INTRODUCTION

The importance of adequate means of water conservation in small terrestrial animals needs no stressing and, as Wigglesworth (1946) has pointed out, the part played by the integument in this respect is of central importance since all other means of water economy are useless if the integument is freely permeable. Epicuticular waxes, investigated by Beament (1944), Lees (1947) and Lees & Beament (1948), have contributed largely to the success of insects and ticks as terrestrial animals. Little is known, however, of the water relations of other terrestrial arthropods, and the woodlice are of particular interest in this connexion since they are the only Crustaceans which have succeeded in colonizing the dry land to any extent. In so far as the water relations of this group have been investigated it is the behavioural aspect which has received most attention, e.g. Gunn (1937), and apart from the work of Lafon (1948) on Ligia, there has been no systematic attempt to investigate the properties of the cuticle as it affects water conservation, though the question is clearly of interest.

It appears to be the opinion of many authors, from Webb & Sillem (1906) onwards (e.g. Vandel, 1943; Cole, 1946; Hatchett, 1947—see discussion below), that woodlice can be arranged in a series from Ligia at the bottom, through such forms as Trichoniscus, Philoscia, Oniscus, and Porcellio to Armadillidiurn at the top, such that their power of water retention varies from least to greatest and that their distribution ranges correspondingly from wetter to drier habitats. While this may very well be so, there has been no satisfactory proof, for we have little information either about the rate of evaporation under controlled conditions, or of the micro-climatic conditions in which the various species live. The work to be described was carried out in an attempt to provide information under the first head, and also in the hope that the results might add to our knowledge of the physiological problems involved when an essentially aquatic group invades the land.

MATERIAL

Seven species of woodlice and a millipede were used. The former were chosen to represent a complete range of habitat as far as humidity conditions are concerned, and their names and notes on the localities from which they were collected follow. Ligia oceanica Linn. is a large, littoral species of which material was obtained from Plymouth. *Philoscia muscorum* Scopoli, is a small species, confined to apparently
damp surroundings such as dead leaves in woodlands and some rubbish heaps. This species was obtained from Surrey gardens and from woodlands in Devon. *Oniscus asellus* Linn. is ubiquitous and material was obtained from several sources. *Porcellio scaber* Latr. is also very common. *Cylisticus convexus* De Geer, is very patchy in occurrence, and not easy to find in large numbers. Material was obtained mainly from a limestone outcrop near Dudley in Staffordshire, known as the Wren's Nest. *Armadillidium nasatum* Budde-Lund was obtained from a greenhouse near Dorking in very large quantities, and *A. vulgare* Latr., the common pill woodlouse, was obtained from Box Hill, from rubbish heaps in Surrey gardens, and from a village near Newmarket.

The millipede, *Glomeris marginata* Koch, was included in this comparative study because it inhabits the same ecological niche as *Armadillidium vulgare*, and material of both animals was very often obtained in the same microhabitat.

In the laboratory, the animals were fed on potato and kept in 12 in. Petri dishes on damp sand together with a few large flat stones. Given clean sand, stones and food every week or so, they will live indefinitely under these conditions.

Animals for experiment were removed from the cultures and kept for 24 hr. in a small Petri dish with moist cotton-wool, but without sand or food.

**METHODS**

In attempting to measure the rate of evaporation from animals the clearly desirable condition that each animal shall be subjected to a constant and known humidity is by no means easy to attain. As Ramsay (1935) has shown, it is extremely difficult to determine the precise humidity conditions to which an animal is exposed when kept in a closed vessel, in 'still' air over sulphuric acid or other humidity-controlling substance. Further, a number of animals kept together in the same experimental chamber, particularly if the animals are in contact or even near to one another, will not all be under the same conditions. In order to minimize these disturbing effects an apparatus was designed in which several animals could be used at the same time but in which they could be kept separate from one another and in moving air of known temperature and humidity. The apparatus is by no means perfect, but it does reduce the two main sources of error while remaining simple in construction.

The essentials are shown in Fig. 1. The animals are kept in a long glass tube and separated from one another by a number of perforated metal disks which are all attached to a central rod. The rod and disks are made to fit snugly enough to prevent any movement of animals from one compartment to another. This 'separator tube' (*S*) is attached to a board which also carries two similar tubes each filled with calcium chloride (in the dry air experiments) through which air passes before entering the separator tube. The board with its three tubes is placed in a large tank where the temperature of the water is controlled to within 0.5° C., and air is circulated through the apparatus by a small pump (*AP*). The air is led through a copper coil in the water tank so that it takes up the temperature of the water before entering the drying tubes. Two taps in the air tube leading from the apparatus back to the air pump can be set so that the rate of output can be measured by collecting the bubbles in a
Evaporation of water from woodlice and Glomeris

graduated cylinder. (A flow-meter inserted at this point would be simpler.) A thermometer is inserted into the top compartment of the separator tube.

Animals exposed in this apparatus to moving air are probably not all subject to precisely the same speed of movement, for there are bound to be small eddies—but the air stream is slow (about 1 l./min.) and consequently the differences will not be great. It may also be objected that the animal in the top compartment is not sub-

Fig. 1. a, diagram of the apparatus used for measuring the rate of evaporation from woodlice under controlled temperature and humidity conditions. The animals are placed one in each compartment of the separator tube (S) and air is circulated at 1 l./min. by the pump (AP). b, ground glass joints (B 29) with perforated glass disks, used in place of the separator tube in later experiments.

jected to dry air, since by the time it reaches this point the air has already passed over several evaporating animals. In fact, the amount of water vapour taken up by the air as it passes along is very small (something in the order of 0.005 mg./l.) and does not significantly affect its drying power when it reaches the later animals in the series.

In later experiments the separator tube was replaced by a series of cones and sockets with ground glass joints (Quickfit & Quartz, B 29; see Fig. 1 b). Each cone has a perforated glass disk sealed into the end so that when several cones are fitted together, compartments are formed in each of which one animal can be placed. This form of apparatus is clearly more versatile than the metal disk type since as many compartments as are needed can be fitted together rapidly, and furthermore there is no risk of damage to the animals as they are put in or removed.

In operation, the temperature of the water-bath and speed of air flow through the
apparatus are first checked. The animals are then weighed separately, and each placed in a compartment. The apparatus is then returned to the water-bath for the prescribed period of time, after which each animal is weighed again. Any animal which shows sign of damage or which has defaecated during the experiment is discarded. For short exposures up to an hour it can safely be assumed that the difference in weight before and after exposure is almost entirely due to loss of water.

