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# PREFACE

> 'If anybody shall reprove me and shall make it apparent unto me that I do err, I will most gladly retract. For it is the truth that I seeke after, by which I am sure that never man was hurt and as sure that he is hurt that continueth in any error or ignorance whatsoever.'
>
> MARCUS AURELIUS

THIS book was conceived largely at the sink, where most modern husbands have to spend so much of their leisure. My deepest thanks are therefore due to my dear wife who shouldered far more than her share of the domestic drudgery in order that I might slip away to jot down my ideas. I would also like to express my gratitude to my friends and colleagues at home and abroad who have so generously sent me reprints of their publications. In many cases I have not been able to quote these in the bibliographies for reasons of space, but my debt to the work of others in attempting to cover a very wide field in a single volume must be abundantly clear to the reader.

J. L. C–T.
*April* 1957

## ACKNOWLEDGMENTS

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# INTRODUCTION

> 'The evaporating power of the air may be the primary factor upon which the organisation of the entire terrestrial fauna depends.'
>
> R. HESSE, W. C. ALLEE and K. P. SCHMIDT

THE Arthropoda is the dominant phylum of the Invertebrates. In the oceans, minute crustaceans comprise the major component of the zooplankton upon which the food chains of the whales and larger fishes are based: on land the medical, economic and biological importance of insects and mites especially, can scarcely be over-stressed. These may be very cogent reasons for their investigation, but they are not the most important. The little creatures are interesting in their own right, and research into the details of their lives provides mental exercise that is a source of unending pleasure and interest.

Questions are sometimes asked as to the use of academic research. The answer may be that it lies in man's nature to explore the secrets of the universe, for comparatively few intellectual and aesthetic pursuits are motivated by purely practical considerations. Scott did not go to the South Pole in search of coal, nor did Beethoven write his string quartets for economic reasons. The best excuse for climbing Mount Everest may have been to get to the top, or simply because it was there. Perhaps the last word on the subject was written by J. S. Bach. 'The aim and final reason of all music is the glory of God and the recreation of the mind.' And so for all the arts and sciences!

Many excellent books have recently been written about insects and of all the terrestrial Arthropoda they are the most catholic. Over 600,000 species are known to science and the total number in existence probably exceeds a million. There are more species of beetles in the world than of all other animals put together. One of these, *Niptus hololeucus* can live on cayenne pepper and thrive on sal ammoniac. This species has been known to live in the corks of entomologists' cyanide killing-bottles and no less than 1,547 specimens were taken from a jar of casein that had been stoppered for twelve years. The fly *Psilopa petrolei* inhabits puddles of crude petroleum; and both flies and beetles abound in certain hot springs in the western United States where the temperature approaches 50° C. The largest insects include the African Goliath beetle, *Goliathus regius* which measures four inches in length and two in breadth, and the Venezuelan *Dynastes hercules*, reaching a length of 6¼ inches, while the magnificent butterfly *Ornithoptera victoriae* of the Solomon Islands has a wing-span exceeding one foot. In contrast some of the parasitic Hymenoptera are considerably less than one hundredth of an inch in length, despite the complexity of their structure.

The diversity and versatility of the insects is nowhere equalled in the animal kingdom, but in this volume I hope to show that the other terrestrial Arthropoda, although somewhat neglected, will well repay further acquaintance.

For many years, the majority of zoologists who have worked on the Arthropoda have tended to concentrate their efforts either on the marine Crustacea or on the insects. Apart from systematists, comparatively few have paid more than superficial attention to the remaining members of the phylum and although increasing numbers are now doing so, there is ample scope for new recruits as the reader will soon realise.

It is now generally recognised that the Collembola are not insects and the same may be true of other Apterygota. Nevertheless, these animals have always come within the scope of the entomologist and receive attention in many well-known entomological textbooks. I have not, therefore, included them in this book even though the Pauropoda and Symphyla have been noticed. Indeed, it is now believed that the latter are closely related to the Insecta. Consequently the selection of groups discussed in the following chapters may appear somewhat arbitrary from a systematic point of view: but it will, I hope, be found to have practical justification.

Life on land entails a number of problems for animals. Larger forms require structural support, respiratory organs must become modified for air breathing and there is no longer the surrounding water into which toxic excretory products can freely diffuse, while mechanisms for the conservation of water and the maintenance of a constant internal medium must be evolved. That these problems are by no means easily overcome is shown by the fact that several invertebrate phyla are almost entirely marine while others as yet possess few terrestrial species. Indeed, the Arthropoda have been unusually successful in exploiting the terrestrial habitat and by adaptive radiation have succeeded in establishing themselves in nearly all the habitable corners of the earth. Each aspect of their adaptation to life on land affects and is affected by other aspects. For example, it might appear a fairly simple matter for an organism to eliminate water-loss by the evolution of an integument completely impervious to water-vapour; but such an integument would also be impervious to oxygen and carbon dioxide. A respiratory mechanism has therefore had to be evolved which permits gaseous exchange without excessive water-loss. If the integument is rigid and provides support, then growth becomes impossible except by moulting and this limits size. The physiology of nutrition and excretion too are closely concerned with water conservation and superimposed upon this basic physiological requirement are the innumerable concomitants of behaviour and ecology.

There are two obvious ways in which small animals can escape desiccation on dry land. One is to avoid dry places and to remain most, if not all of the time, in a humid environment; the other, to evolve an impervious integument. Both methods have been exploited by the Arthropoda and each has its drawbacks and advantages. Indeed, on the basis of this character the terrestrial members of the phylum can be divided roughly into two main ecological groups: the first includes woodlice, centipedes, millipedes and their allies which lose water rapidly in dry air; the second, the Arachnids and insects which are covered with a layer of wax that renders them comparatively independent of moist surroundings.

