Am. Zoologist, 8:309-326 (1968).

Transition from Water to Land in Isopod Crustaceans

E. B. Edney

Department of Life Sciences, University of California,
Riverside, California 92502

Synopsis. The fossil record of land isopods is of little help in tracing the evolution of their terrestrial adaptations; however, we can usefully correlate the traits of various extant species with their various environments. Loss of cuticular water varies greatly between species, generally in relation to habitat, although the mechanism restricting loss is unclear. Both endocuticular and epicuticular barriers have been reported, the latter in *Venizillo arizonicus*. Pseudotracheae are advantageous for respiration in dry air, but again the mechanism is not clear. Excess nitrogen is excreted mainly as ammonia gas. Wide osmotic variation in the hemolymph resulting from dehydration is tolerated. Lethal temperatures vary in general according to habitat, and are affected by size, humidity, permeability of the cuticle, and previous temperature history. Evaporative cooling is sometimes of survival value for short periods. Metabolic rate is affected by season, and both long photoperiod and high temperatures are necessary for gonadal development and breeding. Responses to light, temperature, and humidity are more labile than previously thought. A peripheral hygro-receptor has tentatively been identified. The mechanism of bunching is largely thigmotactic, but olfaction may play a part, as it does in shelter-seeking. More information is now available about the micro-climates of habitats. In *Porcellio scaber*, nightly activity on trees in some situations permits elimination of excess water by transpiration. In *Armadillidium vulgare* nightly activity is greater in moister air, and drowning is a density-dependent mechanism for population control during heavy rains. Isopods are successful as land animals. Further study of population and distribution limits by combined ecological and physiological methods would be fruitful.

The title of this paper has certain evolutionary implications and I should like to comment briefly on these before proceeding. Those isopods which are now terrestrial constitute the sub-order Oniscoidea. The earliest undoubted oniscoid fossils occur in the Baltic amber from the upper Eocene or lower Oligocene, where forms congeneric with the present *Trichoniscus, Porcellio,* and *Oniscus* occur (Straelen, 1928). A fossil named *Eoarmadillidium dolfuss* was found in the Pleistocene of Languedoc, but the dating is doubtful (Vandel, 1960). Records of *Armadillidium* from the Miocene in Switzerland and southern Germany are uncertain. One or two fossils indistinguishable from the present *Porcellio scaber* are known from the Pleistocene of Britain and Austria, and *Armadillidum vulgare* is present as a sub-fossil in recent deposits in Britain. Since representatives of several families are present in the Eocene, it seems probable that terrestrial forms evolved some time before that, but as Straelen tersely puts it, "on ne connaît rien de leur origine."

The fossil record, then, is not helpful, and the question arises as to the extent to which we are justified in drawing phylogenetic conclusions from a study of present forms. On morphological grounds, Vandel (1943, 1965) believes that the Oniscoidea are polyphyletic. The first group (his Série tylienne), represented by *Tylos* and *Helleria* resemble marine valvifers such as *Idotea.* The second (Série trichoniscienne) includes the morphologically primitive, cave-dwelling *Cantabroniscus primitivus* and all other trichoniscoids; and the third group (Série lygienne) contains all the remaining Oniscoidea. The second and third groups are

---

I am grateful to Drs. D. F. Jans, O. H. Paris, A. Vandel, and M. H. Warburg for permission to use illustrations from their published work, and to Dr. W. C. Sloan for permission to refer to unpublished work. Figure 2 is reproduced by permission of the publishers of *Faune de France.*

derived, he believes, from undetermined but distinct sources within the marine isopods.

It is at least highly probable that all present land isopods are derived from marine ancestors. This being so it is reasonable to ask what differences exist between present species and present marine isopods, to inquire whether such differences are correlated with terrestrial life, and to deduce from this information the general direction of the evolution of terrestrial from marine forms. In this limited sense we can speak of the transition to land.

It is also perfectly proper to compare present species of land isopods among themselves as regards the extent to which each is structurally and functionally adapted to its own habitat, and thus to obtain information about physiological mechanisms and degrees of terrestrialness of habitat.

However, it is improper, in my view, to combine these two sets of information and force them to yield conclusions about evolutionary histories of particular species. For example, we should not try to trace the course of evolution, or transition to land, of a semi-xeric species such as the Australian *Buddelundia albinogrisescens* by inference from the littoral *Ligia* spp., the hygric *Trichoniscus,* the mesic *Porcellio,* and so on.

Let it be admitted that phylogenetic inferences, if legitimate, have a certain esthetic appeal. On the other hand, the search for them does not constitute the mainspring that keeps comparative physiologists active. I suspect that even if evolution were not the explanation of the present assemblage of living organisms, the general internally consistent body of knowledge which comparative physiology is discovering would take much the same form and have as much interest and relevance to science in general as it now does. In short I am suggesting that in this discussion it will do no harm if we concentrate on the comparative physiology of land isopods in relation to their several environments, for this is all we really have information about.

THE PHYSICAL ENVIRONMENT

It is well to keep in mind the main differences between aquatic and terrestrial environments so that the significance of morphological and physiological adaptations to the latter can be appreciated. The medium, air, is gaseous and less dense than water; the partial pressure of oxygen is the same, but the amount per unit volume is greater. An aquatic environment may impose an osmotic gradient across an animal's integument in either direction and the resulting loss or gain of water or salts can be offset by active uptake or elimination from or to the liquid environment. In air, an osmotic gradient as such does not exist. Water is indeed lost by evaporation, but in most cases it cannot be replaced by active uptake *via* gills or integument because the water potential in air is usually far too low, and salts are absent.

Both water vapor pressure and temperature vary more rapidly and over wider ranges on land, and at any one time differences in these values may be very great over short distances. Most animals weigh little if anything at all in water, so that mechanisms for support and locomotion in aquatic forms may be very different from those on land. However, the extent of the changes necessary during transition from the one to the other depends greatly on the locomotory structures of the aquatic ancestor. In isopods it seems likely that the walking habit (rather than swimming or jumping) and dorso-ventral compression of some members of the group facilitated a change to terrestrial life. Internal fertilization and retention of the eggs in brood pouches by oöstegites are traits that have great survival value for terrestrial animals, and both these features are characteristic of the marine isopods. These matters have been considered elsewhere (Edney, 1954, 1960; Vandel, 1960).

TABLE 1. *Comparative rates of transpiration.*

Species	Family	Temperature °C	Rate of transpiration in mg/cm²/hr/mmHg × 10³	Authority
ISOPODS				
Ligia oceanica	Ligiidae	30	220	Edney (1951)
Philoscia muscorum	Oniscidae	30	180	Edney (1951)
Oniscus asellus	Oniscidae	23	165	Bursell (1955)
Oniscus asellus	Oniscidae	39	132	Edney (1951)
Cylisticus convexus	Cylisticidae	30	125	Warburg (1965*a*)
Porcellio scaber	Porcellionidae	30	110	Edney (1951)
Porcellio dilatatus	Porcellionidae	28.7	104	Bursell (1955)
Armadillidium vulgare	Armadillidiidae	30	85	Edney (1951)
Armadillidium vulgare	Armadillidiidae	30	78	Warburg (1965*b*)
Hemilepistus reaumuri	Porcellionidae	19	23	Cloudsley-Thompson (1956*b*)
Venezillo arizonicus	Armadillidae	25	15	Warburg (1965*b*)
INSECTS				
Blatta orientalis	Blattidae	25	48	Mead-Briggs (1956)
Tenebrio molitor (larvae)	Tenebrionidae	25	5	Mead-Briggs (1956)
Glossina morsitans (pupae)	Muscidae	25	0.3	Bursell (1958)

Among the most important changes associated with transition from marine to terrestrial life are those which concern the problems of water balance and gas exchange, and to these we shall now turn.