Where the rate of evaporation is being considered, the results are expressed in terms of milligrams of water per square centimetre of surface of the animal per hour. The surface area of each individual was determined by following Wigglesworth's method (1945): the cuticles of a number of weighed specimens were carefully removed and the flattened pieces drawn on graph paper by camera lucida; the surface area and weight of these individuals then enables us to find ‘k’ in the formula \( S = kW^4 \) where \( S \) = surface area in sq. mm. and \( W \) = weight in mg., so that the surface area of any subsequent specimen can easily be estimated from its weight. The values of ‘k’ found for the various species used were as follows: Porcellio, 12·4; Cylisticus, 10·8; Oniscus, 13·6; Philoscia, 10·5; Armadillidium vulgare, 11·5; A. nasatum, 11·8; Ligia, 12·3; Glomeris, 10·5.

**EXPERIMENTAL RESULTS**

(1) **Preliminary experiments**

Before proceeding with the main comparative work, measurements were made to find whether there was any difference in rate of evaporation between the sexes or between living and dead animals.

The estimations were carried out at 30° C. in dry air. The results showed no difference as regards sex for exposure periods of either 15 min. or an hour, and need no further comment. As regards living and dead animals, the results were rather variable, but statistical analysis showed no significant difference so far as short exposures (up to an hour) are concerned.

In view of these results, males and females were used in further work without distinction (except females carrying brood pouches which were never used), and except where the contrary is stated the animals used were living, at least at the beginning of the experiments. Animals were chosen which were of approximately the same size, and colour varieties were excluded.

(2) **The site of water loss**

It has been demonstrated by Mellanby (1934), Wigglesworth & Gillett (1936) and Koidsumi (1934) that the greater part of evaporation from insects takes place through the spiracles. Respiration in woodlice is carried out by the pleopods or ‘gills’ on the ventral abdominal segments. In some genera the pleopods contain bunches of tubules or ‘trachea’ (see Verhoeff (1920) for a detailed description), but in none is there anything so elaborate as the insect spiracular apparatus or tracheal system.

Experiments were carried out to find whether water is lost more readily in the
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region of these pleopods than elsewhere. Specimens of *Armadillidium*, *Porcellio* and *Ligia* were used, and they were exposed, ten at a time, in the apparatus already described, for 1 hr. at 30° C. Recently killed animals were used and they were exposed in three series: (i) uncovered, (ii) the dorsal surface covered with beeswax, and (iii) the gills covered with beeswax. The loss of weight (which can be taken as loss of water) was found in each series and from these results the loss from the dorsal surface only, the whole ventral surface, and the gills only, was calculated. Table 1 contains the results.

Table 1. The absolute and relative amounts of water lost by woodlice from the dorsal, total ventral, and gill areas, when exposed to dry air at 30° C.

<table>
<thead>
<tr>
<th></th>
<th>Dorsal surface only</th>
<th>Total ventral surface</th>
<th>Gill area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Armadillidium:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of original weight lost</td>
<td>2.2</td>
<td>2.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Percentage of total surface</td>
<td>33.6</td>
<td>64.6</td>
<td>1.8</td>
</tr>
<tr>
<td>Rate of loss/unit area</td>
<td>6.5</td>
<td>3.8</td>
<td>83</td>
</tr>
<tr>
<td><strong>Porcellio:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of original weight lost</td>
<td>3.2</td>
<td>3.7</td>
<td>2.9</td>
</tr>
<tr>
<td>Percentage of total surface</td>
<td>38.2</td>
<td>58.8</td>
<td>3.0</td>
</tr>
<tr>
<td>Rate of loss/unit area</td>
<td>8.4</td>
<td>6.3</td>
<td>97</td>
</tr>
<tr>
<td><strong>Ligia:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Percentage of original weight lost</td>
<td>4.2</td>
<td>6.4</td>
<td>2.5</td>
</tr>
<tr>
<td>Percentage of total surface</td>
<td>36.6</td>
<td>59.1</td>
<td>4.3</td>
</tr>
<tr>
<td>Rate of loss/unit area</td>
<td>11.5</td>
<td>10.9</td>
<td>58</td>
</tr>
</tbody>
</table>

If one considers the loss of water from each of the areas concerned as a percentage of the original weight of the animal, the figures show that there is no very great difference: the absolute amount of water lost from the gills, the rest of the ventral surface and the dorsal surface is of the same order. But to make a valid comparison of relative rates we need to know not only the absolute amount of water lost, but the total evaporating surface of each of the areas considered. Measurements of gill area* were made as described above, and expressed as a percentage of the total area of the animal. These figures are also shown in Table 1, and another simple calculation enables one to find the rate of loss per unit area in arbitrary units. When this is done it becomes clear that the rate of loss is very much greater from the gill area than from elsewhere, a fact which is clearly associated with the respiratory function of the gill surfaces.

The figures also appear to show that the rate of evaporation from the dorsal surface is greater than that from the ventral, a finding which if true would be rather surprising. But it is in fact almost impossible to estimate the true evaporating area of the ventral surface of a woodlouse. The figures which appear in the table show the total area, including all surfaces of the legs and so forth, whereas it is very likely

* In this connexion 'gill area' means the area of that part of the body occupied by the gills, not the total surface of all the gill lamellae.
that many of these surfaces are in contact with each other or so close as to inhibit evaporation from them. We can, therefore, make a generous reduction in total area of the ventral surface, and this would bring the rate per unit area up to that from the dorsal surface.

It is somewhat surprising to find the rate of loss from the dorsal surface as high as it is, compared with the ventral surface, for in life the ventral surface of the animal is close to the substratum which is usually moist whereas the dorsal surface is much more exposed, and one might have expected to find water-retaining properties present in the dorsal surface to a much greater extent than in the ventral.

If a comparison is made between the three species considered, it is clear that the rate of loss is greatest in the littoral-living *Ligia* and decreases through *Porcellio* to the drier-living *Armadillidium*. The figures for *Ligia* gill area are an exception to this, and they may well be due to the much greater proportion of the total area occupied by gills in that animal.

(3) The relation between rate of evaporation, temperature and humidity

The rate of evaporation in dry air was determined at 10° intervals from 10° to 60° C., for all the species mentioned above. There were two series of experiments, in the first the animals were exposed for 15 min., and in the second, for an hour. At least ten animals and frequently many more were exposed at each temperature. The rate of evaporation per unit area was calculated for each animal and the mean calculated for the group.

