

PHYSIOLOGICAL ABSORPTION OF LIQUID WATER BY COLLEMBOLA: ABSORPTION BY THE VENTRAL TUBE AT DIFFERENT SALINITIES

GERHARD EISENBEIS

Institut für Zoologie der Johannes Gutenberg-Universität, Saarstrasse 21, D-6500 Mainz a.Rhein,
Federal Republic of Germany

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Abstract The ability to absorb solutions has been examined in the coxal vesicles of the ventral tube in two sympatric surface dwelling Collembola (*Tomocerus sp.* and *Orchesella villosa*) from a beech forest. The net influx of distilled water and different sodium chloride solutions was measured, followed by examination of the effective surface of the vesicles which contacts the medium. The transport rate decreased with increasing salinity of the medium. *Orchesella* always showed higher absorption rates than *Tomocerus*, if the values were related to unit surface area. However, considering that the effective surface area of the vesicles of *Tomocerus* is larger, the total absorption rate by the ventral tube of *Tomocerus* exceeded that of *Orchesella*. Calculating the increase in the total water content, *Orchesella* compensated for its deficit faster than *Tomocerus*, because *Orchesella* is smaller in total weight and water content. In most cases the efficiency of the absorptive epithelium decreased during an absorption cycle; this also occurred before moulting. Some hours after moulting, the absorption rates increased to their former level. Comparing the rates of transpiration, absorption by the ventral-tube vesicles, and drinking, confirmed the dominant role of the ventral tube in the water balance of Collembola. It is an important factor in the strategy of adaptation from the hypogaic to the epigaic life.

Key Word Index: Absorption, coxal vesicles, transport epithelium, adaptation, moulting, Collembola

INTRODUCTION

AMONG arthropods, the ability to absorb water in the liquid phase evolved in different ways. It is especially common in apterygote insects (except for *Zygentoma*) by means of abdominal coxal vesicles, which play an important role in water balance (NUTMAN, 1941; SEDLAG, 1952; NOBLE-NESBITT, 1963; SMITH, 1970; BITSCH and PALEVODY, 1973; WEYDA, 1974; EISENBEIS, 1974, 1976a; HOULIHAN, 1976). Under dry conditions, most hygic Collembola are very susceptible to the loss of water and seek refuge in moist cavities in the soil. They aggregate in the deeper litter. At night and during suitable climatic conditions, they leave the soil and climb plants (BAUER, 1979). The significance of humidity for the stratigraphic and aggregative formation of Collembolan populations is pointed out by JOOSSE (1970, 1971) and KACZMAREK (1975). Rates of life cycles are also influenced by lowered humidity. On the other hand, hygic Collembola lose water if the atmosphere is saturated with water vapour.

If Collembola are dehydrated excessively and replaced on a moist surface, they absorb water by everting their ventral-tube vesicles. The absorption rate is very high and the animals make good their water deficit in a short period. In the present study, two soil-litter dwelling Collembola, *Tomocerus sp.* and *Orchesella villosa* were compared under different experimental conditions. First an attempt was made to measure the net influx of water per unit surface area of vesicles. Then the influence of salinity on the transport rate was examined. The ventral-tube vesicles consist of a transport epithelium underlying a thin permeable cuticle (EISENBEIS, 1974; EISENBEIS and WICHARD,

1975a, b). Subjecting the epithelium to increased salt concentrations causes alterations in the ultrastructure (EISENBEIS and WICHARD, 1977). An attempt was made to compare transpiration and absorption rates and to evaluate the ecological significance of these special water-absorbing organs.

MATERIALS AND METHODS

The springtails were collected from the upper layers of soil litter in a beech forest in the Taunus region near Schlangenbad and Wiesbaden, and were kept in small boxes together with the material from their habitat. As a rule, *Tomocerus* spp. (*Tomocerus longicornis*, *Tomocerus flavescens*) inhabit moist parts between the dry litter and fermentation layer, whereas *Orchesella villosa* can be found mostly in the dry parts of the litter. Identification was based on PALISSA (1964), but the two spp. of *Tomocerus* could not be separated. However, there was no evidence of any differences in response to the treatments.

Measurement of transpiration and of absorption

Weighings were made with a recording Sartorius electrobalance (model 4431; sensitivity 1 μ g) and a mechanical microbalance (Sartorius model 2405; sensitivity 1 μ g). For measuring the weight losses and gains the animals were exposed in a small cage made from wire-mesh (copper or steel with mesh size 0.5 mm). Figure 1 shows the electrobalance fixed in a steel construction to avoid disturbances from the ground. Figure 2 shows a section through the balance and the glass vial, with the animal housed in the cage. Relative humidity was adjusted with saturated salt

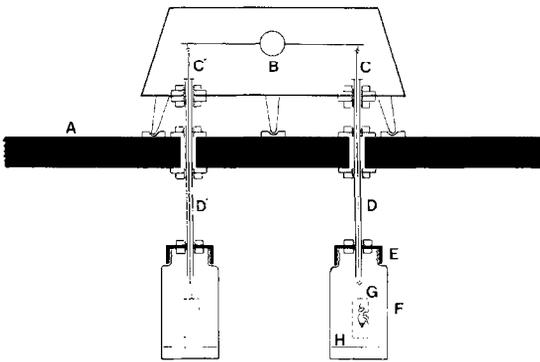


Fig. 2. Section through the ultramicrobalance modified for 'underfloor' measurement. The balance is connected by thin wires of 0.1-mm diameter to small cages (copper or steel), which are located within glass vials (25 ml). (A) Steel plate (thickness: 2 cm); (B) Balance box; (C, C') Balance levers, connected with wires; (D, D') suspended tubes (diameter: 3 mm); (E) Screw cap; (F) Glass vial of 25 ml capacity; (G) Cage, housing the animal; (H) Water or saturated salt solutions.

solutions (WINSTON and BATES 1960) and monitored with a Rotronic thermohygrometer (Hygroscope BT with DMS 100 H sensor).