WATER BALANCE

Loss of water occurs through the general integument, through the respiratory membranes, with the feces and perhaps as a result of nitrogen excretion. So far as transpiration is concerned our interest at present is centered on two aspects: the nature of any waterproofing mechanism that may exist, and the extent to which transpiration from different species differs and is correlated with environmental conditions. In 1954 I concluded from the evidence then available that transpiration through the integument of land isopods is proportional to the vapor pressure of the surrounding air, that temperature within the biological range does not affect the permeability of the integument as such, and that the latter varies between species in a manner inversely related to the dryness of their habitats. These conclusions implied, *inter alia,* that the cuticle of land isopods does not possess the waterproofing mechanism, an oriented layer of polar lipid molecules in the epicuticle, so characteristic of insects and arachnids (Beament, 1959, 1961; Lees, 1947). Certainly most land isopods lose water faster than most insects or ticks (see Table 1), but the question of a waterproofing mechanism needs further consideration.

In 1955 Bursell produced evidence of two breaks in the temperature/transpiration curve for *Oniscus asellus,* at 28° and about 35°C—in other words he found that the rate of transpiration per unit vapor pressure deficit (V.P.D.) increased at these temperatures. For *Porcellio dilatatus* and *Armadillidium vulgare* his evidence suggests a single break in the curve at 28°C. Since recently molted animals, in which the epicuticle is probably complete but in which the endocuticle is only partially laid down, transpire faster than intermolt animals, and since further, abrasion of the surface does not lead to a large increase in transpiration as it does in insects and arachnids, Bursell argued that the mechanism for restricting transpiration in land isopods consists of lipid material deep in the endocuticle of the animals. He confirmed earlier findings (Edney, 1951) that land isopods transpire more rapidly during the first 30 min of exposure than later, and went on to suggest that this is due to an initial rapid loss of water from the outer, unwaterproofed, layers of the cuticle, followed by a gradual reduction in rate as depletion of water leads to a shrinking of the cuticle with consequent concentration of the lipid material.

Bursell also made the point that since transpiration is more rapid at higher temperatures and since loss of water itself leads to a reduction in rate, we should not expect transpiration per unit vapor pressure deficit to be the same at all temperatures (except perhaps during very short exposures); rather we should expect a lower rate at higher temperatures, since more water will have been lost during the initial stages of exposure.

Warburg (1965*a,b*) measured transpiration in several mesic and xeric species but was unable to demonstrate any rapid increase at higher temperatures except in the xeric *Venezillo arizonicus*. In this species but not in others, treatment of the cuticle with warm chloroform also caused a marked increase in transpiration (as it does in many insects) although abrasion apparently failed to do so. Auzou (1953) found that transpiration increased above about 20°C in *Oniscus asellus* and above 30°C in *Porcellio scaber,* but she exposed her animals for at least three hours and her data do not permit any assessment of reliability.

Comparison and evaluation of these various results is difficult since workers have used very different experimental conditions, and expressed their results in various, not always interchangeable, units. However, Figure 1 is an attempt at such a synthesis. The data have all been converted, making certain assumptions, to rates per cm^2 per mm Hg V.P.D. Temperatures are those of the ambient air, for no information is available about the surface temperatures of the animals in most of these experiments, and this, as Beament (1958) has pointed out, can lead to error. Subject to these reservations, the following points emerge. There is a general downward trend in rate per unit V.P.D. as temperature rises over the lower temperature range. Bursell's curve for *Oniscus* shows a break in this trend at about 28°C, and an upward swing for *Porcellio* starting at the same temperature. My curve for *Porcellio* shows the same general features: there is no sharp break, but this if it exists would have been missed because the experimental temperatures were widely separated. There is clearly a difference in shape between Warburg's curves for *Venezillo* and *Armadillidium*—the former rises steeply at high temperatures paralleling that for the insect *Blatella* (derived from Wigglesworth's data, 1945). However, there are many inconsistencies in this and related evidence. For example, *Armadillidium* is said to lose five times as much water during the second half hour of exposure than during the first, while the reverse is true of *Cylisticus* (Warburg 1965*b*). In *Buddelundia,* the rate of transpiration at 35°C is virtually the same whether the V.P.D. is 9.2 or 42 mm Hg (Warburg, 1965*a*). Abrasion, according to Auzou (1953) has no effect on transpiration in *Oniscus* but a marked effect in *Porcellio* while Bursell (1955) found no effect in *Porcellio*. Warburg found that abrasion has no effect in *Venezillo* although chloroform does increase the rate of transpiration.

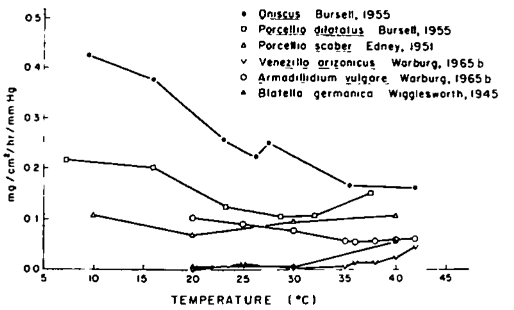

FIG. 1. Transpiration in various species of land isopods and the cockroach *Blatella.* Data from Bursell (1955) refer to the second half-hour of exposure; those from Edney (1951) to the first whole hour; those from Warburg (1965*b*) to the first whole hour, and those from Wigglesworth (1945) to exposures for less than one hour. Data have been recalculated where necessary in terms of surface area and to allow for differences in vapor pressure deficits.

What, if anything, can be rescued from this conflicting evidence? It is fairly clear that permeability of the cuticle is affected by temperature at least in some species. Bursell's evidence for a deep-seated lipid barrier in *Oniscus* and *Porcellio* is strong (although this would seem to be less efficient than an epicuticular barrier since the endocuticle is reduced or interrupted at the arthrodial membranes), and Warburg's evidence for an epicuticular barrier in *Venezillo* is also good. It is not impossible that both mechanisms exist within the group Oniscoidea, but the problem needs further and deeper investigation.

COMPARATIVE RATES OF TRANSPIRATION

We are on firmer ground when comparing rates of transpiration in different species, for although workers have used different techniques and forms of expression, results are internally comparable and, since specific differences are quite large, at least qualitative comparisons can be made. In a very general way there is a correlation between moistness of the habitat and permeability of the integument, as Table 1 makes clear. However, this is a superficial statement which needs qualification. Firstly, "moistness of the habitat" is a very inexact expression indeed and usually represents no more than an overall impression of the local macro-climate. In fact there are large differences in micro-climate often within very short distances as Warburg (1965*c*) and several others have shown, and it may be that differences in permeability are related more closely to the period of time that an animal spends away from saturated air (or the V.P.D. it can tolerate for a given time) than to the overall humidity of its general environment.

Secondly, loss of water by transpiration expressed in terms of weight per unit area gives little guide to survival in unsaturated air, since matters of size are involved. *Ligia*, with a weight of about 1 g, may lose water more than twice as fast per unit area as *Porcellio* weighing 100 mg (Edney, 1951), yet because of its smaller surface/volume ratio *Ligia* lives longer than *Porcellio* in dry air (Miller, 1938). If survival in unsaturated air is a measure of terrestrial adaptation, then large animals have an advantage over smaller ones.

RESPIRATION AND LOSS OF WATER

Oxygen uptake by land isopods occurs mostly through the pleopods which may be simple gill-like structures, as in the littoral *Ligia* species, or modified in various ways (see Fig. 2) by invaginations forming "pseudotracheae." The early work (references in Edney, 1954) leaves little doubt that the development of pseudotracheae in one form or another is associated with respiration in dry air, and Vandel (1943) believes that each of the three main types evolved separately. The amount of water lost by the pseudotracheae is a substantial fraction of the total loss, but the proportion varies according to terrestriality (Edney, 1951); being as high as 42% in *Porcellio*, but only 24% in *Ligia*. Total evaporative loss per unit area is much greater in *Ligia*, so that the high proportionate loss in *Porcellio* is a reflection of the more efficient waterproofing of the non-pleopodal areas in that genus.