The results for exposures of 1 hr. are shown in Table 2, and a selection of them has been graphed in Fig. 2. They show that there is an increase in the rate of evaporation as temperature rises, and that this increase is greater at higher than at lower temperatures. It will also be noticed that the rate of evaporation from *Philoscia* is higher at all temperatures than is that from *Porcellio*, while the rate for *Armadillidium* is lower still. *Glomeris*, it will be seen, gives a curve similar in general shape to those given by woodlice. Fig. 2 also shows the curve for the cockroach *Blatella*, derived from Wigglesworth's data (1945), and the shape of this curve can be seen to differ significantly from the woodlouse curves. It shows no rise in the rate as temperature increases up to about 35° C. after which the rate rises very steeply. It is now well

<table>
<thead>
<tr>
<th>Temperature in ° C.</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>50</th>
<th>60</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Armadillidium</em></td>
<td>1.5</td>
<td>2.7</td>
<td>4.5</td>
<td>6.5</td>
<td>9.5</td>
<td>12.5</td>
</tr>
<tr>
<td><em>Porcellio</em></td>
<td>1.0</td>
<td>1.5</td>
<td>3.0</td>
<td>6.0</td>
<td>10.0</td>
<td>17.0</td>
</tr>
<tr>
<td><em>Cylisticus</em></td>
<td>1.0</td>
<td>3.0</td>
<td>7.0</td>
<td>9.0</td>
<td>13.0</td>
<td>18.5</td>
</tr>
<tr>
<td><em>Oniscus</em></td>
<td>2.0</td>
<td>4.5</td>
<td>7.0</td>
<td>11.5</td>
<td>18.5</td>
<td></td>
</tr>
<tr>
<td><em>Philoscia</em></td>
<td>3.0</td>
<td>4.0</td>
<td>4.5</td>
<td>9.0</td>
<td>14.0</td>
<td>19.5</td>
</tr>
<tr>
<td><em>Ligia</em></td>
<td>2.0</td>
<td>4.0</td>
<td>7.0</td>
<td>12.5</td>
<td>15.0</td>
<td>19.7</td>
</tr>
<tr>
<td><em>Glomeris</em></td>
<td>1.2</td>
<td>3.7</td>
<td>5.5</td>
<td>9.0</td>
<td>14.5</td>
<td>21.0</td>
</tr>
</tbody>
</table>
known that the shape of the curve for insects is attributable to a change in phase of a very thin waxy layer in the epicuticle at the 'critical' temperature, above which the wax does not prevent the passage of water to anything like the extent which it does below this temperature.

Fig. 2 also shows a curve labelled 'vapour pressure'. This represents, on an arbitrarily chosen scale along the ordinate, the water-vapour pressures of saturated air at the temperatures along the abscissa. (This is, of course, the same as a saturation deficit/temperature curve for dry air.) The striking similarity between the shape of this curve and the shape of the evaporation curves for woodlice suggests a close relationship. If the relation is a linear one, as seems likely, then rate of evaporation graphed against saturation deficit instead of temperature, should give a straight line. In Fig. 3 this has been done, and it is clear that an approximately linear relationship does exist for both woodlice and Glomeris (but not, it will be noticed, for the insect Blatella). The significance of the position of the various curves on this graph will be further discussed below.

We may now consider the corresponding results for exposures of 15 min. These are shown in Table 3 and a selection is graphed in Fig. 4. Here again the same general picture appears, the most significant difference being the general increase in rate of evaporation shown over those for an hour's exposure. The curve for Porcellio for 1 hr. exposure has been included in Fig. 4 for comparison, and the figures for
other species show the same effect. The reason lies, of course, in the fact that water is evaporated at a greater rate during the first quarter than during the remaining quarters of a complete hour's exposure. This effect may itself be caused by a drying of the outer layers of the integument which is thus made less permeable, but whatever its cause it is clearly of advantage to the animals since it acts as a regulatory mechanism, reducing the rate of loss of water at a time when conservation is most needed.
Evaporation of water from woodlice and Glomeris

Table 3. Rate of evaporation of water in mg./cm.²/hr. when exposed to dry air for 15 min. at various temperatures

<table>
<thead>
<tr>
<th>Temperature in °C</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>50</th>
<th>60</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Armadillidium vulgare</em> (i)*</td>
<td>6.0</td>
<td>7.0</td>
<td>8.7</td>
<td>12.0</td>
<td>13.0</td>
<td>13.5</td>
</tr>
<tr>
<td><em>A. nasatum</em></td>
<td>4.5</td>
<td>5.2</td>
<td>6.2</td>
<td>13.5</td>
<td>13.7</td>
<td>14.0</td>
</tr>
<tr>
<td><em>Porcellio</em></td>
<td>3.0</td>
<td>4.5</td>
<td>5.7</td>
<td>11.5</td>
<td>15.5</td>
<td>9.0</td>
</tr>
<tr>
<td><em>Cylisticus</em></td>
<td>4.0</td>
<td>4.5</td>
<td>6.0</td>
<td>9.5</td>
<td>14.0</td>
<td>21.0</td>
</tr>
<tr>
<td><em>Oniscus</em></td>
<td>4.5</td>
<td>7.5</td>
<td>12.0</td>
<td>15.0</td>
<td>17.0</td>
<td>23.0</td>
</tr>
<tr>
<td><em>Philoscia</em></td>
<td>4.5</td>
<td>4.5</td>
<td>6.5</td>
<td>8.5</td>
<td>13.2</td>
<td>22.5</td>
</tr>
<tr>
<td><em>Ligia</em></td>
<td>5.0</td>
<td>6.7</td>
<td>9.0</td>
<td>13.0</td>
<td>17.0</td>
<td>26.0</td>
</tr>
<tr>
<td><em>Glomeris</em></td>
<td>1.7</td>
<td>1.7</td>
<td>4.0</td>
<td>8.7</td>
<td>15.2</td>
<td>17.0</td>
</tr>
<tr>
<td><em>Blatella</em>†</td>
<td>0.1</td>
<td>0.1</td>
<td>0.2</td>
<td>3.5</td>
<td>13.0</td>
<td>—</td>
</tr>
</tbody>
</table>

* Group (i) consisted of specimens from the Hogs Back, Surrey; group (ii) from near Newmarket, Suffolk.
† Data from Wigglesworth (1945).