For measurement of transpiration, the animals were taken from soil litter and placed in the balance. The first step was to determine the initial total weight. After taring the balance, the weight loss was recorded in a 33% r.h. atmosphere at 22°C to -20% of the initial water content (Fig. 3, interval T1). T1 was followed by the first absorption phase (interval A1). Then the animal was replaced in the balance for recording the weight gain by absorption and for following a further transpiration measurement (interval T2).

For measurement of absorption, a filter paper of 25-mm diameter was wetted with 100 µl of distilled water or a 50, 125 or 250-mosmol/l NaCl solution. Then the animal was taken from the balance and placed in a glass vial together with the wet filter paper. During this time, the weight recording was continued

to the -20% level (Fig. 3). As a rule the ventral-tube vesicles absorbed during a 5-30 minute period and then the animal was replaced in the balance. There followed a cycle of successive intervals of transpiration and absorption, modified by changing the different solutions for absorption. In most cases, the animals had to absorb 5-10 times. To avoid condensation of water within the glass vial during the absorption period, the vial was placed on wet tissue paper at room temperature (22-24°C).

Determination of the surface area of ventral-tube vesicles

The outer surface of the vesicles represents the apical surface of the transport epithelium. At the end of an absorption cycle the animals were submersed immediately in 70% alcohol. As a rule, the coxal vesicles are everted by haemolymph pressure. The first step was to measure the effective vesicle surface area. During the absorption period, the coxal vesicles are not pressed fully against the wet filter paper. They form a pistil-like organ, which makes water contact only in the distal part (Fig. 4a, b). The surface area determinations were made by drawing the outline of the vesicles in ventral view using a Wild M5 Stereo microscope with a drawing mirror and measuring the area by planimetry. After fixation in Bouin's solution, the animal was macerated carefully, embedded in a polyvinyl-lactophenol medium and pressed under small lead weights for some days. Then followed the determination of the total vesicle surface area. The total body surface area was calculated by the formula of MEEH (see Tables 2, 3 and VANNIER, 1972).

Determination of the water content

Water content of Collembola and other soil arthropods was measured as the difference between the initial total weight and the dry weight (without lipid extraction), determined at 70°C over P₂O₅ (EISENBEIS, unpublished).

RESULTS

Water content of soil-litter inhabiting Collembola varies little, if the animals are kept moist in boxes

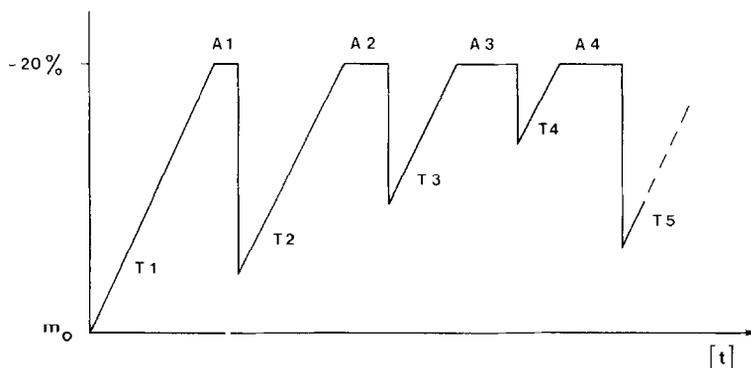


Fig. 3. Sequence of transpiration (T) and absorption intervals (A). During transpiration periods the animals are exposed to 33% r.h. at 22°C. For absorption the animals are placed on wet filter paper. All absorption experiments are started at the same level of dehydration for each animal, nearly -20% of the initial water content (m_0). After a few minutes, when given access to water (in most cases 5-30 min), the absorption period is interrupted. Only after a longer period of about 1 hr, the animals return to their initial weight or more. As a rule, the animals had to absorb 5-10 times.



Fig. 1. The ultramicrobalance (Sartorius model 4431), placed in a steel pyramid and connected to a cooling and recording system. Isolation is achieved by aluminium coated styropore plates which can be removed in the front door of the temperature controlled and ventilated area. (A) Balance chamber; (B) Temperature controlled and ventilated area; (C) Cooling system; (D) Recording system.

