STUDIES ON THYSANURA. II. ORIENTATION REACTIONS OF *MACHILOIDES DELANYI* WYGODZINSKY AND *CTENOLEPISMA LONGICAUDATA* ESCHERICH TO TEMPERATURE, LIGHT AND ATMOSPHERIC HUMIDITY

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INTRODUCTION

Investigations into the responses of Thysanura to their physical environment have been confined to those Lepismatida regarded as household pests (Meyer 1932, Lindsay 1940, Crome 1955). The Machilida have not been studied at all in this respect.

The Thysanura occupy a key position in hexapod evolution. These animals are better able to conserve their body water than are many of the species constituting the typical fores cryptofauna, but they have not achieved the degree of impermeability shown by the Pterygota (Heeg 1967). The extant cryptofaunal arthropods are physiologically the nearest approach to the ancestral land arthropods available for study, and, where studied, have proved to be poorly adapted to withstand the rigours of terrestrial life outside their sheltered habitat. By implication the early land arthropods would, like their present-day cryptofaunal descendants, have been confined to a narrow range of equable physical conditions. Such restriction would have been behavioural. Modifications in the reactions to physical stimuli, directing the animals to conditions physiologically more demanding than those of the ancestral habitat, are thus a prerequisite to the improvement of adaptations to land life, and for this reason the responses of the Thysanura to their physical environment are of interest not only because of their ecological importance, but also for their evolutionary implications.

The present investigation concerns the reactions of *Machiloides delanyi* Wygodzinsky and *Ctenolepisma longicaudata* Escherich to light, temperature and humidity. The autecology of the two species and their collection and laboratory culture are described elsewhere (Heeg 1967 and in preparation).

BEHAVIOURAL RESPONSES TO TEMPERATURE

The eccritic temperatures of *M. delanyi* and *C. longicaudata* were determined using a Herter *Temperaturorgel* (Herter 1924). By noting the retreat of the animals in the face of an advancing temperature gradient in this apparatus, it was also possible to establish the upper avoidance temperature. The latter was confirmed by attempting to force the animals to cross a temperature barrier, and noting the temperature at which an avoiding reaction was elicited. In these experiments the reference is to surface temperature. The effects of ambient temperature on the activity of the animals was investigated in a constant temperature room. The animals were placed in individual containers, each with a grid marked out on the floor; by noting at regular intervals whether a given individual had changed its position, a measure of its activity at

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different ambient temperatures could be obtained. The experiments were carried out in darkness, observations being made with the aid of a faint red light to which the animals were known not to respond.

Figures 1 and 2 show respectively the distribution of *M. delanyi* and *C. longicaudata* in a steady temperature gradient. *M. delanyi* showed no clear cut temperature preferendum in the gradient. When placed in a gradient ranging from 5–14C, 16 out of a total of 17 animals distributed themselves evenly among temperatures of 10C or higher. This is possibly indicative of cold avoidance. *C. longicaudata* shows a general gathering (86 % of the total number of animals used) within the range 8–25C, with a possible preferendum over the range 15–20C. The upper avoidance temperatures for the two species were found to be:

C. longicaudata	40–43C
and *M. delanyi*	35–36C

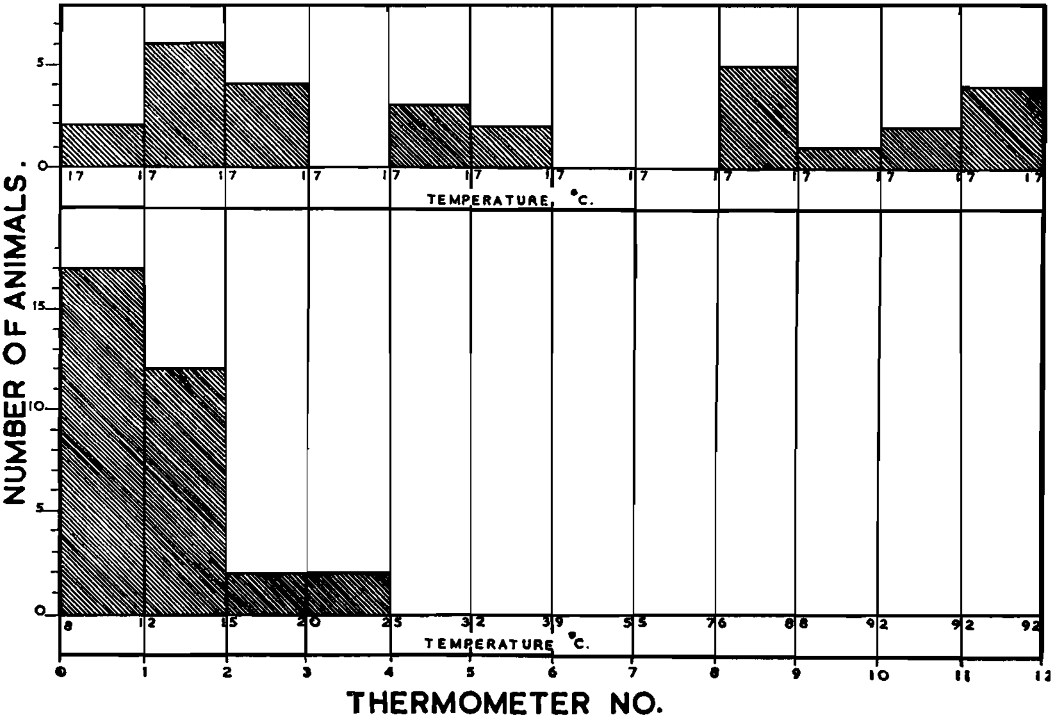

Figure 1. Distribution of *M. delanyi* in a steady temperature gradient. The upper histogram shows the distribution of the animals in the "*temperaturorgel*" before the gradient was established.