There is one interesting exception to this general effect however, and that is shown by Glomeris, whose rate of evaporation during the first quarter of an hour is maintained (except at 60°) during the rest of a complete hour’s exposure. The explanation of this is by no means clear, though its effect is to place Glomeris at or near the top of the scale for 1 hr. exposures, though it is one of the lowest in the scale (particularly at low temperatures) for 15 min. exposures.

In Fig. 5 the results for 15 min. exposures are graphed against saturation deficit, and again an approximately straight line relationship appears (cf. Blatella) except for Glomeris, where the rate falls off significantly above 50° C.
It will have been noticed that *Armadillidium* appears in neither of the last two graphs. This is because its behaviour, like that of *Glomeris*, is anomalous at higher temperatures. Fig. 6 shows this anomalous behaviour for *A. vulgare* (from the Surrey chalk in one series and from Suffolk in another) and for *A. nasatum*. It is clear that in all three species the usual saturation deficit curve is followed reasonably well up to 40°C, above which there is a strong falling off. This takes the form of an absolute drop in rate in *A. nasatum* between 50° and 60° C., and a more or less constant rate in *A. vulgare* from 40° to 60° C. (a relative drop compared with the rate if it followed the s.d. curve). The significant feature is certainly the fact that there is a strong falling off, the extent to which this takes place is of lesser importance.

Now since the effect is observed in both species of *Armadillidium* and in *Glomeris*, all of which are able to curl into a ball, the power to do so seems to offer a likely source of explanation of the effect. Attempts were therefore made to discover whether these species do curl up at high temperatures and to measure the rate of loss when they are kept open. Observation showed that they do indeed curl up above 40° C., but to a variable extent and for variable periods, for they were killed by temperatures just above 40° and after death they always relaxed slightly; and experiment seemed to show that even when kept flat by being encased in gauze envelopes, the animals lost water less rapidly at 50° and 60° C. than would be expected. The technique used for keeping them flat, by enclosing them in wire-gauze envelopes, was by no means satisfactory however, for it was never possible to be quite sure that scratching of the surface or other damage had not occurred; so that the theory of restriction of loss by curling, though apparently quite likely, cannot be said to have been proved, and some other method of keeping the animals open must be found.

It has been shown by the experiments described above that, with certain reservations, the rate of evaporation of water bears a linear relation to saturation deficit when the air is dry. It follows from this that temperature *by itself* has no effect upon
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rate of evaporation, and it should be possible to demonstrate this experimentally by keeping the saturation deficit constant while varying the temperature. The results of such an experiment would also tell us whether the relation between saturation deficit and rate of evaporation holds not only when the air is quite dry, but at other relative humidities as well.

Solutions of sulphuric acid and water were made up for each 5°C interval in temperature from 20°C to 45°C, such that each would give a saturation deficit of 17.5 mm Hg. This meant having a relative humidity of 0% at 20°C and one of 76% at 45°C. Wash bottles containing pumice and the necessary solution then took the place of the calcium chloride tubes in the apparatus, and measurements of loss of weight were made as usual. Porcellio scaber was the animal used, and the results are shown graphically in Fig. 7. Exposures were for both 1 and 2 hr. periods, and the results showed a constant rate of loss for all temperatures up to 35°C. For temperatures higher than this the rate of loss increases slightly for 1 hr. exposures, and to an even slighter extent for 2 hr. exposures. There are two contributory causes for this rise, one theoretically necessary, the other of experimental origin. The latter is probably of greater effect and it arises from the fact that at high temperatures the R.H. has to be rather high, so that after the weighed animals have been put into the apparatus, the humidity takes a little time to reach the desired level. The animals therefore respond to too dry conditions and the initial rate of loss is high. The second and theoretically necessary cause lies in the fact that even ideally the rate of evaporation is not precisely proportional to S.D., for there is an increase approximately in proportion to the square of the absolute temperature, due to the increased rate of diffusion of gases. Making allowances then for these two factors it can safely be said that the effects of temperature upon the evaporation of water from woodlice are such as can be deduced from the laws of gaseous diffusion, and that there is no evidence of an effect of temperature upon the permeability of the integument.

We must now examine the curves for Ligia oceanica which were not included in the graphs discussed above. They are shown in Fig. 8, and it is clear that for both 15 min. and 1 hr. exposures the rate of increase in evaporation falls off significantly above 40°C. This is shown clearly when saturation deficit is used as the abscissa...
(broken lines). Now *Ligia* is considerably bigger than any of the other woodlice used, and weights of 0.9 g. are by no means uncommon, whereas a fairly large *Armadillidium* weighs only 0.2 g., and a *Philoscia* about a fifth of this. Furthermore, the surface of *Ligia* always appears to be slightly moist, and it seems not unlikely that *Ligia* is sufficiently large and has a sufficiently permeable cuticle, to be able to cool itself to such an extent as significantly to reduce its rate of evaporation at high temperatures. The absolute rate of evaporation at all but the highest temperatures is a good deal higher in *Ligia* than in any other species studied, a fact which lends support to the cooling theory, and experiments at present in progress have already shown that the internal temperature of *Ligia* in dry air can be held at several degrees lower than the external temperature.

![Graph](image)

*Fig. 8.* The rate of evaporation of water from *Ligia* in dry air in relation to temperature on a linear scale (continuous line) or to saturation deficit on a linear scale (broken line); for exposures of both 15 min. and 1 hr.

(4) *The effect of humidity upon upper lethal temperatures*

Besides its indirect effect through saturation deficit and rate of evaporation, temperature has of course a direct effect both on general metabolic processes and, presumably, on distribution. Little is known about the range of temperature tolerance in woodlice, and nothing, so far as the writer is aware, of the relation of humidity and temperature tolerance. Here again our knowledge of woodlouse physiology lags behind that of insects, for the effect of humidity on the thermal death points of insects has been known for some time from the work of Mellanby (1932) and others.
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The present series of experiments was designed to find the highest temperature which woodlice can tolerate for periods of either 15 min., 1 or 24 hr., in 0, 50 and 100% R.H. The animals were exposed, ten at each set of conditions, in the apparatus already described, and air of the required humidity was bubbled through at the rate of 1 l./min. The highest tolerable temperature was determined to the nearest degree, very little variation amongst individuals being found in this respect. Almost invariably if half the animals were alive after exposure to \( x \)° C, then all the animals in another batch would be dead at \( x + 1 \)° C, and alive at \( x - 1 \)° C.