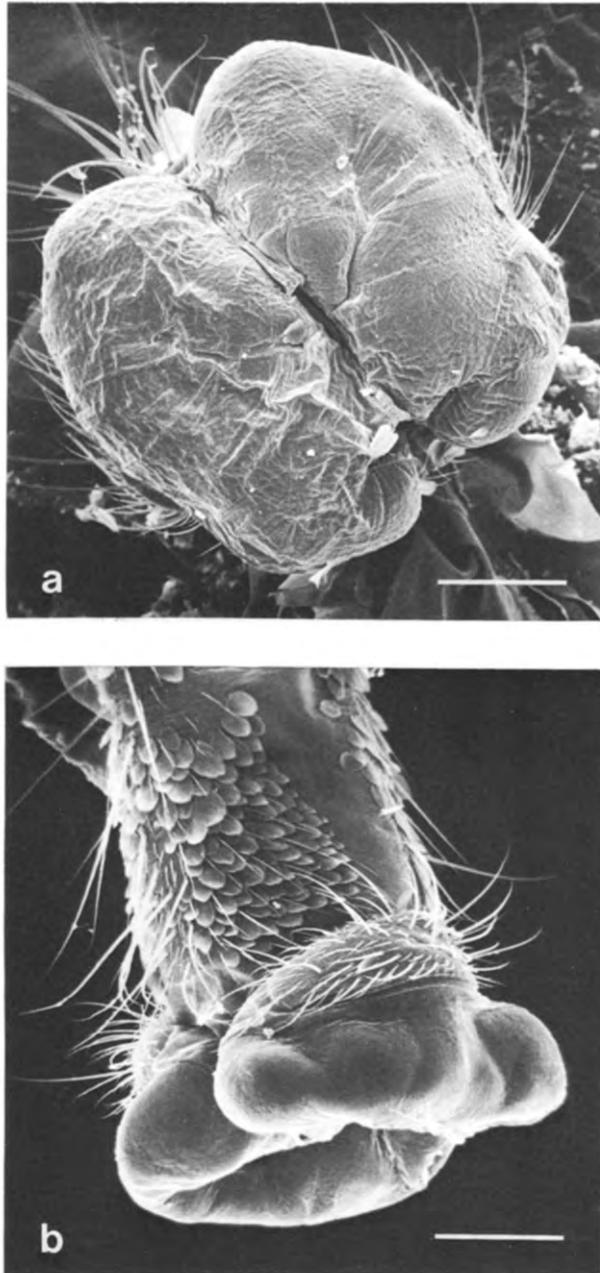


Fig. 4. Scanning electron microscope view of the distal part of *Tomocerus* ventral tube (OsO₂-Fixation;Critical Point Drying).
(a) Ventral view of everted vesicles, showing little signs of shrinking. The outlines represent the area of the effective absorbing surface of vesicles. Scale line: 100 μ m.
(b) Lateral view of partly everted vesicles. Scale line: 100 μ m.

Table 1. Water content of *Tomocerus* and *Orchesella*, as percentage of total weight, based on data from different experimental series

<i>Tomocerus</i>				<i>Orchesella</i>			
<i>n</i>	\bar{x}	<i>s</i>	s/\sqrt{n}	<i>n</i>	\bar{x}	<i>s</i>	s/\sqrt{n}
40	77.1	5.0	0.9	33	75.8	4.3	0.7
9	82.1	1.9	0.6	5	75.3	1.9	0.8
9	80.6	2.7	0.9	9	74.5	3.1	1.0
8	78.2	1.4	0.5	5	76.3	3.4	1.5
11	80.4	3.3	1.0	7	74.2	1.9	0.7
				12	75.3	3.6	1.0

together with material from their habitat. Unpublished data show that there are no remarkable effects of either the animals' size or changing seasonal conditions on the initial water content. After a dry period of about 4 weeks, *Tomocerus* showed no signs of dehydration, when the animals were captured from slightly moistened islets in the dry soil litter of beech forests. The average water content of normal hydrated animals is shown in Table 1. In the present study, the initial water content is calculated as being 80 and 75% of the total weight for *Tomocerus* and *Orchesella* respectively.

Hygic Collembola which are fully hydrated tolerate water loss to about 30% of their initial water content. Then they become motionless and die after a short period. A loss of water content of 20% proved to be the most suitable for absorption experiments and did not affect the animals. Immediately after exposure to a wet filter paper they evert their ventral-tube vesicles by haemolymph pressure and contact the paper. At high salinity of the medium the eversion continues for a few seconds only and then they retract the vesicles into the ventral-tube body. Because the

everted vesicles are visible when a large water deficit is created, it is possible to see that the effective surface area of the vesicles is unchanged within this range of hydration states. Animals with a small water deficit evert their vesicles for a short period only and then they retract them. All absorption experiments have been carried out at the same level of dehydration for each animal.

After a period of about 1 hr, the animals regain or add to their initial weight when given access to water of a low salinity. However, the main absorption period occurs within the first 10–30 min. Within this time animals evert their vesicles for a long period (e.g. for 5–15 min) followed by a short retraction into the ventral-tube body. Retraction periods increase with a lowering of the water deficit. After 1 hr, in most cases, the vesicles are no longer visible. It was not investigated, whether the rate of fluid uptake was greater over the first few minutes compared with later uptake over a short period. But comparing 2 absorption periods of 5 and 10 min, in most cases, double the fluid uptake can be found after 10 min. The uptake of water by means of the vesicles is visible using a simple pocket lens. In most cases the mouth is at a suitable distance from the wet paper, and some animals show drinking movements in pushing and retracting the head. Data from such animals were not used when calculating the rates of absorption by vesicles. The mouths of some animals were closed with histoacryl in order to prevent drinking. Water uptake by the vesicles was not affected by such treatment.