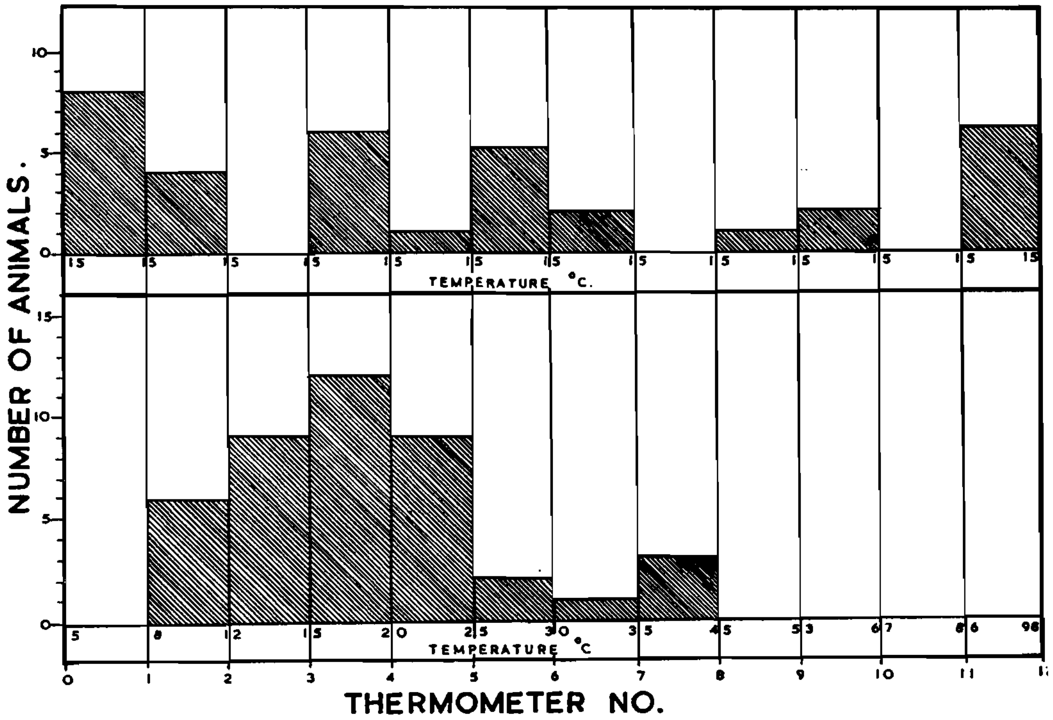

Figure 2. Distribution of *C. longicaudata* in a steady temperature gradient. The upper histogram shows the distribution of the animals before the gradient was established.

Figure 3 shows the effect of ambient temperature on the activity of the experimental animals. Both show orthokinetic responses to low and high temperatures which are in keeping with the preferred ranges as determined in a temperature gradient.

BEHAVIOURAL RESPONSES TO LIGHT

The experimental animals were given a choice between conditions of light and darkness in a light-dark alternative choice chamber, with a light source, a 60 watt incandescent lamp, placed 60 cm above the apparatus. Batches of from four to twelve dark adapted animals were placed in the "light" side of the chamber, and confined to this side by means of a strip of celluloid blocking the access to the "dark" side. The whole operation was carried out under low intensity red light, to which the animals had been shown to be insensitive. They were left to settle, in the dark, for a period of one hour, after which they were given access to the whole chamber by removal of the celluloid strip, and the light was switched on. The number of animals in the light side of the chamber was then recorded at short intervals.

A control experiment was done using twenty animals of each species. These were treated exactly as described above, but no light stimulus was given until the animals had had access to the whole chamber for a period of three hours. During this period counts of the number of animals in the "light" side were made, using a dim red light, at half-hourly intervals.