Land isopods obtain a portion of their O_2-requirements through the general surface (Edney and Spencer, 1955), and measurements of this do provide evidence for the advantage of pseudotracheae in dry air (Table 2). In *Ligia* with blocked pleopods, O_2-uptake in moist air falls to about 50% of normal. In more terrestrial species it falls still further: to about 25% of normal in *Armadillidium*. In dry air, when the integument is also dry, O_2-uptake in normal *Ligia* is reduced to 13% of normal, in *Oniscus* to 33%, but only to 90% and 94% of normal in *Porcellio* and *Armadillidium*, respectively. Blocked pleopods and dry air reduce O_2-uptake to the vanishing point in all species used. *Ligia* and *Oniscus* in the dry air experiments ultimately died, and the cause of death was not desiccation but lack of O_2, because an atmosphere of moist nitrogen failed to prolong life while a high oxygen tension did.

Thus, pseudotracheae are adaptive to respiration in dry air, although it is by no means obvious why this is so. Pseudotracheae of whatever form consist essentially of invaginations of the respiratory surface; but this, by itself, does not reduce water loss per unit O_2-uptake; it simply reduces both, per unit area, by interpolating a longer diffusion path. In insects the advantage of a tracheal system lies in the presence of occlusible spiracles which permit water loss to be reduced except at times of maximum O_2-need, but occlusible spiracles have not been demonstrated in land isopods, so that an explanation of the adaptive value of the pseudotracheae in dry air is still needed. It would be interesting to look for a mechanism whereby the entrances to pseudotracheae may be closed when the whole of the interior respiratory surface is not required for O_2-absorption. Such a mechanism might take the form of a simple apposition against another surface.

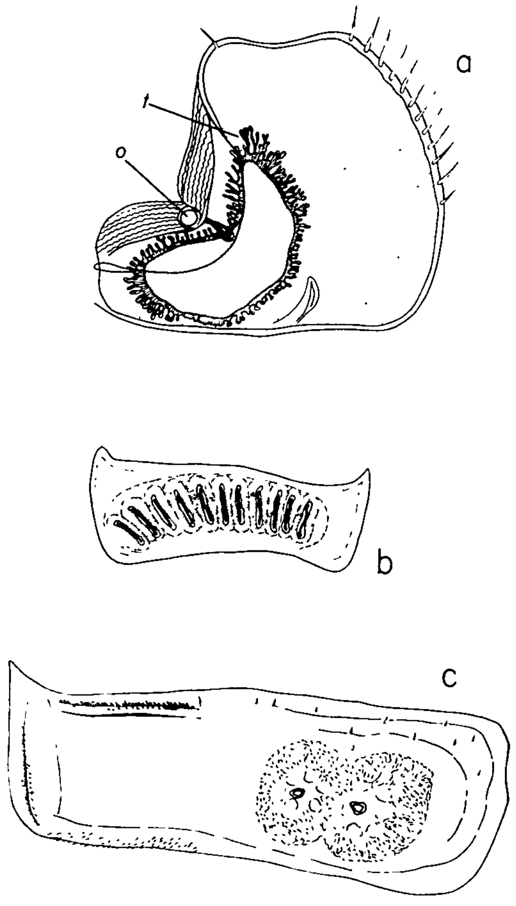

FIG. 2. Three types of pseudotracheae: a, exopodite of the first pleopod of *Porcellio scaber*; b, exopodite of the second pleopod of *Tylos latreillei*; c, exopodite of third pleopod of *Helleria brevicornis*. Type "a" is found in the more terrestrial species. o, air bubble at the opening of the pseudotracheal system; t, terminal twigs of the pseudotracheal bush. From Vandel, 1960, (a, after Verhoeff, 1920).

WATER LOSS BY EXCRETION AND DEFECATION

The nature of the end product of nitrogen metabolism of different animals is often thought to be related to the availability of water: thus, terrestrial animals use uric acid rather than ammonia or urea. Land isopods seem to be an exception, for it was shown by Dresel and Moyle (1950) that ammonia is the main nitrogenous end-product. These authors went on to suggest that adaptation to terrestrial conditions had taken the form of a simple reduction in protein metabolism. The question has been re-examined by Sloan (unpublished), who has good evidence that ammonia is excreted as a gas and that there is no reduction in intake or metabolism of proteins associated with water stress. This is an important finding and we look forward to hearing more about it. Such a mechanism would of course permit elimination without the necessity for liquid water. On the other hand, much unoxidized hydrogen is lost, so that the overall water balance may not be benefited.

The extent of water loss with the feces has not been intensively investigated. Kuenen (1959) in some preliminary work found that *Oniscus, Porcellio,* and *Armadillidium* all produce fecal pellets with less water than their food contained, *Ar-*

TABLE 2. *Oxygen uptake in* $mm^3/mm^3/hr$ *by land isopods in moist or dry air and with free or blocked pleopods. (Data from Edney and Spencer, 1955.)*

Species	Pleopods	O_2 uptake in moist air	O_2 uptake in dry air
Ligia oceanica	Normal	0.155	0.020
	Blocked	0.081	<0.005
Oniscus asellus	Normal	0.075	0.023
	Blocked	0.039	0.005
Porcellio scaber	Normal	0.084	0.075
	Blocked	0.029	<0.005
Armadillidium vulgare	Normal	0.086	0.081
	Blocked	0.022	<0.005

madillidium retaining the highest proportion, *Oniscus* the lowest. But whether or not the amount retained is related adaptively to water needs is not clear.

CAPACITY FOR OSMOREGULATION

There is no doubt that insects, those paradigms of terrestrial adaptation, regulate the osmotic concentration of their hemolymph against the effects of high osmotic concentration in their food or water intake (Phillips, 1964). There is also evidence that volume and osmotic concentration of the hemolymph are regulated against the effects of overall loss of water by transpiration (Edney, 1967). In land isopods there is no such evidence, and what work has been done suggests that they tolerate a wide range of hemolymph concentrations. Parry (1953) found that *Ligia oceanica*, whose normal hemolymph concentration is about Δ 2.0°C (3.3% NaCl), survives a hemolymph concentration induced by desiccation up to Δ 3.48°C (5.8% NaCl). Bursell (1955) found in *Oniscus* a progressive increase in hemolymph concentration from 1.59% to 2.00% NaCl equivalent as evaporation proceeds, the increase in concentration being predictable from the decrease in total water content. This process is to some extent self-regulatory, for a higher hemolymph concentration leads to a lower permeability of the cuticle. It would be of interest to know how the volume of hemolymph changes in these circumstances.

Regulation is by no means absent in all oniscoids, however. Parry (1953) found that *Ligia oceanica* regulates well in sea water between 100% and 50%. Todd (1963) obtained similar results and found that even in 25% sea water there was some regulation, which eventually broke down. Todd's results, which also show the effects of temperature and season on osmotic regulation in *Ligia*, demonstrate that this animal is a better osmoregulator in dilute sea water than the intertidal isopod, *Idotea granulosa*. It is not clear whether osmoregulatory ability in water is preadaptive for success as a terrestrial animal. But these matters are to be discussed later in this symposium.

LETHAL TEMPERATURES AND REGULATION OF TEMPERATURE

Temperature fluctuates more widely and more rapidly in terrestrial than in most aquatic environments, and it is probably also true that, on land, higher ambient temperatures are encountered in the open than in cryptozoic niches. Ability to tolerate high temperature is, in this sense, a mark of terrestrial adaptation.