Biometric data

Tables 2 and 3 show some biometrical data for *Tomocerus* and *Orchesella*. *Tomocerus* is larger than *Orchesella*, but the surface area constants from the

Table 2. Biometrical data for *Tomocerus*

	w_0 (mg)	m_0 (mg)	S_t (mm ²)	S_{Vt-t} (mm ²)	S_{Vt-eff} (mm ²)	S_{Vt-eff}/S_t	S_{Vt-eff}/w_0
\bar{x}	3.542	2.833	24.30	0.359	0.186	0.00768	0.0547
<i>s</i>	0.915	0.732	3.97	0.144	0.026	0.00051	0.0037
s/\sqrt{n}	0.221	0.177	0.96	0.038	0.006	0.00012	0.0009
min	2.327	1.862	18.48	0.227	0.130	0.00655	0.0470
max	6.422	5.137	36.33	0.715	0.238	0.00855	0.0597
<i>n</i>	17	17	17	17	17	17	16

Data on the total weight (w_0), the initial water content (m_0), the total body surface of the animals (S_t : without scales and hairs), the total surface of ventral-tube vesicles (S_{Vt-t}), the effective surface of ventral-tube vesicles (S_{Vt-eff}) and some relations between them. The total body surface has been calculated by the formula of MEEH (see VANNIER, 1972): $S = k_s \times w_0^{2/3}$. ' k_s ' has been experimentally determined as $k_s = 10.53 \pm 0.57$; $n = 30$ (EISENBEIS, unpublished.).

Table 3. Biometrical data for *Orchesella*

	w_0 (mg)	m_0 (mg)	S_t (mm ²)	S_{Vt-t} (mm ²)	S_{Vt-eff} (mm ²)	S_{Vt-eff}/S_t	S_{Vt-eff}/w_0
\bar{x}	2.355	1.767	18.90	0.201	0.110	0.00589	0.0477
<i>s</i>	0.348	0.257	1.86	0.059	0.013	0.00084	0.0086
s/\sqrt{n}	0.096	0.071	0.51	0.016	0.004	0.00023	0.0024
min	1.633	1.247	15.01	0.115	0.088	0.00477	0.0360
max	2.886	2.164	21.67	0.307	0.138	0.00740	0.0625
<i>n</i>	13	13	13	13	13	13	13

Data on the total weight (w_0), the initial water content (m_0), the total body surface of the animals (S_t : without hairs), the total surface of ventral-tube vesicles (S_{Vt-t}), the effective surface of ventral-tube vesicles (S_{Vt-eff}) and some relations between them. The total body surface has been calculated by the formula of MEEH (see VANNIER, 1972): $S = k_s \times w_0^{2/3}$. ' k_s ' has been experimentally determined as $k_s = 10.70 \pm 0.78$; $n = 32$ (EISENBEIS, unpublished.).

formula of MEEH ($S = k_s \cdot w_0^{2/3}$) are nearly identical ($S = \text{surface}; w_0 = \text{initial total weight}; k_s = \text{constant}$). *Tomocerus*: $k_s = 10.53 \pm 0.57$, $n = 30$; *Orchesella*: $k_s = 10.70 \pm 0.78$, $n = 32$. In this study, the means of the effective surface area of the vesicles of *Tomocerus* amount to 0.186 mm^2 and of *Orchesella* to 0.110 mm^2 . The percentage of effective vesicle area relative to the total body surface area is 0.768 for *Tomocerus* and 0.589 for *Orchesella*. The ratio effective vesicle area/total weight gives mean values of 0.0547 for *Tomocerus* and 0.0477 for *Orchesella* (Tables 2, 3). By means of these data it is possible to estimate the effective surface of the ventral-tube vesicles by weighing the animals.

Absorption of water by ventral-tube vesicles

Tables 4 and 5 show the average net rates of water influx in $\mu\text{g}/\text{mm}^2/\text{min}$ related to the effective vesicle

area and for all absorbing cycles. Both *Tomocerus* and *Orchesella* reduce their uptake from water of increased salinity. But for all conditions, *Orchesella* shows higher rates of absorption. In Fig. 5 the maximal rates are compared per unit area and for all animals. The differences between the data in Tables 4, 5 and Fig. 5 are due to the reduction in transporting activity during the absorbing cycles. As a rule, the animals show their maximal rates during the first 3 absorbing periods. Only a few specimens of *Orchesella* were able to absorb from a 250-mosmol/l NaCl solution. It is also shown, that uptake by *Orchesella* is more efficient at lower salinity. But considering, that the effective surface area of the vesicles of *Tomocerus* is absolutely larger, the total absorption rate by the ventral tube of *Tomocerus* exceeds that of *Orchesella*, when the animals were exposed to distilled water and a 50-mosmol/l NaCl solution (Fig. 6). On exposure to

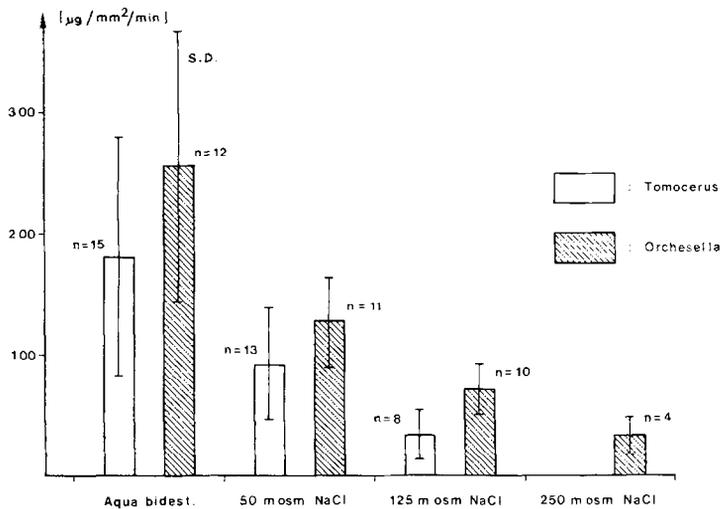


Fig. 5. Absorption by the ventral-tube vesicles of *Tomocerus* and *Orchesella* from different salt solutions. The maximal absorption rates are given in $\mu\text{g}/\text{mm}^2/\text{min}$ related to unit area of the effective vesicle surface.