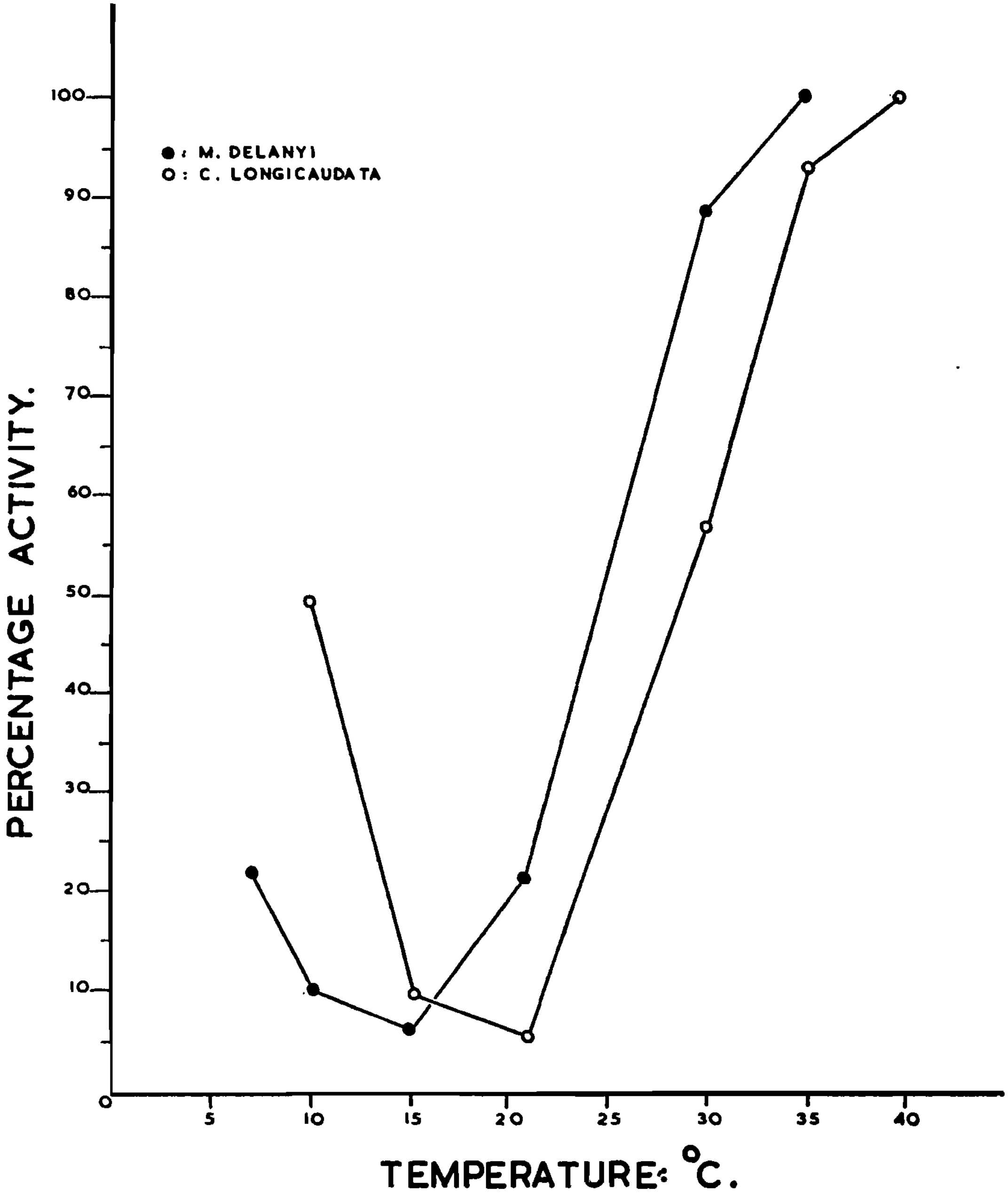

Figure 3. Percentage activity of *M. delanyi* and *C. longicaudata* at different air temperatures.

The experiments were carried out at 20C in a constant temperature room in which the animals had been kept for at least 24 hours before use. No attempt was made to control humidity within the constant temperature room where the ambient humidity was usually in the region of 70% RH.