The highest ambient temperatures that land isopods tolerate is affected by their genetic constitution, the period of exposure, the rate of rise, the ambient humidity, and the previous temperature history (acclimation). Setting aside the effects of acclimation for the time being, some of the effects of interactions between the other factors are shown in Figure 3. For short (1 hr) exposures, tolerable ambient temperatures are lower in saturated

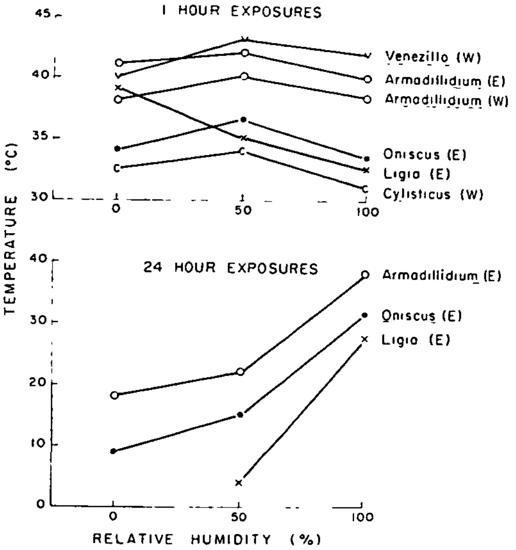

FIG. 3. Lethal temperatures for 1-hr and 24-hr exposures at various humidities. E, data from Edney, 1951; W, data from Warburg, 1965*b*. The effect of size in *Ligia oceanica*, a littoral isopod, at low humidities is apparent.

air than in 50% R.H. (when the body temperature is below ambient owing to evaporative cooling). In dry air the tolerable temperature is somewhat lower because the animals die as a result of desiccation rather than temperature stress. Interestingly enough, *Ligia*, which is much larger than the others and which consequently can withstand a given rate of transpiration per unit area for longer, shows a higher ambient lethal temperature even in dry air. For 24 hr exposures the effects are different. In saturated air, lethal temperatures are all slightly lower than for 1 hr exposures, and the effect of 50% R.H., and still more of dry air, is to lower the lethal temperature greatly. Thus size, duration of exposure, permeability of the cuticle, and humidity are all seen to play significant parts in determining the effects of high ambient temperatures.

If we accept the results of exposure in saturated air as approximating more closely to the true tissue tolerance temperature, the species investigated stand in the same order as they do with respect to general terrestrialness of habitat, *Venezillo arizonicus* showing the highest lethal temperature so far reported, namely 42°C in 100% R.H. for 1 hr (Warburg, 1965*b*).

The ecological significance of some of these facts has been confirmed. For example, *Ligia oceanica* emerges from its moist niches below stones when the temperature there becomes dangerously high as a result of insolation of the upper surfaces. Outside, although in full sunlight, its body temperature is lower, partly as a result of convection to the air, but also owing to evaporative cooling (Fig. 4) (Edney, 1953). Again, the body temperature of *Hemilepistus reaumuri*, which occurs in the Algerian Sahara is reduced as a result of transpiration (see p. 320). Thus, the importance of evaporative cooling in critical circumstances is evident, although the loss of water involved forbids this as a long term measure, so that its significance as an adaptation to land life is probably minimal.

ACCLIMATION TO TEMPERATURE AND SEASONAL EFFECTS

The term "acclimation" is used here to mean an adaptive change in an individu-

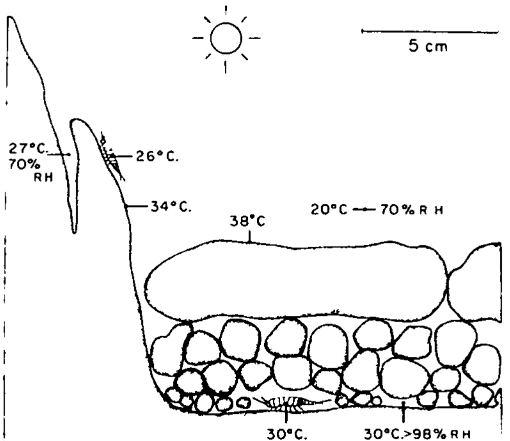

FIG. 4. Diagrammatic section of the base of a red sandstone cliff and shingle inhabited by *Ligia oceanica*, to show microclimatic conditions and body temperatures of the animals. Reduction of body temperature by evaporation of water and by convection occurs when the animals emerge from their cryptozoic niches. After Edney, 1953.

TABLE 3. *Upper and lower lethal temperatures for 30 min exposures at 100% R.H. after acclimation at various temperatures for 14 days. (Data from Edney, 1964.)*

Species	Acclimation temperature, °C	Upper lethal temperature, °C	Lower lethal temperature, °C
Porcellio laevis	30	41.5	5.5
	20	38.5	—0.5
	10	37.5	—2.5
Armadillidium vulgare	30	41.3	3.0
	20	39.5	—1.5
	10	38.5	—3.0

al's temperature response as a result of its previous temperature history. The phenomenon is well developed in some land isopods although it has been held that acclimation is greater in aquatic than in terrestrial animals (Edwards and Nutting, 1950; Scholander, Flagg, Walters, and Irving, 1953). The upper and lower lethal temperatures of *Armadillidium vulgare* and *Porcellio laevis* are affected by previous exposure of these animals to 10°, 20°, or 30°C for a week or more (Table 3). The effect of acclimation on lower lethal temperatures is greater than that on upper lethals in both species. Similarly, the difference between animals acclimated at 20° and 30°C is greater than that between those acclimated at 20° and 10° in both species. There is also a greater effect in *P. laevis,* which is perhaps less terrestrial, than in *A. vulgare.* However, the latter acclimate to a greater extent than the former with respect to standard metabolic rate (Edney, 1964).

Differences in upper lethal temperature were also found among field populations sampled from southern California to British Columbia during August 1962, and these differences were correlated with environmental temperatures (Fig. 5). Further, the differences were environmental rather than genetic in origin, since samples from each locality kept for 14 days at 20°C subsequently all showed the same lethal temperature.

Mention may be made here of Wieser's (1962, 1963*a,b*) interesting work on seasonal and other effects on metabolic rate and gonadal development which, although not immediately relevant to terrestrialness, is generally significant in the biology of land isopods. Wieser worked with the well known *Porcellio scaber* and *Armadillidium vulgare* and with the less well known *A. granulatum* and *Syspastus* (a synonym of *Helleria*) *brevicornis.* The last named is one of Vandel's "Série tylienne," probably derived from an *Idotea*-like stock. No effect of previous temperature history or of size upon O_2-uptake was found in mature *Porcellio scaber.* However, various other factors did affect it in different ways in different species. Thus hunger reduced O_2-uptake in *P. scaber* and in both species of *Armadillidium,* but had no effect in *Helleria.* Activity raised the metabolic rate by a factor of five in *Helleria,* but only doubled it in the other species. The main interest of Wieser's work lies in his discovery of the effect of season of the year on feeding, relative gut weight, and basal metabolic rate. In spring, both wild and laboratory

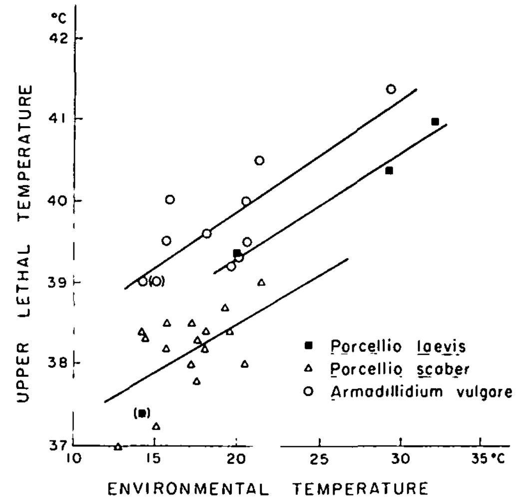

FIG. 5. Upper lethal temperatures (L.T.50) determined soon after capture of animals at various stations from Southern California to British Columbia in August, 1962. Environmental temperature is expressed as the mean daily maximum temperature for 7 days before capture and experiment. Symbols in parenthesis refer to populations from one station (Riverside, Calif.) in the winter. L.T.50's and environmental temperatures are significantly correlated in each of the three species shown. From Edney, 1964.

cultures of *P. scaber* show a rather sudden increase in metabolic rate, relative gut weight, and gonadal development. Photoperiod and temperature jointly control events leading to reproduction in an interesting way: longer day length in spring increases metabolic rate in preparation for gonadal development, but higher temperatures are also necessary as a releaser for the actual development to commence. Thus, in a year when spring is late (so far as temperature is concerned), reproduction is retarded. Wieser (1963*b*) suggests further that the process involves the interaction of an internal clock and hormonal production, for while short day-length inhibits development, if a population subjected to 7 hours of light per day has the light phase shifted to another 7-hr period, the effect appears to be additive and some of the females produce brood pouches.