Table 4. Absorption of solutions by the ventral tube of *Tomocerus*

	<i>Aqua bidest.</i>	50-mosmol/l NaCl	125-mosmol/l NaCl
\bar{x}	150.5	83.6	28.3
s	91.4	44.8	20.0
s/\sqrt{n}	14.8	8.6	5.8
min	28.8	15.1	3.0
max	428.6	209.0	65.5
n	38	27	12

The rates have been related to the effective vesicle surface area; net influx measured in $\mu\text{g}/\text{mm}^2/\text{min}$; all absorption cycles included.

Table 5. Absorption of solutions by the ventral tube of *Orchesella*

	<i>Aqua bidest.</i>	50-mosmol/l NaCl	125-mosmol/l NaCl	250-mosmol/l NaCl
\bar{x}	192.2	116.2	95.4	31.7
s	87.4	44.3	78.0	15.1
s/\sqrt{n}	14.2	9.9	20.8	6.7
min	86.9	20.8	37.9	17.5
max	555.5	164.6	286.4	55.5
n	38	20	14	5

The rates have been related to the effective vesicle surface area; net influx measured in $\mu\text{g}/\text{mm}^2/\text{min}$; all absorption cycles included.

125-mosmol/l NaCl, *Orchesella* always absorbed at higher rates.

The influence of uptake by the ventral tube on the total water content is shown in Tables 6 and 7. The rates are expressed as the percentage uptake over the initial water content. In both cases the rates were lower with increasing salinity, but those of *Orchesella* were higher under all conditions. The rates are related to all absorbing stages. In Figs. 7 and 8 water balance is shown by comparing the transpiration rates at different r.h. and the maximal absorption rates. It is evident that absorption rates at lowered salinities considerably exceed the transpiration rates. The greatest differences were found in *Orchesella*. But both in *Tomocerus* and in *Orchesella* the highest rates of uptake resulted from drinking. In some cases the animals also drank salt solutions.

The influence of moulting on the absorbing activity

is shown in Figs. 9 and 10. Before moulting, animals try to absorb but the rates are very low. Some hours after moulting, the absorption rates increased to their previous level. Premoulting-stage animals also seem to be less able to absorb from the higher salinity media. This indicates that there are considerable differences in the absorbing activity of animals. For example, Tables 5 and 7 show a wider range in the 125-mosmol/l min-max data than in the 50-mosmol/l group, which can be explained by such differences in the absorbing activity of individuals.

DISCUSSION

EDNEY (1977) pointed out, that liquid-water absorption by arthropods is a neglected field so far as quantitative experimental work is concerned. These results are an attempt to quantify the uptake of liquid

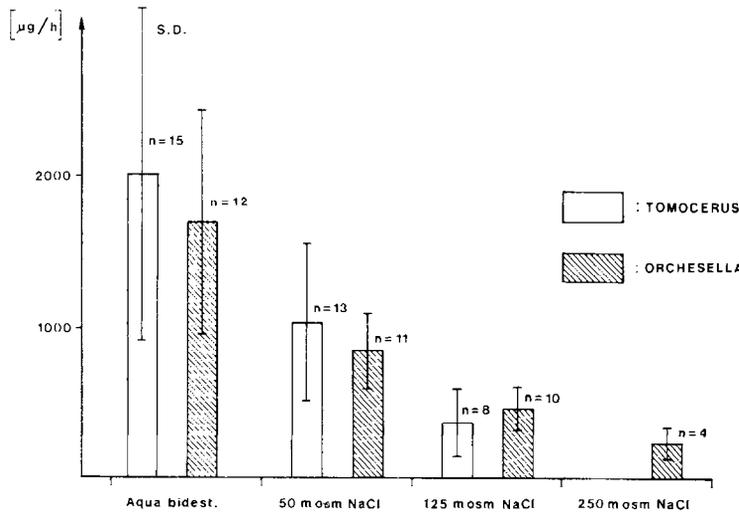


Fig. 6. Absorption by the ventral-tube vesicles of *Tomocerus* and *Orchesella* from different salt solutions. The maximal absorption rates are given in µg/hr related to the total effective vesicle surface area.