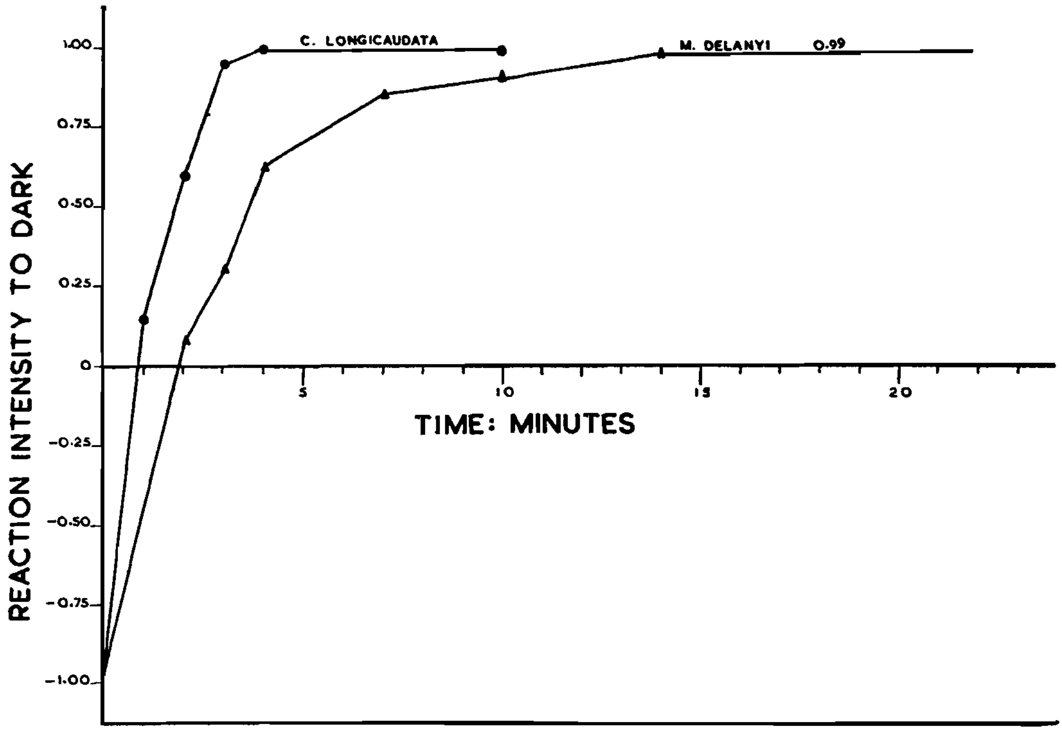

Figure 4. Development of the photonegative responses of *M. delanyi* and *C. longicaudata* in a light/dark alternative choice chamber.

Both *M. delanyi* and *C. longicaudata* were found to be photonegative. Figures 4 and 5 illustrate the development of this reaction, the reaction intensity being expressed as:

$$\frac{\text{No. of animals in dark—No. in light}}{\text{Total no. of animals used.}}$$

This gives a range of reaction intensities from 1·0 (all in dark) through 0·0 (completely random) to —1·0 (all in light).

BEHAVIOURAL RESPONSES TO ATMOSPHERIC HUMIDITY

Dodds and Ewer (1954) have shown that desiccation reverses the reactions of adult *Tenebrio molitor* to atmospheric humidity, the desiccated animals becoming hygropositive whereas normal individuals have a preference for dry conditions. In considering the humidity responses of *M. delanyi* and *C. longicaudata* it was therefore necessary to establish the humidity preferences of both normal and desiccated specimens.

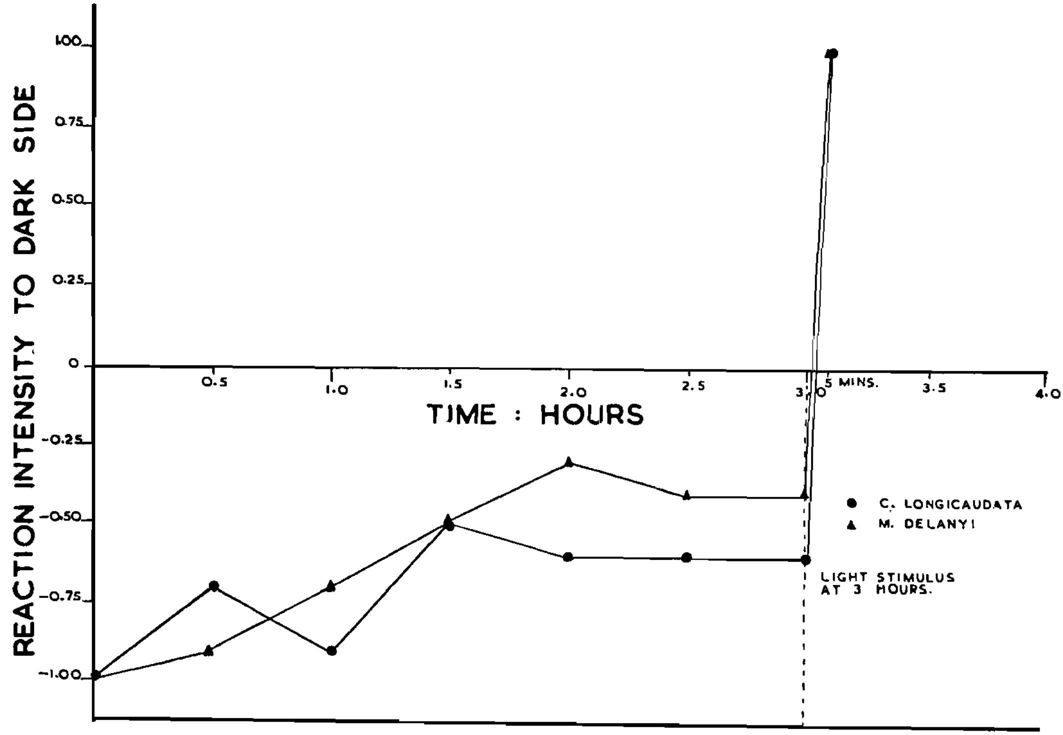

Figure 5. Distribution of *M. delanyi* and *C. longicaudata* in a light/dark alternative choice chamber before and after the application of light stimulus.

Humidity preferences of normal individuals

The humidity responses were tested in a choice chamber consisting of a plastic dish with a false floor of perforated zinc overlying containers holding humidity controlling substances. These were in close juxtaposition, thus giving a very sharp gradient between the two sides of the chamber. After the controlling substances had been introduced, the chamber was closed with a tight-fitting lid sealed with vaseline. The animals were introduced into the chamber by way of a hole drilled into the centre of the lid, the hole being closed by means of a tight-fitting rubber stopper.