Wieser (1965) has also found an interesting relationship between copper metabolism and terrestriality. Although the absolute content of hemocyanin is independent of the habitat of a species, terrestrial isopods are more dependent upon copper in their food than marine ones are—they conserve copper and show higher, more constant amounts in the hepatopancreas. We look forward to hearing more about isopod metabolism during the present symposium.

ORIENTATION AND BEHAVIOR: INTRODUCTION

We come now to an aspect of terrestrial adaptation of great importance, and one which fortunately has been the subject of several investigations during the last decade. Poorly equipped as most isopods are to resist the effects of dry air and high temperatures, sensory and behavioral mechanisms that permit them to avoid such conditions to a greater or lesser extent assume added significance.

The older work made it clear that most species of land isopods at most times aggregate in dark moist places as a result of certain kinetic and possibly tactic responses (references in Edney, 1954). Obviously, if these mechanisms were inflexible, all the animals would be confined to dark, damp crevices. More recent work has therefore been concerned with the variability of such mechanisms, their interactions, and their relationship to natural conditions in the field.

Cloudsley-Thompson, (1952, 1956*a*) for instance, found a circadian rhythm of activity in *A. vulgare* and *O. asellus* which is partly endogenous and also associated with changes in photo- and hygro-responses in such a way that the animals emerge and become active after nightfall and retreat to cover at daybreak.

SENSORY ORGANS

Before reviewing some recent developments in behavioral mechanisms I shall refer briefly to what little is known of the sensory organs involved. One kind of receptor which would seem to be advantageous on land but not in water is a hygroreceptor. Early work by Gunn (1937) and others failed to locate such receptors, and the problem was reexamined by Jans and Ross (1963) who carried out a survey of all peripheral receptors in *P. scaber* and *O. asellus* by means of complete serial sections. Six types of receptor were identified. By inference from their structure and position, three seem to be mechanoreceptors, and of the remaining three, one has been tentatively identified as a hygroreceptor (Fig. 6). These organs are on the under side of the lateral plates, in such a position that mechanical or olfactory functions seem unlikely. They are protected from damage and liquid water, yet they are exposed to the air. Their structure resembles that of the few other hygroreceptors known in arthropods (references in Jans and Ross, 1963), but such a function has not yet been confirmed experimentally.

No other sense organs known to be specifically associated with the terrestrial habit have been described.

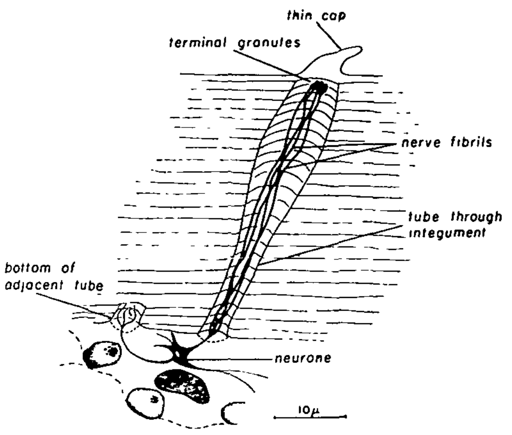

FIG. 6. The structure of a "lateral pit," believed to be a hygroreceptor, on the under surface of a lateral plate of *Porcellio scaber*. From Jans and Ross, 1963.

BEHAVIORAL MECHANISMS

Recent work on behavioral mechanisms has underlined their complexity and variability. I shall discuss this aspect of the work before proceeding to the even more complex situation with regard to distribution in the environment.

Friedlander (1963, 1965) investigated the process of thigmokinesis in land isopods and was able to quantify this response satisfactorily for the first time. He showed that even smooth glass is preferable to no contact, but that rougher surfaces are preferred to smooth ones. The intensity of the response, which is greatest in *O. asellus*, less in *P. scaber*, and least in *A. vulgare*, is in all three species greater in dry than in moist air. Unfortunately, we do not know whether the state of the animal's water reserves affects its response. When contact shelter was pitted against high humidity in an experiment with *A. vulgare*, high humidity without contact was preferred to low humidity with contact (Table 4).

Aggregation is a characteristic of the behavior of many species of land isopods. It is certainly effective in reducing loss of water (although Friedlander found no greater degree of aggregation in 80% R.H. than in saturated air) and seems to be mediated mainly by thigmokinesis. This is not the whole story, however, for although animals aggregate around roughened clay models, they aggregate to a greater extent around each other. Friedlander found no chemical attraction between individuals, but in 1963 Kuenen and Nooteboom did (see below).

No particular significance should be attached to the fact that thigmokinetic responses occur in aquatic isopods, for they occur in several other groups of aquatic animals as well. In this respect isopods are no more pre-adapted for land life than, for example, decapods.

Kuenen and Nooteboom (1963) asked the important question: how do isopods find daytime shelters after their nightly excursions? Thigmokinesis, they point out, is not effective until an animal is already in a crevice, and high photokinesis is probably not the explanation since the animals often take shelter long before the night is over. Low hygrokinesis is a possible answer and so is olfaction. They investigated the latter.

Their results show (1) that the smell of each species (*O. asellus, P. scaber,* and *A. vulgare*) is attractive to other individuals of the same species (and in some cases to other species, although less distinctly) (Table 5), and (2) that the attraction is greater the lower the water content of the responding animal (Fig. 7). There was even an indication of negative response in *P. scaber* when fully hydrated. These conclusions are securely based, and the ecological significance is apparent: if Den

TABLE 4. *Choice chamber experiments with* Armadillidium vulgare *showing the effects of dorsal mechanical contact or its absence in wet and dry air. (Data from Friedlander, 1963.)*

	CHOICE	
Moist with contact	or	Dry without contact
91.4%		8.6%
	CHOICE	
Moist without contact	or	Dry with contact
69.8%		30.2%
	CHOICE	
Moist without contact	or	Dry without contact
93.3%		6.7%

TABLE 5. *Response of land isopods in an olfactometer to the smell of their own and other species. (Data from Kuenen and Nooteboom, 1963.)*

Species tested	Species providing smell	% positive reactions	P
Oniscus asellus	*O. asellus*	68	<0.001
Oniscus asellus	*A. vulgare*	55	>0.5
Porcellio scaber	*P. scaber*	63	<0.001
Porcellio scaber	*A. vulgare*	64	<0.001
Armadillidium vulgare	*A. vulgare*	62	<0.001
Armadillidium vulgare	*O. asellus*	49	>0.5

Boer's conclusions (see below) are correct, land isopods emerge at night and lose excess water by transpiration. When they have reduced their water content sufficiently, they are attracted to crevices by their own species' smell; until then they remain in the open.