Table 6. Absorption rates by the ventral-tube vesicles of *Tomocerus* as percentage gain of water content per hour (+m^o₀/hr) related to the initial water content (m₀); all absorption cycles included

	<i>Aqua bidest.</i>	50-mosmol/l NaCl	125-mosmol/l NaCl
\bar{x}	61.1	34.7	11.3
<i>s</i>	35.5	19.9	7.7
<i>s/Vn</i>	5.9	3.8	2.2
min	18.1	6.4	1.3
max	170.8	90.1	27.4
<i>n</i>	36	27	12

Table 7. Absorption rates by the ventral-tube vesicles of *Orchesella* as percentage gain of water content per hr (-m^o₀/hr). related to the initial water content (m₀); all absorption cycles included

	<i>Aqua bidest.</i>	50-mosmol/l NaCl	125-mosmol/l NaCl	250-mosmol/l NaCl
\bar{x}	72.8	43.3	33.2	12.5
<i>s</i>	36.2	17.7	22.4	4.3
<i>s/Vn</i>	5.9	3.9	6.0	1.9
min	29.5	7.1	15.3	6.7
max	213.1	66.1	92.4	17.9
<i>n</i>	38	20	14	5

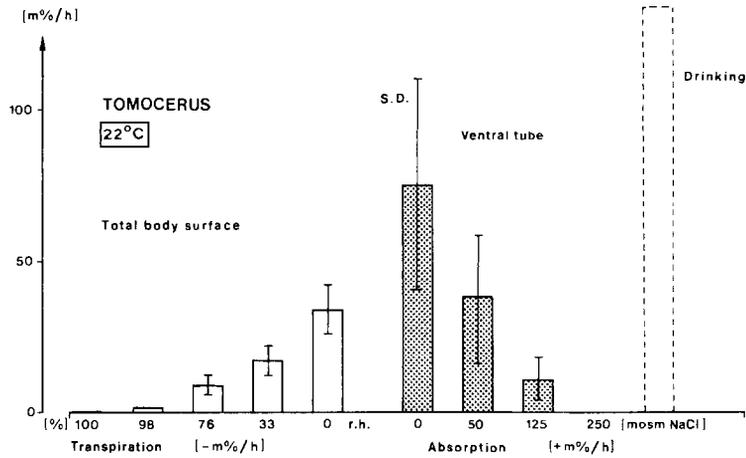


Fig. 7. Water balance of *Tomocerus*. On the left: transpiration rates at different r.h. as percentage loss of water content per hour ($-m^{\circ}_o$ /hr), related to the initial water content (m_o); on the right: maximal absorption rates by the ventral-tube vesicles and rate of drinking by mouth as percentage gain of water content per hour ($+m^{\circ}_o$ /hr), related to the initial water content (m_o). The animals also lose water in a 100% saturated atmosphere, but the transpiration rate is very low, e.g. -0.28°_o /hr.

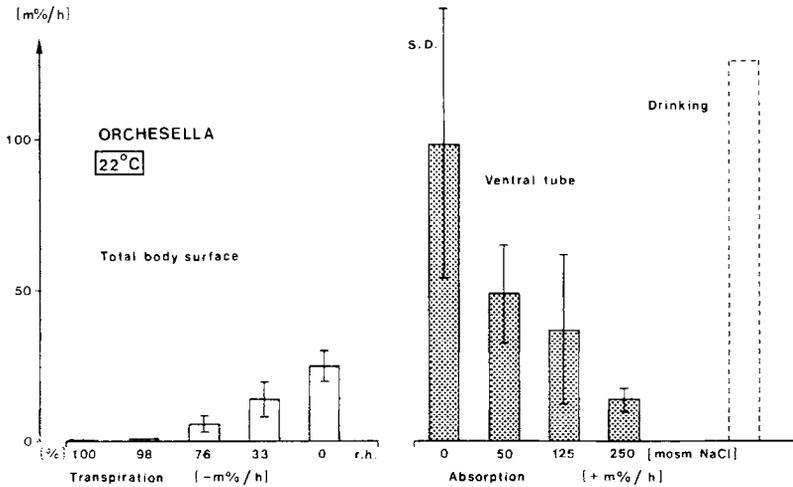


Fig. 8. Water balance of *Orchesella*. On the left: transpiration rates at different relative humidities as percentage loss of water content per hour ($-m^{\circ}_o$ /hr), related to the initial water content (m_o); on the right: maximal absorption rates by the ventral-tube vesicles and rate of drinking by mouth as percentage gain of water content per hr ($+m^{\circ}_o$ /hr), related the the initial water content (m_o). The animals also lose water in a 100% saturated atmosphere, but the transpiration rate is very low, e.g. -0.27°_o /hr.

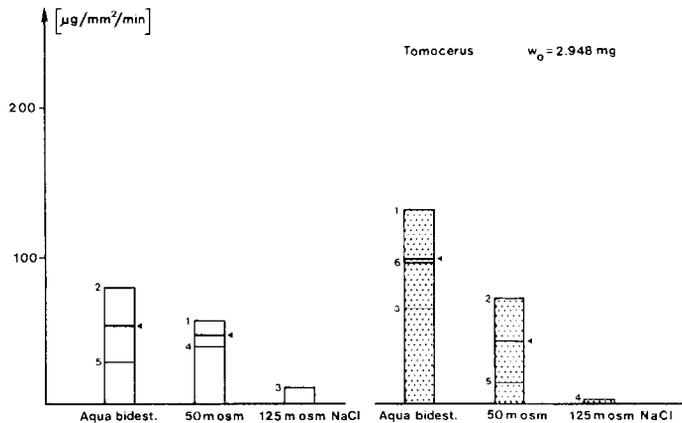


Fig. 9. Absorption by the ventral-tube vesicles of a specimen from *Tomocerus* with the initial weight $w_o = 2.948$ mg. On the left: uptake rates in the premoulting stage; on the right: uptake rates after moulting. The rates are related to unit area of effective vesicle surface. The sequence of absorption is given by numbers; the arrows mark the mean values.

