised position, so that the pleopods did not directly touch the surface of the wet paper. However, the whole vicinity of the pleopods was stained dark red, because of the accumulation of red-colored water (Fig. 2C, black circle). No obvious difference between using seawater and distilled water was seen in the actual mechanism of water uptake or in the behavior of the animal.

Structure of pereiopods VI and VII

We found three specialized structures that seemed responsible for the observed red stain on the two caudal pereiopods. Both pereiopod pairs VI and VII had hollow structures, here termed *gutters*, on the 1st and 2nd podites (Fig. 3D, black arrow). These gutters were located at the center of each pereiopod, oriented longitudinally along the podites. The gutter on the 2nd podite of pereiopod VII extended to only 80% of its length, but it ran the entire length of the 2nd podite on pereiopod VI. These gutter structures were not observed on other pereiopods or on other podites of pereiopods VI and VII.

On pereiopod VI, many narrow cuticular protrusions were seen on the surface of the cuticle in the gutter of the 2nd podite. These cuticular protrusions were in a longitudinal line (Fig. 3D, white arrow). Similar protrusions were also observed on the surfaces of the 3rd, 4th, and 5th podites, but gutters were not present (Fig. 3A, E). A number of lines were formed into a regular arrangement, following the longitudinal direction of each podite. The regular lines were observed from the distal end to the proximal end of the 3rd, 4th, and 5th podites, but were only seen at the proximal