The complex interplay of light, temperature, humidity, and time of day in determining behavioral responses is illustrated by Warburg's (1964) work on a variety of isopod species from mesic and xeric habitats, particularly *Venezillo arizonicus* and *Armadillidium vulgare*. The results in terms of preferences for, and activities in, the many different combinations of these factors used by him are difficult to summarize, and I shall draw attention to only three points of interest: (1) Warburg found marked differences between species in their responses to the same situation. (2) Light seems to be of relatively minor importance in determining behavior; however light does have more effect on *V. arizonicus* than on other species, and Warburg believes this to be adaptive for an animal in a xeric habitat. (3) The experimental results emphasize that the sign of a response may change, even abruptly. Thus, during the first 15 min of exposure to a choice between 40% R.H. and light on the one hand, against 70% R.H. and darkness on the other, both at high temperatures, *A. vulgare* and *V. arizonicus* both showed a preference for the dark side, but this was reversed during the rest of the first hour, an effect which Warburg ascribes to water loss.

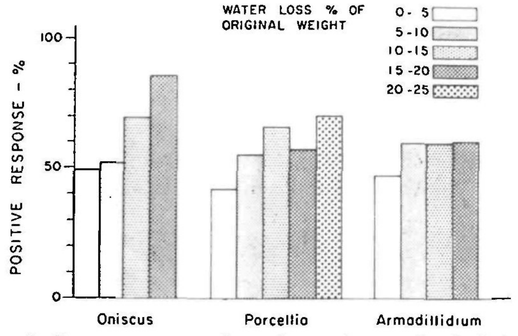

FIG. 7. Responses of isopods to the smell of their own species when the responding animals have suffered various degrees of water loss. In *Oniscus*, positive responses at 10-15% and 15-20% water loss are significant. In *Porcellio* there is a significant negative response at 0-5% water loss and significant positive responses at 5-10% and 10-15% water losses. The responses of *Armadillidium* are not significantly different from chance. Data from Kuenen and Nooteboom, 1963.

CONDITIONS IN THE HABITATS OF LAND ISOPODS

Much has been written about different degrees of terrestrialness of habitat, but rather few measurements have actually been made. The earlier work is referred to by Edney (1954).

Cloudsley-Thompson (1956*b*) and Edney (1958) contributed further information about the microclimates inhabited by both mesic and xeric species. The so-called desert isopod, *Hemilepistus reaumuri*, digs neat vertical holes in the sand of alluvial plains and spends a lot of time in them. During April 1955, when I visited an area near Biskra on the northern fringes of the Sahara Desert, very large numbers of these animals were active on the desert surface up to 1100 hr and after 1500 hr. Temperatures and humidities measured in their habitats showed that conditions in the holes were indeed far more equable than those outside. Even at 2″ below the surface the R.H. never fell below 80% even when it was only 20% outside. By tethering living and dead dry animals on the surface I found that eva-

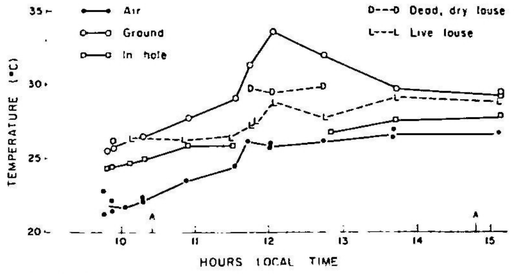

FIG. 8. Temperatures in the habitat of *Hemilepistus reaumuri*, a "desert" land isopod in Algeria. The effect of transpiration on body temperature is evident from a comparison of the data for a dead, dry animal with those for a living specimen. From Edney, 1958.

poration from the former reduced the body temperature some 2.5°C below that of the dry specimen. Such evaporative cooling, for short periods, may have survival value, since animals caught in the open by a sudden increase in heat load scurry for the shelter of a hole. One set of temperature observations is shown in Figure 8.

In direct sunlight *Hemilepistus* lost 5.4 mg $H_2O/cm^2/hr$ (or 5.6% of its body weight) and this is sufficient to account for the temperature depression recorded. *Hemilepistus* is large for a land isopod, about 2.0 cm long, and walks with the body raised well above the ground when the latter is hot.

One of the fullest investigations of mesic and xeric habitats is that of Warburg (1965*c*) who measured conditions in three habitats in Arizona during a week or more in mid-summer. His data (Fig. 9) confirm that there is less variability in temperature and humidity in cryptozoic niches, and also suggest, rather unexpectedly, that in mesic habitats occupied by *A. vulgare*, midday conditions under logs (temperatures up to 40°C, humidities down to 16% R.H.) may become less tolerable than those in the open. In xeric habitats occupied by *V. arizonicus* mean and maximum temperatures are generally higher and humidities lower, but, owing to the lack of protection from trees or bushes, the open areas are uncrossable during the day.

A point of interest is that Warburg's data do not include a single instance of saturated air. His highest R.H. is 90% under a stone in the mesic environment, and none of his mean maximum humidities are higher than 80%. Since there is good evidence that land isopods lose water in anything but saturated or very nearly saturated air, it must be presumed that such conditions were reached during the night (no data are given for this period) or that a moist substrate was available from which the animals could absorb water (Spencer and Edney, 1954).

MOVEMENT WITHIN THE ENVIRONMENT

Much of the work on water and temperature relationships of land isopods has been concerned with the "perils" attendant upon water loss. It is salutary, therefore, to be reminded of the converse problem, namely the danger of becoming waterlogged, and this is drawn to our attention in important papers by Den Boer (1961) and Paris (1963).

Den Boer, in a series of well conceived and logically satisfying experiments, showed that a large part of the locomotor activity of a population of *Porcellio scaber* near Den Haag, subserves the function of elimination of excess water. During the day these animals are found in

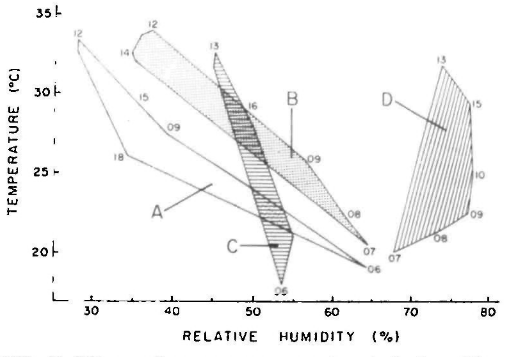

FIG. 9. Thermohygrograms constructed by Warburg (1965*c*) from data obtained by him in a land isopod habitat in Arizona at an elevation of 5400 ft. Conditions under a large stone are less variable and more humid than under a log or on the ground. A, air at 1 meter height; B, ground; C, log; D, large stone.

various shelters: in the woodland litter or in shelters either at the bases of trees or farther up. They move about from one to another at night. Brereton (1957) also noticed nightly activity on trees by *P. scaber*, and concluded that these animals exhibit seasonal migration, moving into the upper parts of the trees in summer. However, this situation is not strictly comparable with that in Den Boer's work, for Brereton's trees were much taller and provided more shelters high above the ground.

Den Boer found that vertical activity is negatively correlated, and horizontal activity positively correlated, with vapor pressure deficit. The search for food was not responsible for the nightly increase in activity in his animals, since food was always available in or near their shelters. Neither was sexual activity responsible, for there was no increase in activity during the breeding period. The animals did, however, absorb water from moist surfaces and from saturated or near-saturated air in their shelters, and then showed a preference for lower humidities, particularly in the dark. Normal excretion is not capable of maintaining water balance in saturated air, but evaporation is. Hence, Den Boer suggests that the extent and duration of vertical migration into the upper part of trees at night are associated with the fact that lower humidities, permitting transpiration, are to be found there. This hypothesis was confirmed by field observations and measurements, and by experiments with models in the laboratory. There is little doubt that Den Boer has established an important point.

Paris and his colleagues have also contributed important information about the ecology of *A. vulgare* in California. The work of Paris and Pitelka (1962) on the population dynamics of the species is the most complete study of its kind on isopods. Hubbell, Sikora, and Paris (1965) and Paris and Sikora (1965) describe studies on food preferences, ingestion, and assimilation in this species using radio tracers. However, Paris' work (1963, 1965) on the effects of climate on activity, dispersion, and population control of *A. vulgare* is most relevant in the present context and I shall restrict comment to this.