Relative humidity in the choice chamber was controlled by using saturated solutions, made up as described by O'Brien (1948) and Winston & Bates (1960), as well as KOH solutions prepared according to Solomon (1951). Before use the atmosphere within the chamber had to be allowed to come into equilibrium with the subtending controlling solutions. The minimal time for this was found experimentally to be 20 minutes, but one hour was allowed in all experiments.

All experimental animals were fed and watered before use. The animals were introduced into the chamber in batches of four to six and their distribution recorded after one hour, preliminary tests having shown that they take from 15 to 20 minutes to settle after having been disturbed. The animals were then stimulated to activity by tapping the sides and lid of the chamber, and a further reading was taken one hour later, when they had once again come to rest. In this way seven recordings were made for each batch of animals tested, and the mean of these recordings, taken to the nearest whole number, was regarded as the actual distribution in the chamber for that particular batch. Animals which had come to rest in the middle of the chamber in any observation were not included in the count. Reaction intensity was determined in the same manner as for the response to light. The experiments were carried out in the dark, and at a constant temperature of 20C. Counting was done with the aid of a faint red light.

Control experiments were carried out in a choice chamber without any humidity controlling substances and which thus had a uniform humidity throughout.

The results obtained for a choice between 94 and 25% Relative Humidity, obtained using distilled water and fused granular $CaCl_2$ as controlling agents, are shown in Table 1. These clearly show that *C. longicaudata* is indifferent to atmospheric humidity. Neither the control, nor the experimental results, differed significantly from random. This precludes the possibility of extraneous factors having influenced distribution. *M. delanyi*, however, shows a distinct dry preference, suggesting an eccritic humidity below 94% RH. Further experiments were therefore conducted on this species using lower humidities; the results of these are summarised in Table 2. They suggest that the humidity preferendum of *M. delanyi* lies within a fairly wide range between 70 and 85% RH, which corresponds closely with the actual conditions observed in its habitat in the field (Heeg in preparation). The inability to distinguish between humidities well outside the normal range is not peculiar to *M. delanyi*, having also been shown for the amphibious crab *Potamon depressus* by Dandy and Ewer (1961). The result obtained for the 15–0% RH choice, if a correct reflection of normal behaviour, would, however, suggest that the animals can discriminate between the presence and absence of water vapour even at low relative humidities.

TABLE 1

DISTRIBUTION OF *M. delanyi* AND *C. longicaudata* IN A CHOICE CHAMBER WITH 94 AND 25% RH AS ALTERNATIVES. (P=PROBABILITY OF DIFFERENCE BETWEEN EXPERIMENT AND CONTROL BEING DUE TO CHANCE).

Species	*Distribution of animals*				*Chi-squared*	*P*
	Experiment		*Control*			
	94% *RH*	25% *RH*	*Left*	*Right*		
M. delanyi	19	63	42	40	13·8	0·001
C. longicaudata	27	31	33	25	1·2	0·1

The result presented here for *C. longicaudata* conflicts with those obtained for *Lepisma saccharina* L. by Crome (1955) summarised in Table 3. In the absence of control experiments

TABLE 2

REACTIONS OF *M. delanyi* TO DIFFERENT RELATIVE HUMIDITIES IN AN ALTERNATIVE CHAMBER. (P=PROBABILITY OF THE DISTRIBUTION DIFFERING FROM THE CONTROL EXPERIMENT IN TABLE 1 DUE TO CHANCE).

Humidity choice (% RH)†	*Distribution*		*Reaction intensity to dry*	*Chi-squared*	*P*
	Wet	*Dry*			
100 -90*	2	22	+0·83	14·1	0·001
96·5–80	2	18	+0·80	10·4	0·001
96·5–75	3	15	+0·67	7·1	0·01
90·0–75*	8	34	+0·64	12·9	0·001
90·0–80*	5	19	+0·58	6·9	0·01
85·0–75	14	17	+0·13	0·3	0·5
85·0–75*	22	16	–0·16	0·5	0·5
80·0–75	16	13	–0·10	0·2	0·5
80·0–70*	18	16	–0·06	0·2	0·5
80·0–60*	25	7	–0·56	7·9	0·01
80·0–55	16	2	–0·78	8·7	0·01
75·0–60*	25	5	–0·67	9·4	0·01
75·0–55	19	3	–0·73	9·5	0·01
60·0–50*	24	9	–0·39	7·6	0·01
50·0–25*	26	29	+0·05	0·2	0·5
25·0–15*	27	22	–0·10	0·3	0·5
15·0–0*	21	3	–0·75	10·1	0·01

*KOH solutions used in humidity control. Saturated solutions of various salts used in all other instances.