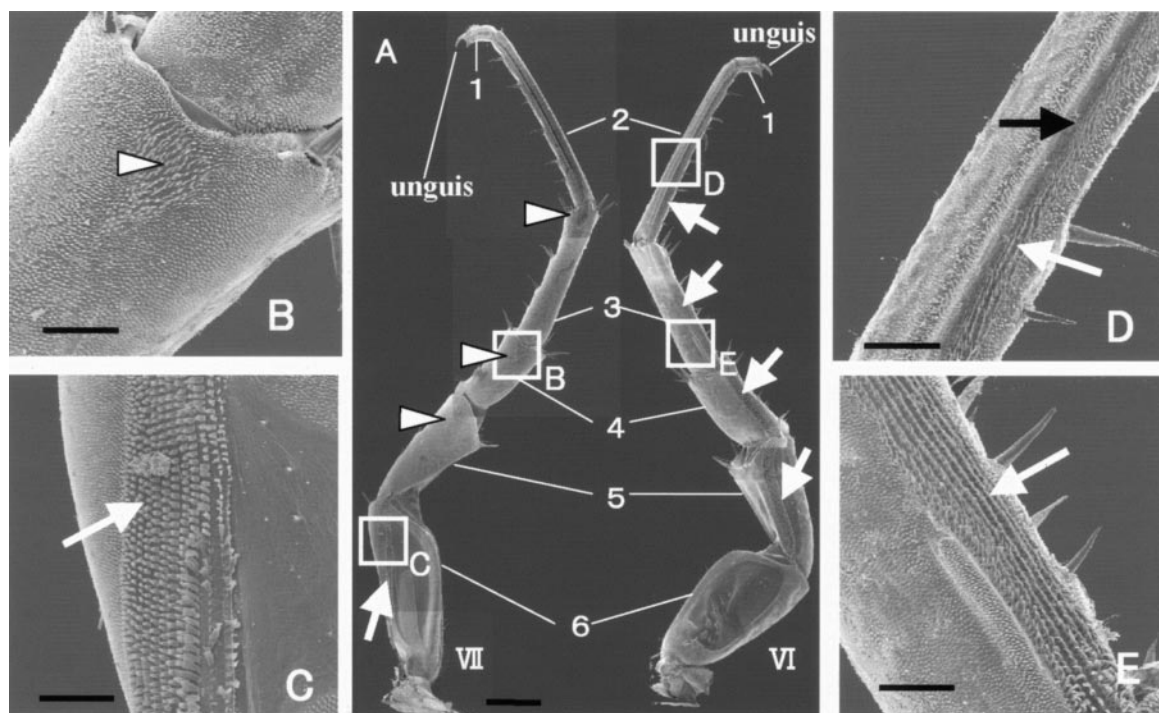


Figure 3. Scanning electron micrographs of pereiopods VI and VII (from a specimen of 30.5 mm in body length). (A) Pereiopods VI and VII with gutter on 1st and 2nd podite. White arrows indicate regular lines of protrusions; arrowheads indicate long cuticular hairlike protrusions of pereiopod VII. Rectangles B–E indicate positions of higher magnification in B–E. The scale is 1.5 mm. (B) The 4th podite of pereiopod VII with patch of long cuticular hairlike protrusions (arrowhead), and (C) 6th podite with closely spaced rows of pegs (arrow). (D) The 2nd podite of pereiopod VI, showing gutter (black arrow) and well-defined lines of cuticular hair protrusions (white arrow); (E) 3rd podite with closely aligned cuticular hair protrusions, forming well-defined longitudinal lines of hairs (arrow). The scale in B, C, D, and E is 300 μ m.

half of the 2nd podite. The regular lines of protrusions were not observed on the 1st and 6th podites of pereopod VI.

On pereopod VII, the regular lines of protrusions were observed only on the 6th podite (Fig. 3C, arrow). In addition, there were small areas of thin, relatively long cuticular protrusions at the distal ends of the 3rd, 4th, and 5th podites of pereopod VII. These cuticular protrusions were not aligned in longitudinal and regular lines (Fig. 3B, arrow-head).

Structural comparison of the regular lines of protrusions in animals of different sizes

The width of the regular lines of the cuticular protrusions, the greatest width between the longitudinal lines of the cuticular protrusions, and the number of lines involving the 3rd, 4th, and 5th podites of pereopod VI were measured from scanning electron micrographs of *L. exotica* in three size classes: small (ca. 1.5 cm), medium (ca. 2.0 cm), and large (ca. 3.0 cm). The data follow allometric relationships ($y = ax^k$; $\log y = k \log x + \log a$) as illustrated in Figure 4. The width of the regular lines, which is the distance from the end line to the line of the other side, on each podite of the large specimens was about twice that of the small specimens, and the scaling exponent k in the width of the regular lines was about 1.0 (Fig. 4A). The width between the lines, which corresponds to the distance between one line and its adjacent line, followed a consistent pattern: widest at the center; narrower towards the periphery. The widest gaps were used for comparisons between the animals. The widths between the lines varied little over the range of animal sizes monitored. The width between the lines in large specimens was only about 1.3 times greater than that of small specimens for each podite, and the k value was about 0.3 (Fig. 4B). The number of lines in large specimens was about 1.5 times greater than that in small specimens for each podite (Fig. 4C). All three parameters showed proportionality with body size, but the k values were different. The lowest value was the ratio of the width between the lines.

Water flow along the isolated pereopods

Water flow along the isolated pereopods is illustrated in Figure 5. When the middle part of the 2nd podite of pereopod VI was dipped into the water, water started to flow upward against gravity, following the regular lines, as far as the joint between the 2nd and 3rd podites (Fig. 5B). When the distal end of the 3rd podite touched the surface of the water, water again flowed upward within a few seconds, reaching the joint between 5th and 6th podites, but not any farther onto the 6th podite (Fig. 5C). Even with the distal end of the 6th podite dipped into water, no further upward flow was observed (Fig. 5E).