The work was done in Californian grassland near San Francisco — a very different situation from Den Boer's — in an attempt primarily to obtain information about population control. Food was normally abundant. Dead leaves of the tar-weed, *Picris*, were preferred, but in their absence almost any other dead vegetation would do. Predation by reptiles was not heavy, and spiders and centipedes did not feed on *A. vulgare* at all. In passing we may note that Gorvett (1966) considers that the lobed tegumental glands opening on the uropods and lateral plates have been evolved in the land isopods (they occur in no others) specifically as a protection against predation by spiders.

After ruling out predation, parasitism, and cannibalism as important population control mechanisms, Paris investigated the effects of weather. During periods of drought in this area, the isopods descend in soil fissures to a depth of between 15 and 45 cm. They emerge at night to feed, and estimates of their activity on the surface showed a strong negative correlation with V.P.D. (Fig. 10).

These results appear at first to conflict

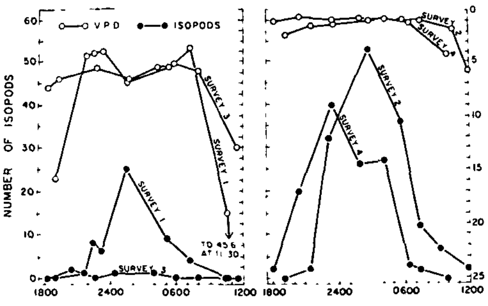

FIG. 10. Samples of data obtained by Paris (1953). The data as a whole show an inverse correlation between deficit in vapor pressure and the degree of nightly activity in a population of *Armadillidium*. Curves on the left refer to a dry night, those on the right to a moist night.

with Den Boer's data for *P. scaber*. However, if we accept that these animals were out to feed while Den Boer's were not, that these animals were not over-hydrated in their daytime retreats, and that in any case this was not vertical activity, the two sets of observations are seen to be complementary rather than contradictory.

During the rainy season, the picture that Paris obtained was different in one respect — the animals remained near the surface all day, although they still became active at night with a peak at midnight. Most importantly, he found that the main cause of mortality during the winter rains was drowning — a conclusion based on field observations and experimental determination of the effects of submergence for different periods of time. Again we see complementarity between Den Boer's experiments and those of Paris. In the latter, prolonged, heavy rain led to waterlogging of the animals and ultimately to death since there were no trees on which to escape. According to Paris the effect is density-dependent since, although there are some places where the animals can and do obtain protection from drowning, these are too few to protect a large population.

What indications of terrestrial adaptation, if any, emerge from Den Boer's and Paris' work? In the former the answer is clear: a terrestrial animal that is largely cryptozoic on account of the need to conserve water is sometimes subject to a superabundance of this material and must possess behavioral mechanisms that permit elimination as well as retention of water according to the needs of the moment. Paris believes that isopods became terrestrial originally in response to the availability of a particular trophic niche — dead vegetation — and that their subsequent success results in part from an ability to utilize a wide variety of food materials. His results also underline the necessity for such animals to possess behavioral mechanisms which are tied in very closely with water requirements.

CONCLUSIONS

Kuenen and Nooteboom (1963) probably express a generally held opinion when they comment that "Land isopods are not very well adapted to land life." Yet the plain fact is that they are among the most common of terrestrial invertebrates. They are found from the littoral zone to great heights, from the perpetually humid forest leaf litter to habitats that are described as deserts and in which such plants as saguaro and barrel cacti flourish. In France alone Vandel (1960) recognizes 166 species in 54 genera and 13 families, and in the family Porcellionidae with a world-wide distribution, some 500-600 species have been described. They are, in fact, successful as land animals, and our knowledge of their physiology, behavior, and population dynamics is beginning to let us see why.

There are many important gaps in this knowledge, and in conclusion I shall refer to some of these. Limitation of water loss resulting from transpiration is one of the most important traits of a good terrestrial animal, and we do know that land isopods vary in this respect, but there is still uncertainty as to the means whereby such waterproofing is achieved. The effect of the various kinds of pseudotracheal apparatus on oxygen uptake and water loss through the respiratory membranes is also unclear. In both these fields further comparative study would be fruitful.

Very little indeed is known about the physiology of nitrogen excretion in land isopods, despite Sloan's intriguing discovery that *A. vulgare* and *P. scaber* excrete gaseous ammonia (*cf.* Hartenstein in this symposium).

The osmoregulatory capabilities of land isopods seem to be very limited. What evidence there is suggests that apart from *Ligia* in water they are passive in this respect, and that evaporation of water leads to a proportionate increase in hemolymph concentration. However, the effect of dehydration on hemolymph volume has not been measured, so that we cannot yet say how this compartment of body water is affected by overhydration or underhydration.

In addition to physiological adaptations, behavioral mechanisms are of the greatest significance, and some important recent advances have been made in this field. Behavioral responses to climatic and other physical variables are proving to be much more labile than was originally thought, and sorting out the contributions of each to the final behavioral response is becoming increasingly difficult. Animals in nature are subjected to a multiplicity of physical and physiological variables, and their behavior at any one time is the result of a complex interplay of all these factors. Attempts to analyze such behavior in the laboratory by varying one parameter at a time are of course desirable, but laboratory conditions, the insides of glass containers in particular, are far from natural, so that the animals are often not answering the question which we think we have put to them. The issue may also be confused by illogical inferences. If 60% of a population of *Oniscus asellus* moves to the warm end of a temperature gradient, and 40% settles for the other, are we justified in concluding that *Oniscus* shows a slight preference for the higher temperature? If, as it seems, 60% show a complete preference for one temperature and 40% show a complete preference for the other, then surely the question as to how these two kinds of individuals differ is the important one.

Despite some formidable difficulties, behavior in nature, in relation to actual micro-climatic conditions, is likely to be one of the most rewarding fields for study. Den Boer's work on *P. scaber* is a case in point, and we need a lot more information of this kind if only to assess the extent to which land isopods face the problem of too much water as well as too little.

Finally, apart from Paris' work we know very little about the factors that control population numbers and limit distributions of species in nature, and this is a serious gap in our understanding of the successes and limitations of isopods as land animals. It is certainly not sufficient to say that population size and distribution are limited by (for example) humidity. If four individuals of *Venezillo arizonicus* can live under one of Warburg's stones, why do not a hundred so live? Is food a limiting factor here? In other situations is living space a factor? These are questions which can be tackled effectively only by close combination of physiological and ecological methods. They are difficult questions, but their investigation is, in my view, not only desirable but essential if we want to gain a fuller understanding of terrestrial adaptation in land isopods.

REFERENCES

Auzou, M. L. 1953. Recherches biologiques et physiologiques sur deux isopodes onisciens: *Porcellio scaber* Lat. et *Oniscus asellus* L. Ann. Sci. Nat. (Zool.) Paris 15:71-98.

Beament, J. W. L. 1958. The effect of temperature on the waterproofing mechanism of an insect. J. Exptl. Biol. 35:494-519.

Beament, J. W. L. 1959. The waterproofing mechanism of arthropods. I. The effect of temperature on cuticle permeability in terrestrial insects and ticks. J. Exptl. Biol. 36:391-422.

Beament, J. W. L. 1961. The water relations of the insect cuticle. Biol. Rev. 36:281-320.

Brereton, J. le G. 1957. The distribution of woodland isopods. *Oikos* 8:85-106.

Bursell, E. 1955. The transpiration of terrestrial isopods. J. Exptl. Biol. 32:238-255.

Bursell, E. 1958. The water balance of tsetse pupae. Phil. Trans. Roy. Soc. London 241:179-210.