The results of these experiments are shown in Table 4, and a selection is represented graphically in Fig. 9. It is clear from these results that for any one species (with the exception of Ligia), the lethal temperatures for a 15 min. exposure are substantially the same at all three humidities used (though slightly lower at 100% R.H. than in drier air, and slightly higher at 50% R.H. than at other humidities). For exposures of 1 hr., the findings are parallel, but all the temperatures are slightly lower (from 1° to 5° C). For exposures of 24 hr., however, the picture is very different. Here the humidity has a profound effect, for in dry air the lethal temperature is about 20° lower than it is in saturated air, and even at 50% R.H. the lethal temperature is very greatly depressed.

In the main then it can be said that the animals are dying from high temperature at the short exposures (of 15 min. and an hour) but that they are drying out and dying from desiccation during the long exposure (except at 100% R.H. of course). The lethal temperatures found at 100% R.H. probably represent the true tissue tolerance, and it is significant that these do not differ widely with different periods of exposure. During brief exposure periods it appears that there is some benefit to be derived from evaporation (and hence cooling) in non-saturated atmospheres; the

Table 4. The highest temperature which various species of woodlice and other arthropods can tolerate at different humidities for various periods of time

<table>
<thead>
<tr>
<th>Period of exposure</th>
<th>15 min.</th>
<th>1 hr.</th>
<th>24 hr.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>50</td>
<td>100</td>
</tr>
<tr>
<td>Armadillidium vulgare</td>
<td>43</td>
<td>46.5</td>
<td>42</td>
</tr>
<tr>
<td>A. nasiatum</td>
<td>42.5</td>
<td>45.5</td>
<td>41</td>
</tr>
<tr>
<td>Porcellio</td>
<td>42.5</td>
<td>43</td>
<td>38</td>
</tr>
<tr>
<td>Omicus</td>
<td>40</td>
<td>41.5</td>
<td>37</td>
</tr>
<tr>
<td>Cylitcicus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philoscia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ligia</td>
<td>41.5</td>
<td>40</td>
<td>34.5</td>
</tr>
<tr>
<td>Glomeris</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Period of exposure</th>
<th>1 hr.</th>
<th>24 hr.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>Pediculus*</td>
<td>46</td>
<td>46</td>
</tr>
<tr>
<td>Xenopsylla larvae*</td>
<td>39.5</td>
<td>39.5</td>
</tr>
</tbody>
</table>

* Data derived from Mellanby (1932).

The lethal temperatures found at 100% R.H. probably represent the true tissue tolerance, and it is significant that these do not differ widely with different periods of exposure. During brief exposure periods it appears that there is some benefit to be derived from evaporation (and hence cooling) in non-saturated atmospheres; the
effect is rather greater at 50% R.H. than in completely dry air where the rate of evaporation is probably so great that the cooling effect cannot be maintained over the whole period.

Fig. 9. The highest temperature which various woodlice, *Glomeris* and the insects *Pediculus* and *Xenopsylla* (larvae) can tolerate, at different humidities and for various periods of time.

*Ligia* behaves somewhat differently from the rest, and the differences are again very readily explained by its greater size and therefore greater water evaporating capacity. At 15 min. and 1 hr., there is in all but saturated atmospheres a cooling effect which raises the apparent temperature tolerance above the true tolerance of the tissues. In 24 hr. exposures, the temperature tolerated is much lower at 50% R.H. than it is when the air is saturated, and this is to be expected in an animal whose water-conserving powers are so feeble.
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In Fig. 9 the woodlice are also compared with *Glomeris* and with the insects *Pediculus* and *Xenopsylla*, the data for the insects being taken from Mellanby (1932). The various species of woodlice stand in approximately the same order as they do in respect of rate of evaporation; that is *Armadillidium* has the highest temperature tolerance and the lowest rate of evaporation, *Ligia* has the lowest temperature tolerance and the highest rate of evaporation, the remainder being intermediate. *Glomeris*, it will be noticed, has a ‘true’ temperature tolerance just above the highest woodlouse, and in 24 hr. exposures its capacity to resist high temperatures does not fall to nearly the same extent as that of the woodlice, and in this respect it resembles the insects. Both of the insects to which Fig. 9 refers have an upper temperature limit which is independent of humidity for short exposures but, like woodlice, they show a drop in temperature tolerance in dry air for long exposures, though the drop is not so great as it is in woodlice.

(5) Recovery after desiccation

We have seen that water is easily lost from woodlice, and it remains to find out whether they can re-absorb it if they are returned to suitable conditions after desiccation. It was shown by Verhoeff (1920) that land isopods can absorb liquid water by means of the uropods, which convey it to the pleopods or the rectum. Presumably such liquid water can also be imbibed through the mouth. What is uncertain is whether the animals can absorb water vapour from damp air, as a number of insects and ticks can.

This question was investigated by subjecting individuals of various species to desiccation either for 45 min. at 0% R.H. and room temperature (15° ± 2° C.) or to 50% R.H. for 23 hr. at the same temperature, after which they were kept without food and again at the same temperature in small Petri dishes with moist cotton-wool where the air was presumably saturated with water vapour, or in desiccators at 98% or 95% R.H. They were weighed before desiccation, immediately after, and then at approximately 2 hr. intervals for the first 6 hr. and daily thereafter for 8 or 10 days. All of those which were kept at 95% R.H. after desiccation lost weight and ultimately died. Those which were kept at 98% showed somewhat erratic behaviour, and of those kept in saturated air, all survived and the great majority gained weight.

In Fig. 10 an attempt is made to show the changes in weight of these groups. In each graph the thin horizontal line represents the weight immediately after desiccation, and the thick line represents the changes in weight shown by the animals during the experimental period expressed as a percentage of the post-desiccation weight. The thick vertical line at the commencement of each graph represents the weight lost during desiccation, but this does not apply to column C where the animals were desiccated for 23 hr. and the amount of weight lost was too great to be included conveniently in the graphs as set out: losses of 50% of the post-desiccation weight were common under these conditions. Column A refers to animals which were desiccated in dry air for 45 min. and subsequently allowed to recover in 98% R.H. Those represented in column B suffered the same desiccation, but recovered in 100% R.H., while those in column C were desiccated for 23 hr. at 50% R.H. and
allowed to recover in 98% R.H. Six animals of each species were treated in each of the conditions represented, and the relevant curve shows the mean behaviour of the six animals. Where the behaviour was too variable for this treatment three curves are shown on the one graph representing the two extremes and a central example.