In pereopod VII, despite gradual sequential immersion

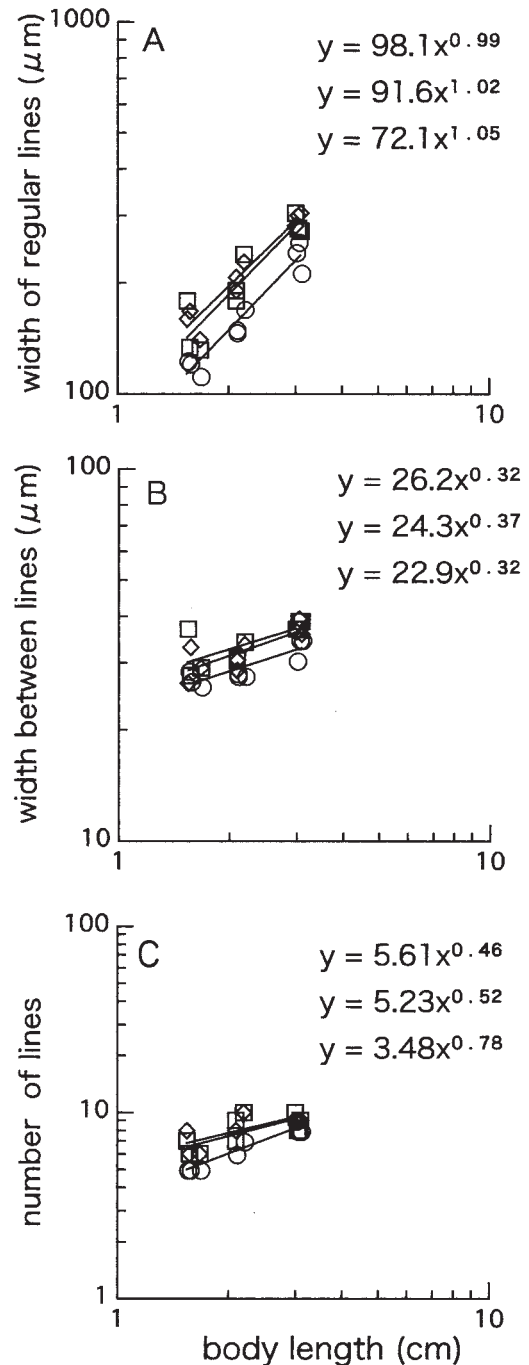


Figure 4. Relationships between regular lines of cuticular protrusions for different body size classes of *Ligia exotica* (abscissa). The ordinates show (A) width of the regular lines of the cuticular protrusions, (B) width between the widest rows of cuticular hair lines, and (C) number of lines. The symbols mean the following: circle, 3rd podite; square, 4th podite; diamond, 5th podite. Each symbol indicates the mean ($n = 10$) of small, medium, and large animals in A and B. The regressions for each podite are drawn as solid lines.

from the unguis to the 5th podite (Fig. 5G, H), no water flow was observed until the distal end of the 6th podite itself touched the surface of the water. Only then did water begin

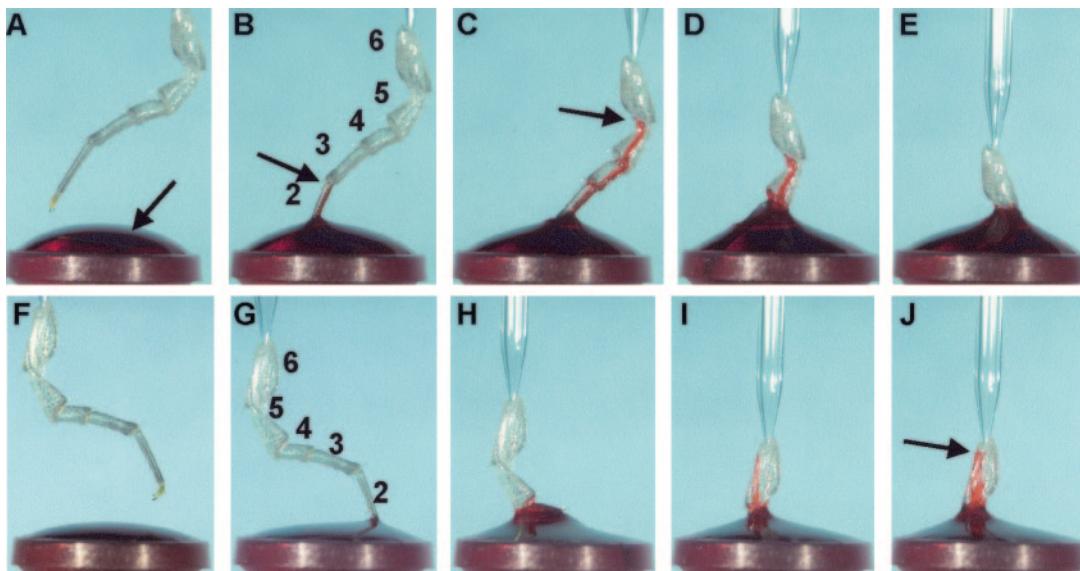


Figure 5. Illustration of water flow along the caudal side of pereopod VI (A–E) and the frontal side of pereopod VII (F–J). (A) Just prior to contact with water of pereopod VI (arrow indicates meniscus of red-colored water at top of tube); (B) water rises only as far as the proximal end of the 2nd podite (arrow); (C) on dipping the 2nd podite into water, the water moves up podites 3–5; (D, E) even after full immersion there is no further upward flow. (F–J) A similar experiment with pereopod VII. Note that water flows upward only when the distal end of the 6th podite is in contact with the water (I and J).