†RH values in gradients of 16% RH or more will be slightly in error owing to the distillation process in the choice chamber.

these are difficult to evaluate, and it must be concluded that either *C. longicaudata* differs from *L. saccharina* in being indifferent to atmospheric humidity or that Crome's experimental animals had suffered desiccation, possibly during the light adaption process. This was carried out in closed petri dishes on a windowsill; the animals were protected from the direct effects of sunlight by means of a "transparent paper screen". *C. longicaudata* survives only one hour of exposure to direct sunlight in a closed container, and it seems possible that, although the paper screen afforded sufficient protection to allow Crome's animals to survive, enough solar radiation passed through or radiated from the screen to impair cellular activities. This could affect the active water-retaining mechanism described by Heeg (1967) and it may therefore be that Crome's results are representative of desiccated rather than normal animals.

Humidity preferences of desiccated specimens

Experimental animals were desiccated to reduce their internal water content and tested in a choice chamber using distilled water and $CaCl_2$ as humidity controls. Desiccation of the animals was carried out over $CaCl_2$ for 48 hours and 120 hours in the cases of *M. delanyi* and

TABLE 3
DISTRIBUTION OF *Lepisma saccharina* IN A HUMIDITY GRADIENT.
(SUMMARISED FROM CROME, 1955).

Temp.	*Light or dark adapted*	*No. of animals**	*No. of recordings*	*Distribution*				
				5% RH	35% RH	55% RH	80% RH	100% RH
10–12C	Light	13	55	26	4	0	1	24
18–22C	Light	21	120	4	4	5	7	100
18–22C	Dark	18	100	12	11	5	10	62
30–32C	Light	13	36	1	5	1	1	28

*All animals drawn from a total stock of 22.

C. longicaudata respectively, since these times subjected the two species to approximately the same percentage water loss. The results for *C. longicaudata* are based on three counts per batch only, since these animals are able to absorb water vapour from a subsaturated atmosphere (Heeg 1967).

TABLE 4
DISTRIBUTION OF DESICCATED *M. delanyi* AND *C. longicaudata* IN A CHOICE CHAMBER WITH 94 AND 25% RH AS ALTERNATIVES.
(P=probability of the distribution differing from the control experiment in Table 1 due to chance).

Species	*Distribution*		*Reaction intensity to 94% RH*	*Chi-squared*	*P*
	94% RH	25% RH			
M. delanyi	60	27	0·38	5·5	0·05
C. longicaudata	43	3	0·87	17·4	0·001

Both species showed a distinct preference for the wet side of the choice chamber after desiccation, as shown in Table 4. The response was far more marked in *C. longicaudata* than in *M. delanyi*, possibly due to the extreme variability in the individual rates of water loss shown by the latter (Heeg 1967). Although the difference between the results obtained for desiccated *M. delanyi* in a choice chamber and normal controls in a uniform humidity chamber is only just significant, the reaction to the wet displayed by the desiccated specimens become highly significant when compared with the reactions of normal animals in a choice chamber (Chi-squared=35·5).

INTERACTION OF THE BEHAVIOURAL RESPONSES TO TEMPERATURE, LIGHT, AND HUMIDITY

Animals are never subjected to only one category of stimulus, to the exclusion of all others, at any given time. Thus whilst one physical factor in a particular environment may be within the preferred range, another might be unfavourable. Clearly there must be some interaction between the responses to all the stimuli impinging on the sense organs, and this will decide whether an animal will avoid a particular microhabitat or occupy it. Whilst it would be impossible to investigate combinations of all the possible factors which may be encountered, the more important of these, temperature, light and humidity, were considered for both *M. delanyi* and *C. longicaudata*. For obvious technical reasons, only two factors were considered at any one time.

TEMPERATURE-LIGHT INTERACTION

The interaction between temperature and light was investigated using the *Temperaturorgel.* A mask of black cartridge paper was constructed which could be used to darken 10 cm of the length of the trough housing the experimental animals, leaving a space of only 0·5 cm between the floor of the trough and the mask to allow the animals free entry to and exit from the darkened area. The mask was placed so as to darken the middle region of the apparatus. The experimental animals were allowed to distribute themselves in the trough, in the dark, over a period of one hour, after which two 60 watt incandescent lamps, placed 35 cm above the apparatus, were switched on. This caused the animals to congregate in the darkened region, the treatment ensuring that only animals with normal light responses were used. With the overhead lights remaining on, heat was applied to the apparatus to set up a temperature gradient. The temperature at which the animals retreated from the shelter of the mask then gave a measure of the relative importance of the temperature and light responses.

Temperatures above 30C would cause *M. delanyi* to leave the shelter provided by the mask, whilst *C. longicaudata* would remain in the dark until a temperature of 35C was reached. These temperatures are somewhat lower than those normally eliciting an avoiding reaction, but they do approximately correspond to the temperatures at which there is a high level of activity due to the temperature activity orthokinesis.

TEMPERATURE-HUMIDITY INTERACTION

The interaction of temperature and humidity on the behaviour of the experimental animals was investigated insofar as it affected the temperature activity orthokinesis of *M. delanyi* at a humidity within its preferred range. The experimental animals were placed in a uniform humidity chamber in which the controlling solution was a saturated solution of sodium chloride, which subtends a near constant Relative Humidity of between 74 and 76% RH over the temperature range 5C to 50C. The chamber was set up in a constant temperature room at 15C; a thermometer passed through the rubber stopper closing the central hole in the lid of the chamber allowed a constant check on the temperature within. The activity of the animals in the chamber was recorded by periodic observation over four hours, after which the temperature was increased to 30C, at which temperature a further recording of activity was made over a period of five hours. The effect of temperature on the actual choice of the animals in a humidity choice chamber was not determined, as it was found impossible, with the means available, to set up suitable temperature alternatives in such a chamber.