Fig. 10. Change in weight after desiccation in woodlice and Glomeris. Thick vertical line: the extent to which weight was lost during desiccation; thin horizontal line: immediate post-desiccation weight. A, animals desiccated for 45 min., recovery in 98% R.H.; B, similar desiccation, recovery in 100% R.H.; C, animals desiccated for 23 hr. at 50% R.H., recovery in 98% R.H. All at room temperature (15°±2° C).

of the behaviour. It should be emphasized that all these animals (except Philoscia in column A and Glomeris in A and B) were still alive at the end of the experimental period, even though many of them lost weight.

No species was capable of recovery in 95% R.H. and no graphs referring to this condition are shown. The graphs in column A show that most species lose weight in 98% R.H. after desiccation. Armadillidium, however, appears to be just about able to hold its own in this humidity, and in many instances the weight gained is actually more than the original weight lost during desiccation. Ligia, surprisingly, manages to survive and increase in weight after an initial loss, though the degree to
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which weight is recovered is very variable. Glomeris is quite incapable of regaining weight and loses rapidly even in 100% R.H.

Column B shows that all species are capable of surviving and gaining weight in 100% R.H. after desiccation, though it is a doubtful point as to whether this is by the absorption of water vapour or of liquid water, for it was found to be impossible to keep saturated air without small droplets condensing on surfaces. Even if kept at a constant temperature small energy systems set up inside the vessel lead to slightly different conditions in one part of the vessel from others and so to condensation.

Column C shows that after desiccation for 23 hr. at 50% R.H. rather more animals are capable of recovering weight in 98% R.H. than in the corresponding series in column A, but the results are irregular, and sufficient material was not available to experiment with all the species. The parallel series of experiments showing recovery in 100% R.H. after desiccation for 23 hr. at 50% was not carried out on all species. The two species which were used, Oniscus and Porcellio, both showed good recovery of weight in 100% R.H., and it can safely be assumed that the rest would have done, for as mentioned above there is plenty of liquid water about.

In general then, it can be said that after suffering water loss by desiccation, all the species of woodlice studied are capable of recovering at least some of the water lost if they can reach saturated air, and that Armadillidium and Ligia but not other species can do so from a relative humidity of 98%. On the other hand, no recovery of water takes place from 95% R.H. or below. The behaviour is very variable, but perhaps this is only to be expected since the animals were subjected to treatment very near the limit of their tolerance.

Having shown that at least some animals are capable of absorbing water vapour from unsaturated air, the question remains as to whether this is a property of living animals only, or whether the same phenomenon can be observed in dead ones. Specimens of Oniscus and Armadillidium vulgare were killed with ammonia vapour and subjected to the same desiccation as living ones, after which they were allowed to recover at 100 and 98% R.H. In saturated air the behaviour of the dead animals was variable, they frequently showed a gain in weight, but they never gained as much as the most successful living ones, and occasionally they remained steadily at the same weight (until putrefaction began to have its effect). This variable behaviour is probably nothing more than a result of the fact that in a closed vessel where there is a free water surface, the condensation of water droplets takes place in an unforeseeable way and leads to extremely doubtful results. In 98%, no dead animal recovered weight at all, though in Oniscus the amount lost was smaller than that lost by living animals. The results are shown in Fig. 11.

A further point of interest in this connexion is that an animal which died during the recovery period invariably lost water very rapidly before doing so. It is as though 98% R.H. is very near the lower limit of humidity which Oniscus can withstand: in some individuals the metabolic machinery concerned is tipped slightly over in the wrong direction, all control is lost and the animals lose water rapidly until exhausted, whereas in others, a precarious equilibrium is just maintained and water gained just balances water lost.
It has so far been assumed that relative humidity is the factor involved in determining whether a woodlouse shall or shall not be able to regain lost water from the atmosphere. This is not necessarily true, for the limiting factor might be saturation deficit, and the following experiment was designed to discover which of the two measures is involved.

Specimens of *Armadillidium vulgare*, a species able to hold its own when allowed to recover from desiccation at $17^\circ$ C. and $98\%$ R.H., were allowed to recover in the same relative humidity, but at either $4^\circ$ or $30^\circ$ C., and their weights plotted. Now if saturation deficit is involved, an animal which holds its own at $17^\circ$ C. should be able to recover very well at $4^\circ$ C., since the saturation deficit is only $0.12$ mm. Hg at $4^\circ$ C. whereas it is $0.29$ mm. at $17^\circ$ C. At $30^\circ$ C. and the same R.H. the saturation deficit is $0.64$ mm., more than five times the value at $4^\circ$ C., and one would expect the animal to lose water rapidly. However, as the graphs in Fig. 12 show, there is little significant difference between the behaviour of the animals at all three temperatures, and we are safe in inferring from this that relative humidity is the limiting factor.

**DISCUSSION**

It will be convenient to discuss: first, the extent to which the present results agree with what is already known of the water relations of woodlice; secondly, their
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significance when compared with parallel results for insects; and thirdly, any new light which they throw upon the subject of woodlouse ecology.

As stated above, very few measurements have been made of the rate of evaporation from woodlice. Allee (1926) showed that Oniscus and Cylisticus if kept singly lose water more rapidly than if they are allowed to bunch, but his findings are qualitative only. Numanoi (1934), working with Ligia exotica only, kept them suspended in air over sulphuric acid at 25° C. and found the time taken to die at different relative humidities varied from 5 hr. at 2% R.H. to 16–20 hr. at 76% R.H., and that the amount of water lost before death occurred was about 13% at all humidities save 100%. These figures do not conflict with those found for L. oceanica in the present work, but they do not tell us much about the nature of the relation between humidity and evaporation beyond the qualitative fact that in drier air evaporation is faster.

Miller (1938), working on the isopods of the San Francisco Bay region, exposed a number of species to different humidities at different temperatures (four temperatures and eighteen combinations of temperature and humidity in all) in desiccators, and noted the times taken to die. Expressing the results in terms of saturation deficit he obtained the best linear relationship by using an exponential equation of the form \[ T = ae^{-mS} \], where \( T \) = survival time, \( a \) and \( m \) are constants, and \( S \) = saturation deficit. For Ligia however, he found that a good straight line fit was obtained if the reciprocal of \( T \) were plotted against the saturation deficit. It should be noted, however, that his animals bunched in the desiccators and were therefore not exposed to the humidities arranged. Rate of evaporation is, of course, not being measured in an experiment of this sort (even under ideal conditions), for we do not know how
survival time is related to rate of evaporation, so that a simple relation between survival time and saturation deficit is not necessarily to be expected. Miller's results therefore, do not really conflict with the present set.