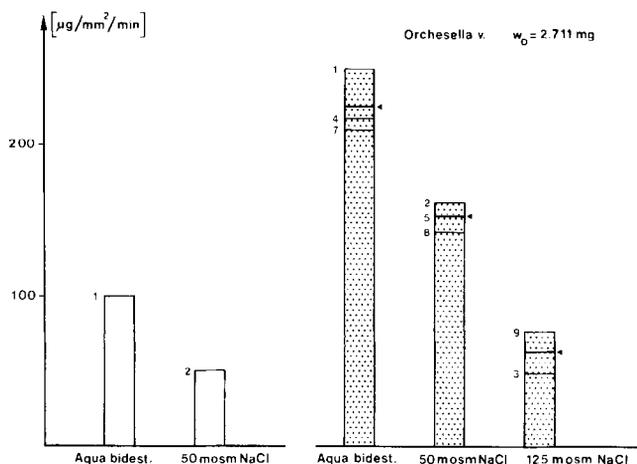


Fig. 10. Absorption by the ventral-tube vesicles of a specimen from *Orchesella* with the initial weight $w_0 = 2.711$ mg. On the left: uptake rates in the premoulting stage; on the right: uptake rates after moulting. The rates are related to unit area of effective vesicle surface. The sequence of absorption is given by numbers; the arrows mark the mean values.

water during lengthy absorption cycles and under changing conditions. The main interest was to study the influence of salt concentrations on the absorption rates and the effect on the absorption efficiency after several absorption intervals.

VERHOEFF and WITTEVEEN (1980) showed that individuals of *Tomocerus minor* and *Orchesella cincta* could compensate partly a water deficit of about 10% of their total weight within few minutes. *Orchesella cincta* absorbed slightly faster than *Tomocerus minor*. But no measurements have been made on the effective surface area of ventral-tube vesicles and, therefore, the real differences between the two transporting systems could not be measured. Also the possible uptake of water by drinking has not been excluded.

The ventral-tube vesicles of *Tomocerus* and *Orchesella villosa* are different in size and efficiency as shown in the present study. Differences are also related to the water contents. Based on unit area, the absorption rates of *Orchesella* were larger than those of *Tomocerus*, but regarding the different sizes of the vesicles, the ventral tube of *Tomocerus* absorbed more fluid within the same time, on being exposed to a low salinity. At higher salt concentrations, *Orchesella* absorbed more efficiently in all cases. Calculating the increase in the total water content, *Orchesella* also compensated for its deficit faster than *Tomocerus* because *Orchesella* was smaller in total weight and water content.

Very high absorption rates were measured for *Petrobius brevistylus* by HOULIHAN (1976). These animals compensated for a loss of water of about 40% initial water content in 7 min. This corresponds to a rate of about $-340\%/hr$. Another machilid, *Trigoniophthalmus alternatus*, absorbed with a rate of $+162\%/hr$ from distilled water (EISENBEIS, unpublished). Uptake rates decreased with increasing salinity in all experiments; this has been shown for *Petrobius* too. It is assumed that ions are directly affecting the transport mechanism. In Table 1 from ARLIAN and VESELICA (1979), a comparison is made between water activity, osmolality and pressure difference in atmospheres. Changing the osmolality from 50 to 250-mosmol/l the water activity is

influenced over a small range, e.g. from about 0.9995 to 0.9950. In this study, the strongest reduction of absorption rates occurs between distilled water to 50-mosmol/l NaCl solution.

Water cannot be transported only by the osmotic pressure of the haemolymph, because animals show reduced rates before moulting. Some hours after moulting the rates again increase. In addition, there is a decline in rates during successive absorption intervals, as if the epithelium becomes exhausted. This implies that active mechanisms are probably involved in fluid uptake. This interpretation is supported by ultrastructural data, especially the abundance of mitochondria within the transport epithelium, which lines the vesicles. (EISENBEIS, 1974).

Earlier measurements of the osmolality of the haemolymph (free from haemocytes) revealed it to be about 200-mosmol/l for *Tomocerus* and 300-mosmol/l for *Orchesella*. Besides this, EISENBEIS (1974) showed differences in the ultrastructure between *Tomocerus* and *Orchesella*. In general, both genera show the same organisation, but in *Orchesella* 'membrane stacks' have been found within the zone of apical infoldings of the transport epithelium, which points to a some membrane-bound transport system. Furthermore the ultrastructure is very sensitive to changing salinity of the medium. Short-time adaptation (< 1 day) induces alterations in the apical foldings of the transport cells. Long-time adaptation under natural conditions (epineustic forms from salt lakes) reduces the number of mitochondria (EISENBEIS and WICHARD, 1977). It must be noted, that all the data from this study are related to the outer surface of the vesicles. The apical surface of the transport epithelium is enlarged by many delicate foldings like a 'brush border' in other transporting systems.