The temperature activity orthokinesis of *M. delanyi* was displayed even when conditions of relative humidity were in the preferred range. The percentage activity increased from 7% at 15C to 90% at 30C.

LIGHT-HUMIDITY INTERACTION

The interaction between light and humidity was investigated in a humidity choice chamber, half of which could be darkened by means of a black paper mask. The humidity alternatives in the chamber were 94 and 25% Relative Humidity at a constant temperature of 20C. The experimental animals, which had been dark adapted and had had free access to food and water before the experiment were given a choice between 94% RH + darkness and 25% RH + light (giving rise to conflicting stimuli in the case of *M. delanyi*) in the experiment and between 94% RH + light and 25% RH 2 darkness in a control experiment. These experiments were repeated using *M. delanyi* which had been desiccated over $CaCl_2$ for 48 hours and *C. longicaudata* subjected to desiccation for 176 hours. It was necessary here to do a further control experiment in order to ensure that desiccation alone had no effect on the light responses of the animals. Here the desiccated animals were placed in a light-dark alternative choice chamber with a uniform humidity throughout, and their light responses were noted.

TABLE 5

DISTRIBUTION OF *M. delanyi* AND *C. longicaudata* IN A HUMIDITY CHOICE CHAMBER WITH ONE HALF DARKENED.

Species and condition	94% RH + *dark*	25% RH + *light*	94% RH + *light*	25% RH + *dark*
M. delanyi				
Normal	15	0	0	15
Desciccated	18	0	17	1
C. longicaudata				
Normal	16	0	0	16
Desciccated	18	0	15	3

Normal animals of both species showed their usual positive reaction towards the dark side of the choice chamber, regardless of the associated humidity. Although desiccation was found to have no effect on the normal light responses of the animals when tested in a uniform humidity chamber at 70% RH, it did reverse the order of precedence of the humidity and light responses. Desiccated animals congregated in the region of highest humidity, irrespective of whether this region was dark or not. These results are summarised in Table 5.

The results obtained here for normal *C. longicaudata* are not in agreement with those of Crome (1955) for *Lepisma saccharina*. In the latter species the positive response to the highest available humidity is said to overrule the light response in both light- and dark-adapted specimens, which has been shown to be characteristic of desiccated *C. longicaudata*. This lends some support to the suggestion made earlier that Crome's animals had been subject to water loss prior to the experiments.

DISCUSSION

The normal responses of *M. delanyi* and *C. longicaudata* to temperature, light and humidity are such that the animals are kept in conditions within their physiological range. Experiments have shown that the avoidance of high temperature, the factor most likely to be lethal, takes precedence over all other factors investigated. The temperature preferendum of *C. longicaudata* agrees with the temperature optimum for maximal fecundity in this species (Lindsay 1940). Light can only be regarded as a token stimulus associated with radiant heat and thus with body temperature and the negative photoresponse shown by both species keeps the animals from direct contact with the full rigours of the terrestrial environment. The hygroresponses too agree with the conditions found in the habitats normally inhabited by the two species (Heeg in preparation).

However, the hygroresponses of *M. delanyi* and *C. longicaudata* have further implications. Animals which lose water readily have humidity preferenda at or near saturation (Bursell & Ewer 1950; Perttunen 1953). The evolution of improved adaptations in the water economy of such animals requires initially that they come into contact with physical conditions which demand such adaptations. Competition, predation and disease all constitute selection pressures which favour the abandonment of the near-saturation conditions prevalent in the humus/litter complex, and in yielding to those selection pressures the animals will be exposed to conditions which demand adaptations for water retention. Furthermore, such movement away from the humus/litter complex cannot occur without an initial modification of those behaviour patterns associated with a high humidity preferendum; either the animal must display a humidity preference for sub-saturated atmospheres, or become indifferent to the prevailing humidity. The latter condition will reflect a greater emancipation from the restrictions imposed by a high rate of water loss than the former.

It has been demonstrated that both *M. delanyi* and *C. longicaudata* are better able to retain body water under sub-saturation conditions than are the typical arthropods of the forest cryptofauna (Heeg 1967). The present findings are in keeping with these results. *M. delanyi*, by avoiding both high and low humidities, is confined to a region below saturation, but where the saturation deficit is nevertheless not so high as to bring about excessive water loss. *C. longicaudata*, in addition to losing water more slowly than does *M. delanyi*, also has the ability to take up water vapour from an atmosphere where the humidity is as low as 60% RH and consequently is less restricted by atmospheric humidity (Heeg 1967). This would explain its normal indifference to humidity.