to flow to the proximal end of the 6th podite, following the regular lines within a few seconds (Fig. 5I, J).

Water flow along the isolated pereopods could not be observed when the pereopods were completely desiccated, so they were given appropriate moisture before the observation.

Discussion

Cuticular microstructures in peracaridan crustaceans, including aquatic (Meyer-Rochow, 1980) and terrestrial isopods (Schmallfuss, 1978a, b) as well as amphipods (Meyer-Rochow, 1981), are extremely varied and often highly elaborate. In *Ligia exotica*, the structural specializations found on pereopods VI and VII are clearly part of the water-conducting apparatus that Hoese (1982) termed “*Ligia*-type-system.” Hoese (1982) correctly concluded that water was sucked in by grooves on pereopods VI and VII through capillary action, and he proposed that the water-conducting system of the *Ligia*-type helped distribute moisture over the body surface and was involved in respiration, thermoregulation, excretion, osmoregulation, and cleaning. Hoese (1982) did concede, however, that “die Rezeption des Wasserbedarfs, d. h. der oder die Auslöser, die die Wasseraufnahme verursachen” (in English: “the perception of water-need, i.e., the trigger or initiators that caused water uptake”) were not known to him. Furthermore, he did not determine why both pairs of pereopods (i.e., VI and VII) were necessary for the water uptake.

We now know that despite some behavioral anti-desiccation measures taken by *L. exotica*, like crouching and keeping the pleopods motionless close to the body, an animal with a body length of about 2.5 cm and a pre-desiccation weight of about 500 mg will steadily and linearly lose weight to 90% of the initial weight in 3 h; longer periods of desiccation with no access to water will prove fatal. Therefore, regular access to water is essential for *L. exotica*, and if an individual wishes to forage on dry land, as has been pointed out before by, for example, Edney (1951), it needs to reduce its body temperature through evaporation of water from the extensive surface area of its dorsoventrally depressed body.

Water-uptake behavior in *L. exotica* commences when the antennae touch the surface of a water-containing substrate. The animals then crawl onto the wet area and scrape their caudal pereopods several times across the surface, before placing the two most caudal pereopods on each side together and moving them around as a unit, seemingly to locate the most suitable place to absorb water. In our experiments, the pleopods then quickly stained red even though the pleopods themselves were never in direct contact with the wet area. No other regions of the body (except for limited areas on the pereopods) were stained.

Although we observed no difference in the water-uptake mechanism between seawater and distilled water, there was a slight difference in the recovery of body weight. This observation suggests that *L. exotica* has a tendency to more

effectively (or preferentially) absorb seawater rather than distilled water. It will sometimes be forced to accept puddles filled with rainwater, and thus it might be able to use both freshwater and seawater, but it clearly gains more weight from seawater. This could be a reason why these isopods rarely venture far from the edge of the sea. Further studies with choice experiments will be needed to test whether *L. exotica* detects water bodies of different salinity.

L. exotica has seven pairs of pereopods, but the characteristic structures—here referred to as “the regular lines”—were found only on the caudal pereopods VI and VII. When individuals of *L. exotica* scrape their caudal pereopods against each other before water uptake commences, long cuticular protrusions on podites 3–5 of pereopod VII will presumably be brought into contact with the regularly arranged cuticular protrusions referred to as the regular lines. With individual, autotomized caudal pereopods, water flow along the regular lines of both pereopods VI and VII was observed, but no water flow was observed when the pereopods were desiccated. The scraping movements at the beginning of the water uptake seem to encourage water flow along the surface of the regular lines of each pereopod by elevating the affinity to water of the cuticular protrusions.

