STUDIES ON THE ONYCHOPHORA

III. THE CONTROL OF WATER LOSS IN *PERIPATOPSIS*

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ALL terrestrial animals have to solve the problem of resistance to desiccation, and adaptations associated with this difficulty are of two main types: (1) the development of waterproof external surfaces, and (2) the reduction of the amount of water lost by excretion. In some animals there is also an increase in the formation of metabolic water. In a previous paper it has been shown that the second method has been employed by the Onychophora (Manton & Heatley, 1937). A uricotelic metabolism has been acquired, and nitrogenous excretion by the intestine has reduced the water passing out by the segmental excretory organs to a minimum. The presence of large fat stores in the body may indicate that a fatty metabolism is also increasing the production of metabolic water.

The methods of formation of waterproof coverings in animals are various. The Onychophora resemble the other terrestrial Arthropoda in possessing a dry integument. It is formed of chitin covered by a very thin cuticle, the whole being not more than 1 μ thick. The cuticle is raised into primary papillae bearing sensory spines and numerous secondary papillae or scales; these appear to prevent the cuticle from being wetted by water. The cuticle of the oral region is smooth and can be made wet.

Although the Onychophora have developed a dry skin and a uricotelic metabolism, they are still unable to control their water loss sufficiently to enable them to live in environments which are not permanently damp. As shown in Text-fig. 9 in the second paper of this series (Manton & Heatley, 1937) the loss of water by *Peripatopsis* in room atmosphere is rapid, 33 per cent of its weight being lost in 3½ hours. This loss can be regained only through the mouth. The dry skin, unlike the wet skin of the newt, cannot absorb water, and no uptake of water occurs in a saturated atmosphere unless the animal is allowed to suck wet material.

The present investigation was undertaken to ascertain why *Peripatopsis* has so little control of its water loss in comparison with other terrestrial animals better able to withstand desiccation. Experiments, under standard conditions, were carried out to determine the rate of evaporation of an earthworm with a wet skin and several Arthropods, including *Peripatopsis*, in which the integument is dry.

Two forms of apparatus were used: (*a*) a wind tunnel through which conditioned air was passed at 7·0 m./sec. (Ramsay, 1935), and (*b*) a simpler apparatus: the animals whose rates of evaporation were to be compared were placed separately in parallel flues of 1 × 1 in. cross-section through which a current of dry air was passed at 0·25 m./sec. The flues were mounted in a thermostatically controlled bath.

In both cases the temperature was 30 ± 0·1° C. In the apparatus (*a*) the relative humidity was 27·5 ± 1 per cent, and the results obtained with dry air in apparatus (*b*) were referred to 27·5 per cent R.H. on the assumption that at constant temperature the rate of evaporation is proportional to the humidity. This is not strictly true, but the error introduced almost certainly does not exceed 10 per cent. As will be seen from the results, such an error is inconsiderable in comparison with the differences in evaporation rates of the animals studied.

Standard conditions of 30° C. *and* 27·5 % *relative humidity*

0·25 m./sec. wind velocity			7·0 m./sec. wind velocity		
Animal	Original weight in gm.	% of original weight lost in 30 min.	Animal	Original weight in gm.	% of original weight lost in 30 min.
Blatta orientalis	0·768	0·24	*Periplaneta americana*	0·981	0·54
Amphipyra pyramidea (caterpillar)	0·292	0·42	Earthworm	1·692	18·00
			Peripatopsis Sedgwicki	0·303	39·00

The caterpillar and *Peripatopsis* were of about the same size, and the caterpillar was smooth skinned. *Peripatopsis* is seen to evaporate more than twice as fast as the earthworm, and eighty times as fast as the cockroach. It is probable that a wind velocity of 7 m./sec. would not do more than double the rate of evaporation of the caterpillar, so that *Peripatopsis* must evaporate at least forty times as fast as the caterpillar.

It has been shown that practically all the water evaporated from insects is lost from the tracheal system, and only at high temperatures does the body wall of the cockroach, for example, become permeable to water. The control of water loss from the tracheae of insects is maintained by efficient mechanisms for closing the spiracles (Mellanby, 1935).

The integument of *Peripatopsis* is much thinner and may be less waterproof than that of the caterpillar used in the above experiments where it is about 4–5μ thick. However, the chitin in *Peripatopsis*, as in insects, is covered by a thin cuticle, and even in insects possessing very thin cuticles, such as the larvae of the flea and clothes moth, the integument is nearly watertight. Thus it is probable that the integument of *Peripatopsis* is not freely permeable to water.

The tracheae of *Peripatopsis* are about 2μ wide and do not branch, and their external openings are much more numerous than they are in insects, arachnids and myriapods, where the number of spiracles is few. In the Onychophora groups of tracheae extend from the base of small pits about 80μ deep and 14μ wide. These pits may be separated by a distance of only 80μ, and hence their number in one animal is enormous. They penetrate through the subcutaneous connective tissue to reach the outer layer of muscles, but no contractile structures supply the walls of these pits which cannot be closed. Thus it is probable that the relative inefficiency of the Onychophora in controlling water loss is due to the enormous number of spiracles which lack a closing device, rather than to the presence of a thin integument. This conclusion is supported by the comparison with the earthworm, which loses water less rapidly than *Peripatopsis* in spite of its wet skin. In experiments such as the above, rapid loss of water results in a drying up of the wet surface, and this in turn appears to cause a greater resistance to the passage of water through the outer layer of the animal, so that the rate of evaporation falls off as the experiment proceeds. But in *Peripatopsis* the surface through which the water passes must be the whole lining of the tracheal system, and, owing to its relative enormous area, the rate at which water passes through unit area will be much less than the rate at which it passes through unit area of the earthworm's surface under the same conditions. Drying of the surface and increased resistance will therefore be less marked.

Thus, although the Onychophora have developed many features associated with their terrestrial habitat, such as a dry skin through which water is not readily lost, a uricotelic metabolism, a suitable method of reproduction, and adequate feeding and defensive mechanisms, in common with other successful land animals, the type of tracheal system evolved by the Onychophora has made water control impossible. The group is thereby restricted to permanently damp environments and prevented from becoming eminently successful and widespread. There may be genetical and other factors responsible for the absence of adaptive radiation in the Onychophora, but the type of tracheal system alone might have been a sufficient impediment.

SUMMARY

1. Under standard conditions *Peripatopsis* loses water twice as rapidly as an earthworm, forty times as rapidly as a smooth-skinned caterpillar, and eighty times as rapidly as a cockroach.

2. Water loss almost certainly takes place through the tracheae.

3. Lack of control of water loss is due to the large numbers of spiracles which have no closing mechanism.

4. Although the Onychophora have many efficient adaptations for a terrestrial habit, the type of tracheal system alone may have been responsible for the group not becoming widespread and successful.

REFERENCES

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