The normal humidity responses of an animal living at humidities substantially below saturation must change as its internal water content changes. Thus water loss must give rise to a preference for the highest available humidity, which is likely to indicate a source of replenishment. But the photoresponses of the animal are also of importance here, since the interaction between light and humidity, as it affects the behaviour of an animal, is a complex one. It depends upon (i) the resistance of the animal concerned to water loss, (ii) the normal environment of the animal, and (iii) the state of its internal water balance. Thus it is found that ambient humidity, in the absence of desiccation, may affect the normal light responses of an animal. Waloff (1941) and Cloudsley-Thompson (1952) both show that the intensity of the photonegative response of *Oniscus asellus* L. is markedly less at low humidities, and Perttunen (1961) notes the same phenomenon in *Ligia italica* F. These Crustacea all lose water rapidly (Edney 1954) and sub-saturation conditions cannot be tolerated by them for long periods. For such animals a lowering of the light barrier when conditions favour water loss will have a selective advantage. This effect is also shown by animals which do not lose water readily, but to which a particular humidity may be unfavourable. Perttunen and Lahermaa (1958) show that adult *Tenebrio molitor* L. are less photonegative at 100% than at 77% RH; this is possibly concerned with a detrimental effect of high humidity on some stage in the life history. The light responses of *M. delanyi* and *C. longicaudata* are unaffected by ambient humidity, since for undesiccated animals the intensity of the photonegative response is 100% regardless of humidity. Saturation conditions are detrimental to *M. delanyi* in that they foster fungal attack, whereas dry conditions give rise to water loss, although neither of these is immediately fatal to the animal. Exposure to direct sunlight, however, rapidly induces hyperthermia due to radiant heat, and also exposes the animal to attack by diurnal predators. Correlated with this it is found that the photonegative response overrules the humidity response.

Not only is the photonegative response of *M. delanyi* and *C. longicaudata* unaffected by the prevailing humidity, but it is also not affected by desiccation in the absence of a humidity gradient. This result appears surprising since such a photonegative response might trap an animal in conditions where water loss would be lethal. It would therefore be expected that desiccation should lead to a modification of the response of the animals to light, as appears to be the case in the terrestrial isopods. Abbott (1918) showed that the photonegative responses of *Porcellio scaber* Latr. and *Oniscus asellus* were abolished when the animals had been kept in dry culture. Waloff (1941) claims a reversal of sign from photonegative to photopositive on desiccation of *Oniscus asellus*, but her results, as presented, do not validly allow for this conclusion, which appears to be based on the fact that, as desiccation proceeds, more animals tend to settle in the light than in the dark. However, at best, only six of her experimental animals were sedentary (five in the light side of the choice chamber and one in the dark), and there is no indication of the distribution of the 14 animals actually moving about in the chamber. If the *total* number of animals, irrespective of whether they are moving or settled, does not bear out the results obtained for sedentary animals only, Waloff's results are more likely to be a reflection of the abolition of the photoresponse shown by Abbott (1918). Cloudsley-Thompson (1952) claims to have confirmed the reversal of the photoresponse of *Oniscus* as reported by Waloff, but he gives no details of his results. In animals susceptible to rapid water loss, a reversal of the photoresponse to photopositive may well prove detrimental unless reinforced by favourable humidity stimuli, since conditions outside its shelter may well prove worse than within. It is, however, equally important that light should not prove restrictive in the search for water, thus the abolition of the light response under conditions of water stress would have a definite advantage. *Ligia italica*, although it loses water more rapidly than does either *Porcellio* or *Oniscus* (Edney 1954), shows a reversal from photonegative to photopositive on desiccation (Perttunen 1961), which tends to refute the reasoning above. However, its surroundings on the sea shore ensure an abundance of water in close proximity to its microhabitat and thus minimal exposure in its search for water. Both *M. delanyi* and *C. longicaudata* lose water much more slowly than do the terrestrial Isopoda discussed above. *M. delanyi* can survive conditions of 0% RH at 20C for as long as 200 hours and *C. longicaudata* is even less liable to succumb to these harsh conditions (Heeg 1967). Thus the need for these animals to replenish their internal water store would, under natural conditions, never be so great as to necessitate a search for water by day; indeed, it is doubtful whether desiccation of the animals would ever be so severe as to cause them to abandon shelter even under the influence of favourable humidity stimulus.

SUMMARY

1. *M. delanyi* and *C. longicaudata* actively avoid surface temperatures of 35–36C and 40–43C respectively. In a temperature gradient *M. delanyi* will congregate at temperatures below 17C, but shows no clear-cut preferendum. *C. longicaudata* shows a possible preferendum between 15 and 20C. Both species show an activity orthokinesis in response to changes in ambient temperature. For *M. delanyi* activity is minimal at 15C and for *C. longicaudata* at 21C.
2. Both species show a strong negative photoresponse.
3. *M. delanyi* shows a marked avoidance of humidities outside the range 70–85% RH, but *C. longicaudata* is normally indifferent to atmospheric humidity. Upon desiccation both species react positively to the highest available humidity.
4. The avoidance of high temperatures overrules both the light and humidity responses of both species. In normal animals the negative photoresponse overrules the humidity reactions of the two species, but on desiccation the order of precedence is reveresd.
5. The ecological and evolutionary implications of these findings are discussed.

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