Cloudsley-Thompson, J. L. 1952. Studies in diurnal rhythms. II. Changes in the physiological responses of the woodlouse *Oniscus asellus* to environmental stimuli. J. Exptl. Biol. 29:295-303.

Cloudsley-Thompson, J. L. 1956*a*. Studies in diurnal rhythms. VII. Humidity responses and nocturnal activity in woodlice (Isopoda). J. Exptl. Biol. 33:576-582.

Cloudsley-Thompson, J. L. 1956*b*. Studies in diurnal rhythms. VI. Bioclimatic observations in Tunisia and their significance in relation to the physiology of the fauna, especially woodlice, centipedes, scorpions and beetles. Ann. Mag. Nat. Hist. 9:305-329.

Den Boer, P. J. 1961. The ecological significance of activity patterns in the woodlouse, *Porcellio scaber* Latr. (Isopoda). Arch. Neerland. Zool. 14:283-409.

Dresel, I. B., and V. Moyle. 1950. Nitrogenous excretion of amphipods and isopods. J. Exptl. Biol. 27:210-225.

Edney, E. B. 1951. The evaporation of water from woodlice and the millipede *Glomeris*. J. Exptl. Biol. 28:91-115.

Edney, E. B. 1953. The temperature of woodlice in the sun. J. Exptl. Biol. 30:331-349.

Edney, E. B. 1954. Woodlice and the land habitat. Biol. Rev. 29:185-219.

Edney, E. B. 1958. The microclimate in which woodlice live. Proc. Xth Intern. Congr. Entomol. 2:709-712.

Edney, E. B. 1960. Terrestrial adaptations, p. 367-393. *In* T. H. Waterman, [ed.], The physiology of Crustacea. Academic Press, New York.

Edney, E. B. 1964. Acclimation to temperature in land isopods. I. Lethal temperatures. II. Heart rate and standard metabolic rate. Physiol. Zool. 37:364-394.

Edney, E. B. 1968. The effect of water loss on the haemolymph of *Arenivaga* sp. and *Periplaneta americana*. Comp. Biochem. Physiol. 25:149-158.

Edney, E. B., and J. Spencer. 1955. Cutaneous respiration in woodlice. J. Exptl. Biol. 32:256-269.

Edwards, G. A., and W. L. Nutting. 1950. The influence of temperature upon respiration and heart activity of *Thermobia* and *Grylloblatta*. Psyche (Cambridge, Mass.) 57:33-44.

Friedlander, C. P. 1963. Thigmokinesis in woodlice. Animal Behavior 12:164-174.

Friedlander, C. P. 1965. Aggregation in *Oniscus asellus* Linn. Animal Behavior 13:342-346.

Gorvett, H. 1956. Tegumental glands and terrestrial life in woodlice. Proc. Zool. Soc. London 126:291-314.

Gunn, D. L. 1937. The humidity reactions of the woodlouse, *Porcellio scaber*. J. Exptl. Biol. 14:178-186.

Hubbell, S. P., A. Sikora, and O. H. Paris. 1965. Radiotracer, gravimetric and calorimetric studies of ingestion and assimilation rates of an isopod. Health Physics 11:1485-1501.

Jans, D., and K. F. A. Ross. 1963. A histological study of the peripheral receptors in the thorax of land isopods, with special reference to the location of possible hygroreceptors. Quart. J. Microscop. Sci. 104:337-350.

Kuenen, D. J. 1959. Excretion and water balance in some land isopods. Entomol. Exptl. Appl. 2:287-294.

Kuenen, D. J., and H. P. Nooteboom. 1963. Olfactory orientation in some land isopods (Oniscoidea, Crustacea). Entomol. Exptl. Appl. 6:133-142.

Lees, A. D. 1947. Transpiration and the structure of the epicuticle in ticks. J. Exptl. Biol. 23:379-410.

Mead-Briggs, A. R. 1956. The effect of temperature upon the permeability to water of arthropod cuticles. J. Exptl. Biol. 33:737-749.

Miller, M. A. 1938. Comparative ecological studies on the terrestrial isopod crustacea of the San Francisco Bay region. Univ. Calif. Publ. Zool. 43:113-141.

Paris, O. H. 1963. The ecology of *Armadillidium vulgare* (Isopoda: Oniscoidea) in California grassland: food, enemies and weather. Ecol. Monogr. 33:1-22.

Paris, O. H. 1965. Vagility of P^{32} labeled isopods in grassland. Ecology 46:635-648.

Paris, O. H., and F. A. Pitelka. 1962. Population characteristics of the terrestrial isopod *Armadillidum vulgare* in California grassland. Ecology 43:229-248.

Paris, O. H., and A. Sikora. 1965. Radiotracer demonstration of isopod herbivory. Ecology 46:729-734.

Parry, G. 1953. Osmotic and ionic regulation in the isopod crustacean *Ligia oceanica*. J. Exptl. Biol. 30:567-574.

Phillips, J. E. 1964. Rectal absorption in the desert locust *Schistocerca gregaria* Forskal. I. Water. II. Sodium, potassium and chloride. III. The nature of the excretory process. J. Exptl. Biol. 41:15-80.

Scholander, P. F., W. Flagg, V. Walters, and L. Irving. 1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26:67-92.

Spencer, J. O., and E. B. Edney. 1954. The absorption of water by woodlice. J. Exptl. Biol. 31:491-496.

Straelen, W. Van. 1928. Contributions à l'étude des isopodes méso- et cénozoiques. Mém. Acad. Roy. Belg. Clin. Sci. 9 (5):1-68.

Todd, M. E. 1963. Osmoregulation in *Ligia oceanica* and *Idotea granulosa*. J. Exptl. Biol. 40:381-392.

Vandel, A. 1943. Essai sur l'origine, l'évolution et la classification des Oniscoidea (Isopodes terrestres). Bull. Biol. France Belge. Suppl. 30:1-143.

Vandel, A. 1960. Isopodes terrestres. Faune de France 64:1-416.

Vandel, A. 1965. Sur l'existence d'oniscoides très primitifs menant une vie aquatique et sur le polyphylétisme des isopodes terrestres. Ann. Spéléologie 20:489-518.

Verhoeff, K. W. 1920. Über die Atmung der Landasseln. 21. Isopoden Aufsatz. Z. Wiss. Zool. 68:365-447.

Warburg, M. R. 1964. The response of isopods towards temperature, humidity and light. Animal Behavior 21:175-186.

Warburg, M. R. 1965*a*. The evaporative water loss of three isopods from semi-arid habitats in South Australia. Crustaceana 9:302-308.

Warburg, M. R. 1965*b*. Water relations and internal body temperature of isopods from mesic and xeric habitats. Physiol. Zool. 38:99-109.

Warburg, M. R. 1965c. The microclimate in the habitats of two isopod species in southern Arizona. Am. Midland Naturalist 73:363-375.

Wieser, W. 1962. Parameter des Sauerstoffverbrauches. I. Der Sauerstoffverbrauch einiger Landisopoden. Z. Vergl. Physiol. 45:247-271.

Wieser, W. 1963*a*. Parameter des Sauerstoffverbrauches. II. Die Wirkung von Temperatur, Licht und anderen Haltungsbedingungen auf den Sauerstoffverbrauch von *Porcellio scaber* Latr. (Isopoda). Z. Vergl. Physiol. 47:1-16.

Wieser, W. 1963*b*. Die Bedeutung der Tageslänge für das Einsetzen der Fortpflanzungsperiode bei *Porcellio scaber* Latr. (Isopoda). Z. Naturforsch. 18:1090-1092.

Wieser, W. 1965. Electrophoretic studies on blood proteins in an ecological series of isopod and amphipod species. J. Mar. Biol. Assoc. U. K. 45:507-523.

Wigglesworth, V. B. 1945. Transpiration through the cuticle of insects. J. Exptl. Biol. 21:97-114.