NOBLE-NESBITT (1963) and HOULIHAN (1976) reported the influx of Na^{22} through the vesicles of *Podura aquatica* and of *Petrobius brevistylis*. Considering all data on the structure and function of coxal vesicles in apterygote insects, these organs seem to be very important for water and ionic balance. But at high salinity of the medium (> 250 -mosmol/l NaCl), the animals retract their vesicles after a

very short eversion period. This strengthens the assumption of EISENBEIS (1976b), that ciliary sense organs, which are integrated into the transport epithelium, function as hygro- or osmoreceptive sense organs. *Orchesella*, living in drier parts of the soil litter than *Tomocerus*, shows a higher transporting activity by the ventral-tube vesicles. This confirms, that the ability to absorb water from surfaces under relatively dry conditions, if no water is available for drinking, plays an important role in the life strategy of these animals, extending their range from hypogaic to epigaic conditions. Experimental work will continue to study the permeability of the cuticle for molecules of different size and the influence of extreme temperatures on the absorption rate. Finally the influence of fluid transport on the ultrastructure of transporting cells must be regarded as a very interesting field.

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REFERENCES

- ARLIAN L. G. and VESELICA M. M. (1979) Water balance in insects and mites. *Comp. Biochem. Physiol.* **64A**, 191–200.
- BAUER Th. (1979) Die Feuchtigkeit als steuernder Faktor für das Kletterverhalten von Collembolen. *Pedobiologia* **19**, 165–175.
- BITSCH J. and PALEVODY C. (1973) L'épithélium absorbant des vésicules coxales des Machilides (Insecta, Thysanura). *Z. Zellforsch. mikrosk.* **143**, 169–182.
- EDNEY E. B. (1977) Water balance in land arthropods. *Zoophysiology and Ecology*. Vol. 9, Springer, Berlin.
- EISENBEIS G. (1974) Licht- und elektronenmikroskopische Untersuchungen zur Ultrastruktur des Transportepithels am Ventral tubus arthropleoner Collembolen (Insecta). *Cytobiologie* **9**, 180–202.
- EISENBEIS G. (1976a) Zur Feinstruktur und Histochemie des Transport-Epithels abdominaler Koxalbasen der Doppelschwanzart *Campodea staphylinus* (Diplura: Campodeidae). *Ent. Germ.* **3**(3), 185–201.
- EISENBEIS G. (1976b) Zur Feinstruktur und Funktion von Sensillen im Transport-Epithel des Ventraltubus von *Tomocerus* und *Orchesella* (Collembola: Tomoceridae; Entomobryidae). *Ent. Germ.* **2**, 271–295.
- EISENBEIS G. and WICHARD W. (1975a) Histochemischer Chloridnachweis im Transportepithel am Ventraltubus arthropleoner Collembolen. *J. Insect Physiol.* **21**, 231–236.
- EISENBEIS G. and WICHARD W. (1975b) Feinstruktureller und histochemischer Nachweis des Transportepithels am Ventraltubus symphypleoner Collembolen (Insecta, Collembola). *Z. Morph. Ökol. Tiere* **81**, 103–110.
- EISENBEIS G. and WICHARD W. (1977) Zur feinstrukturellen Anpassung des Transportepithels am Ventraltubus von Collembolen bei unterschiedlicher Salinität. *Zoomorphologie* **88**, 175–188.
- HOULIHAN D. F. (1976) Water transport by the eversible abdominal vesicles of *Petrobius brevistylis*. *J. Insect Physiol.* **22**, 1683–1695.
- JOOSSE E. N. G. (1970) The formation and biological significance of aggregation in the distribution of Collembola. *Neth. J. Zool.* **20**, 299–314.
- JOOSSE E. N. G. (1971) Ecological aspects of aggregation in Collembola. *Rev. Ecol. Biol. Sol.* **8**, 91–97.
- KACZMAREK M. (1975) Influence of humidity and specific interactions on collembolan populations in a pine forest. *Progress in Soil Zoology* (Ed. by Vaněk J.), pp. 333–349 Prague.
- NOBLE-NESBITT J. (1963) A site of water and ionic exchange with the medium in *Podura aquatica* L. (Collembola, Isotomidae). *J. exp. Biol.* **40**, 701–711.
- NUIMAN S. R. (1941) The function of the ventral tube in *Onychiurus armata* (Collembola). *Nature, Lond.* **148**, 168–169.
- PALISSA A. (1964) Apterygota—Urinsekten *Die Tierwelt Mitteleuropas* IV. (Ed. by BROHMER P., EHRMANN P. and ULMER G.) (Ia) Quelle & Meyer, Leipzig.
- SEDLAG U. (1952) Untersuchungen über den Ventraltubus der Collembolen. *Wiss. Z. Univ. Halle (Mathe.-Naturw.)* **1**, 93–127.
- SMITH E. L. (1970) Biology and structure of some California bristletails and silverfish (Apterygota: Microcoryphia, Thysanura). *Pan-Pacif. Ent.* **46**, 212–225.
- VANNIER G. (1972) Estimation de la surface corporelle d'évaporation d'un Insect aptérygote: *Allacma fusca* (L.). Collembole Symphypléone. *C. R. hebdom. Séanc. Acad. Sci., Paris* **274**, 258–261.
- VERHOEFF H. A. and WITTEVEEN J. (1980) Water balance in Collembola and its relation to habitat selection: cuticular water loss and water uptake. *J. Insect Physiol.* **26**, 201–208.
- WEYDA F. (1974) Coxal vesicles of Machilidae. *Pedobiologia* **14**, 138–141.
- WINSTON P. W. and BATES D. H. (1960) Saturated solutions for the control of humidity in biological research. *Ecology* **41**, 231–237.