Allometric relationships ($y = ax^k$) between the widths of the regular lines, the widths between the lines, and the number of lines in relation to body size are shown in Figure 4. The k value of the widths of the regular lines was about 1.0; meaning that it was almost proportional to body length and that a doubling in body length resulted in regular lines twice as wide. However, the k value of the widths between the individual lines of protrusions was about 0.3. The widths between the lines were relatively constant and independent of body size, which suggests that the width between these lines of protrusions is functionally constrained. Instead of enlarging the widths between the lines, *L. exotica* increases the number of lines at each molt. Further study on the physics of this arrangement will be needed to test this “optimal separation hypothesis.”

Marked differences in water flow were observed with the autotomized caudal pereopods. As pereopod VI was dipped into water from the unguis, water flow did not occur unless the middle part of the 2nd podite was also brought into contact with the water. When the distal end of the 3rd podite was immersed, water flowed rapidly, but not beyond the 6th podite. There are no regular lines on the 6th podite of pereopod VI. With pereopod VII, no water flow was observed unless the distal end of the 6th podite was in contact with the water. This corresponds to the only region of the 6th podite that possesses the regular lines. On both pereopods, water flow was observed only in the region where there were the regular lines of protrusions, and thus water conduction was impossible along the entire length of either pereopods VI or VII alone. When *L. exotica* brings pereopods VI and VII together, it seems that a small pipe

forms along the gutters of the 1st and 2nd podites through which water can flow by capillary action. Water flow along the separated (*i.e.*, non-apposed) pipe does not occur. This would explain Hoesé's (1982) observation that *L. exotica* can take up water only when putting pereopods VI and VII together. A system such as this may prevent unstoppable, passive water absorption and have a regulatory function.

The pleopods of truly terrestrial Oniscidea are used for air breathing (Warburg, 1993), but in *L. exotica* they closely approach gills in their way of functioning and thus require large amounts of moisture (Schmidt and Waagele, 2001). Desiccation of the body surface, and in particular the pleopods, may therefore cause *L. exotica* to suffocate. Water uptake, using the two pairs of caudal pereopods, enables *L. exotica* to supply water directly to the pleopods. After *L. exotica* had taken up red-colored water with its pereopods, we dissected some animals to inspect the digestive tract. The foregut and oral cavity were not stained, but the hindgut near the anus (a slit-like opening on the ventral side of the terminal segment) was deeply stained red. This suggests that the increase in body weight in desiccated individuals occurs when water, taken up by them in the way described, moves up the anus. In our experimental conditions we saw neither drinking behavior resembling that described by Carefoot and Tayler (1995), nor signs that water was being lapped up to then be distributed around the body by mouth, as suggested by Hoesé (1982). Water uptake through the anus, however, is a well-known phenomenon in many crustaceans (Fox, 1952) and has been known in crayfish for more than a hundred years (Huxley, 1880). The results presented here clearly show that the semiterrestrial crustacean *L. exotica* is also able to absorb water through the anus. A similar rectal uptake of water in *Porcellio scaber* was suggested by Drobne and Fajgelj (1993). According to earlier reports referred to above, oral uptake of water may also occur in *L. exotica*, but clearly under conditions different from those used in our study. Only further experiments will be able to clarify whether two points of water entry exist in this species.

Barnes (1932) thought water uptake in *L. exotica* was assisted by the uropods. But in agreement with Hoesé (1982), we found no direct evidence for this assertion when wet paper was used as a substrate. However, there may be some relationship between the method of water uptake and the amount of water in the substrate. The use of the pair of caudal pereopods appears to be most suitable for the absorption of water from an area containing limited amounts of moisture, such as a wet surface film of water on rocks exposed to the spray of seawater. Several semiterrestrial crabs can extract interstitial water from damp sand by using closely spaced tufts of long cuticular protrusions on their legs (Walcott, 1976). In this paper, we revealed that *L. exotica* has a specific method to replenish water loss, but one that requires this species to remain close to the edge of

the sea and not venture farther inland. The evolution of a system that controls salinity under these situations is a question that remains to be investigated for this species.

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