Waloff (1941) found that no woodlouse could live indefinitely (over a month) without food in any humidity below saturation, although Armadillidium lived from 2 to 10 days in a relative humidity of 93%. Porcellio did rather worse than Armadillidium at each humidity, and Oniscus did worse still; results which are supported by the present experiments. She also measured the percentage weight lost by evaporation from Oniscus at 0, 50 and 75% R.H. and at room temperature, and found, as Numanoi did for Ligia, that evaporation is greater in drier air. (Her conclusion that the 'loss of water by evaporation is proportional to time and to the percentage of relative humidity' is, however, unjustified, for her figures do not even show a linear relationship between rate of evaporation and R.H. let alone a proportionality.) She also kept desiccated Oniscus in saturated air, and found that the animals usually gained in weight. The same results were found for all the species used in the present work, which is not surprising since there are bound to be droplets of water available.

Heeley (1941) found difficulty in maintaining cultures of various isopods in the laboratory until he found the right humidity for each species. These humidities varied from 84% R.H. for Trichoniscus pusillus to 65% for Armadillidium vulgare. It is difficult to say just what these results mean, for the humidity in the Petri dishes was controlled by dropping water on to filter-paper from time to time and measured by small paper hygrometers. The animals were also provided with fresh moist carrot, so that the actual humidity conditions to which they were subjected may have been very different from those measured by the paper hygrometers. Nevertheless, the fact that the air in these Petri dishes was by no means saturated does suggest that in nature the animals can survive in less than saturated air provided moist food is available. A study of the amount of water obtained by land isopods from their food might show interesting results.

In the present work no difficulty at all was experienced in obtaining good humidity conditions for keeping and rearing isopods of various species—in fact they all seemed to thrive in saturated air, or at least in air exposed to free water surfaces, and Miller (1938) had a similar experience.

We may now compare the present results with the situation as it is known in insects. It has been shown that, with a few exceptions in certain conditions, the rate of evaporation from isopods bears a straight-line relationship to the humidity expressed as a saturation deficit. In insects as Mellanby (1935) has shown, the same principle is at work, but, as we now know, the effect of factors other than saturation deficit upon the rate of evaporation is often so great as to reduce the original relation to insignificance. The two main reasons why saturation deficit and evaporation are not simply related in insects are (i) that the greater part of the loss takes place through the spiracles, which can be closed, and (ii) that there are relatively impermeable waxes in the epicuticle which depress the evaporation very greatly unless their critical temperature is passed. Now the fact that in woodlice the saturation deficit-evaporation relation is linear over a wide range of temperature suggests
Evaporation of water from woodlice and *Glomeris* strongly that there is neither control of water loss from respiratory surfaces by a mechanism such as the spiracles of insects, nor a layer in the integument offering serious resistance to the evaporation of water. On the other hand, water does evaporate more rapidly from some species of woodlouse than from others—and there must be differences in their cuticles to account for this. Why is the cuticle of *Armadillidium* less permeable than that of *Philoscia* for instance? This aspect of the problem deserves further study—it has not been considered in the present work.

Lafon (1948) has come to a similar conclusion from work on *Ligia*. He showed that at 25°C and in dry, still air, specimens abraded with alumina dust did not lose water more rapidly than the unabraded control specimens, and further that the incidence of death did not affect the course of water loss during the exposure period.

In woodlice the area from which the greatest evaporation takes place (if the latter is measured per unit area) has been shown to be the pleopods, but the absolute amount of water evaporated is no greater from there than from the rest of the ventral surface, or from the dorsal surface. In insects, something like 60 or 70% of the water evaporated escapes through the spiracles—and if this were expressed as a rate per unit area (of spiracular opening) it would obviously be very high indeed. The difference then lies in the fact that in woodlice the respiratory area is not protected against evaporation by spiracular mechanisms, neither is the rest of the surface protected by impermeable waxes.

It might be considered surprising to find no difference in the rate of evaporation from living and dead woodlice. But it must not be forgotten that this finding refers to relatively short exposures, of 15 min. or an hour; for such short periods (recalling that evaporation takes place from the whole surface as well as from the pleopods, and that there is no control of evaporation even from the latter) there is no reason why evaporation should be cut down in dead specimens. The finding is confirmed by the general smoothness of the curves relating rate of loss to saturation deficit, for at some temperatures the animals were alive all the time, at others only part of the time, and distinct breaks in the curves could be expected if death had altered the rate to an appreciable extent. Similar results were also obtained by Lafon (1948) for *Ligia*. For long periods such as 24 hr. no comparisons have been made.

In spite of these differences between insects and woodlice there are certain similarities in water relations. One is the depression of the upper temperature limit by low humidities in long exposures, and it indicates that in some insects, as in woodlice, there is a significant loss of water despite the wax layer. There are, however, insects (e.g. *Tenebrio* larvae, *Xenopsylla* adults (Mellanby, 1932)) where there is no such depression even at 0% R.H. for 24 hr. and this is testimony to the very effective powers of water conservation which they possess, powers which cannot be matched by any woodlice.

Some species of insects, notably *Chortophaga* (Ludwig, 1937), *Tenebrio* (Mellanby, 1932), *Xenopsylla* pre-pupae (Edney, 1947), can absorb water vapour from unsaturated atmospheres. This property is also possessed by ticks (Lees, 1946). So far as is known the faculty is confined to insects which may be exposed to very dry habitats, and it has clearly helped to open such habitats to their advance. The present
work has shown that woodlice are for the most part incapable of coming into equilibrium even with such high relative humidities as 98%, and this must be a powerful limiting factor in their distribution.

On the other hand, we have evidence from the present work that some woodlice are capable of suffering very considerable water loss without dying, in some cases as much as 50% of the weight can be lost in this way without killing the animals. In normal conditions woodlice subjected to such treatment would, one supposes, subsequently regain their weight either by absorbing liquid water or by feeding or both, so that the capacity for withstanding great losses may be regarded as being of advantage to them in terrestrial existence.

A corollary to this is suggested by the temperature-tolerance curves which show that a higher temperature than the true tissue tolerance may be withstood for short periods, an advantage which is likely to be due to the cooling effect of a rather rapid loss of water.

Taken as a whole the present results show, in the species studied, a considerable range both as regards temperature tolerance and rate of evaporation. The species can be arranged in a series as regards rate of evaporation per unit area, with *Armadillidium vulgare* at the top showing the lowest rate and *Ligia* at the bottom showing the greatest. They can be arranged in the same series in respect of temperature tolerance, *Armadillidium vulgare* showing the highest tolerance. This strongly suggests that the animals are adapted for terrestrial existence differentially and according to the series mentioned above. We now know that this is certainly true so far as resistance to evaporation goes, but the other side of the picture, the measurement of conditions in which the various species do actually occur, has still to be made.

Miller's (1938) work on the terrestrial isopods of San Francisco Bay, in so far as he used the same genera as those in the present work, suggests a similar order in resistance to drought and as regards actual habitat. But it is little more than a suggestion as regards habitat, for no microclimatic measurements were made, and moistness was estimated by general impression and by height above the sea. Cole (1946), in the course of a useful study of the Cryptozoa of an Illinois woodland, did measure temperature and soil moisture under experimental boards where woodlice occurred and correlated their aggregation and vertical migration with these factors. But as he remarks, 'It will be necessary to measure microclimatic factors actually within the cryptozoic niche' in future work.

Hatchett (1947), after studying the biology of the isopods of Michigan, also correlates distribution with moistness of the environment, but supports the statement with no microclimatic data.

It may also be worth pointing out that the distribution of the common woodlice in this country is by no means certainly related to moisture: for instance *Armadillidium, Glomeris, Porcellio, Oniscus* and *Philoscia* have all been found abundant in a single rubbish heap in Surrey.

*Glomeris*, which was treated together with woodlice in the present work, is interesting in that it shows some similarities to and some differences from them as
Evaporation of water from woodlice and *Glomeris* regards its water relations. Thus its evaporation-saturation deficit curve shows the same general linear relation as do those of woodlice, and the absolute rate like that of the woodlice is a good deal higher than most insects. On the other hand, its temperature-tolerance curves show on the whole a higher tolerance than woodlice, which suggests that it may be nearer the insects in this respect. Its powers of recovery after desiccation, however, are worse even than those of woodlice.

The general similarity between the water relations of woodlice and *Glomeris* throws additional light on the findings of Lafon (1943) that millipede cuticle resembles isopod cuticle in having a high calcium and low chitin content. He also showed that the other large myriapod group, the centipedes, have a cuticle which is more insect-like in gross chemical content, being much lower in calcium and higher in chitin content than the millipedes. It will be interesting to see whether the centipedes are more insect-like in their water relations than the millipedes.

In conclusion, we now know that woodlice can be considered as fairly simple physical bodies in so far as evaporation from them is concerned, and although no direct evidence is offered in the present work on the composition of the integument, there is a very strong suggestion that it lacks the waxes characteristic of insect cuticles. (It is hoped to present direct evidence on this point in a further publication.) The relatively permeable nature of their integuments limits their distribution on dry land, but some genera such as *Armadillidium* would appear to be better adapted in this respect for terrestrial existence than others such as *Philoscia*.

What we still need to know as regards the effect of water relations on woodlouse distribution is the precise conditions, of temperature and humidity in particular, to which the various species are subjected in their natural habitats.

**SUMMARY**

1. Comparative studies have been made on seven woodlice and the millipede *Glomeris* to determine: (i) the site of water loss, (ii) the effect of temperature and humidity on the rate of evaporation of water, (iii) the effect of humidity on their upper temperature tolerance, and (iv) their capacity to regain water after desiccation.

2. An apparatus was constructed in which several animals can be exposed simultaneously but separately to a slowly moving stream of air of any required humidity and temperature.

3. There is no difference between the sexes as regards rate of water loss, and no difference was found in this respect between living and dead animals for exposures up to 1 hr.

4. In *Armadillidium* and *Porcellio* the pleopodal area loses water some ten to twenty times faster per unit area than the dorsal or ventral surface (some five times only in *Ligia*), but the absolute amount of water lost per unit time by the pleopods is less than that from either of the other areas mentioned.

5. Tables and graphs are given showing the rate of loss of water in mg./cm.²/hr. in dry air at various temperatures for each species studied, both for 15 min. and 1 hr. exposures. These show a linear relationship between rate of evaporation and saturation deficit except for *Armadillidium* and *Glomeris* above 40° C. (where the
rate falls off), and *Ligia*. Reasons for these exceptions are suggested: curling in the first two, absolute size in the last.

6. The animals studied can be placed in a series as regards rate of loss of water, from *Ligia* (which shows the greatest rate) through *Philoscia, Oniscus, Porcellio, Cyclisticus* and *Armadillidium nasatum* to *A. vulgare*, which shows the lowest rate of loss. *Oniscus, Porcellio* and *Cylisticus* do not differ very greatly from one another in this respect. *Glomeris* loses water less rapidly than the majority of species of woodlice if exposed for 15 min., but, because the average rate of loss from woodlice falls if they are exposed for an hour, *Glomeris* appears to lose more rapidly than they do for an hour’s exposure.

7. The highest temperature tolerated by woodlice for short exposures (15 min. or 1 hr.) does not vary greatly with humidity—temperatures are somewhat above 40° C. for 15 min. exposures—it is slightly higher at 50% R.H., due to a cooling effect, than in dry or saturated air; but for 24 hr. exposures, the animals die of desiccation and consequently the highest tolerable temperature is very much lower in dry air than in moist. These findings are also true, but to a less marked extent, of *Glomeris*.

8. The species can be arranged in a series as regards temperature tolerance which corresponds with the rate of evaporation series, *A. vulgare* having the highest temperature tolerance, *Ligia* the lowest.

9. After exposure to desiccation for 45 min. in dry air, or for 23 hr. in 50% R.H., both at room temperature, no species could live or recover weight if subsequently kept at 95% R.H. *Armadillidium* (but no others) could live and recover weight by absorption of water vapour if kept at 98% R.H., and all species could live and recover weight if kept in saturated air. Only living animals recovered weight by absorption of water vapour or liquid water. Animals which died after a period in the ‘recovery’ dishes always lost water very rapidly before doing so. The power to recover water from air at 98% R.H., possessed by *Armadillidium*, is limited by relative humidity not by saturation deficit.

10. The above results are discussed and the need for microclimatic data is stressed.

I should like to express my thanks to the Council of the Department of Scientific and Industrial Research for financial assistance during the course of this work. My thanks are also due to Dr S. J. Green for suggesting the improved form of separator tube described on p. 93.
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REFERENCES