In the following chapters the significance of this generalisation will become apparent. Forms lacking an epicuticular wax-layer are almost entirely nocturnal in habit, and can wander abroad only after nightfall when the temperature drops and the relative humidity of the air rises. In contrast, most insects, spiders and most other Arachnida are potentially diurnal except perhaps in deserts and other regions with rigorous climates where, anyway, the majority of the inhabitants avoid the excessive mid-day heat and drought by their nocturnal behaviour. (Conversely, arctic animals are nearly always diurnal in habit.) The more primitive groups such as scorpions, whip-scorpions, spiders of the families Liphistiidae, Theraphosidae, Dictynidae, Dysderidae and so on, have probably become secondarily adapted to nocturnal habits as a result of competition with more efficient species. At the same time, however, many of them are large and somewhat vulnerable and may need to escape the attentions of potential predators in this way.

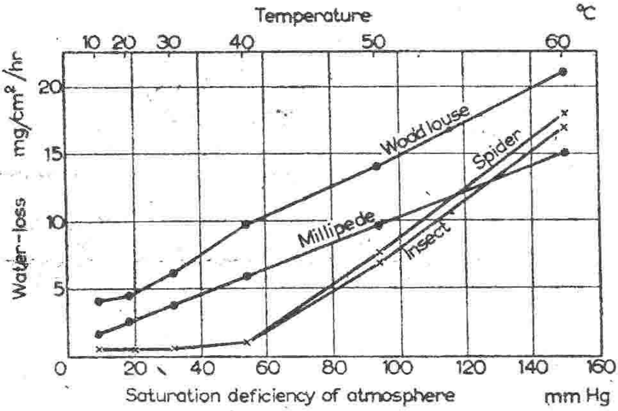


FIG. 1. Rate of water-loss in dry air at different temperatures, and corresponding saturation deficiencies, from a woodlouse (*Porcellio*), millipede (*Oxidus*), spider (*Lycosa*) and insect (*Pieris* larva). In the woodlouse and millipede the rate of water-loss is proportional to the saturation deficiency of the atmosphere, but in the spider and insect it is negligible below about 30° C, the critical temperature at which their epicuticular wax-layers become porous. Rate of water-loss is expressed in milligrams per square centimetre of surface area per hour. (After Cloudsley-Thompson, 1955.)

On the other hand, liquid water can also be very dangerous to small animals that may become water-logged, or trapped by surface tension. Their environment must be neither too wet nor too dry. This is especially true of species lacking a waterproofing wax-layer. Because they are susceptible to desiccation, they are also susceptible to water uptake by osmosis: consequently they tend to inhabit thick leaf-litter, or burrow deep into the soil where they are less liable either to become water-logged or desiccated.

Rigid, mechanistic behaviour patterns in response to environmental stimuli have been evolved by means of which the animals find and maintain themselves in suitable habitats. Physiological and morphological adaptations alone would obviously be insufficient to support the life of any free-living animal. Orientation and behaviour mechanisms must also be evolved to retain organisms in environments to which they are suited, to enable them to find food, mate, and indeed to carry out the innumerable functions essential for their continued existence.

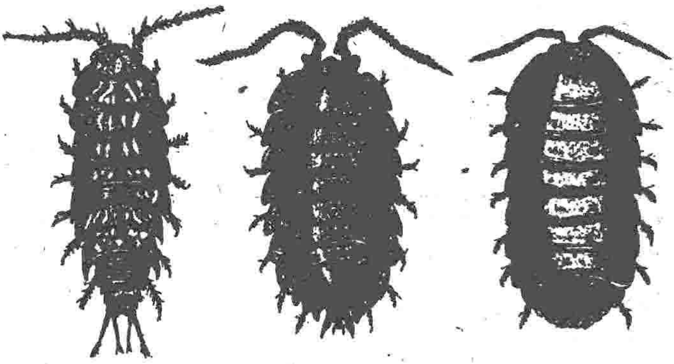

FIG. 2. Woodlice. *Trichoniscus pusillus* (length 4 mm), *Porcellio scaber* (length 14 mm) and *Armadillidium vulgare* (length 15 mm). (After Webb and Sillem, 1906.)

The ecology of animals is therefore governed not only by the factors of their environments, physical and biological, but also by their own physiological requirements and behaviour. The interrelationships between living organisms and their environments include both inter-specific and intra-specific factors. These relationships are specific for every organism and continuous throughout its life: they are reciprocal in that the organism is not merely influenced by, but at the same time positively affects its environment, and are indissoluble because the organism cannot exist independently of its environment. Consequently ecology is a vast and complex subject about which comparatively little is yet known. One advantage of this lies in the fact that it is still possible, as

Charles Elton pointed out in 1927, for almost anyone doing ecological work on the right lines, to strike upon some new and exciting fact or idea.

Ecology has been described as scientific natural history and accurate identification must be made of any animals studied. One of the objects of this book is to indicate some of the innumerable problems awaiting elucidation and to provide a guide to sources for the identification of the British species in particular, as well as to other relevant literature.† It is hoped that it will interest natural history workers in this country and abroad: it may also be of use to upper school biology teachers. At the same time, however, I believe that many university students may find in it information, although simply portrayed, that will be of value to them both in the joys of the field and the gloom of the examination hall.

† Inevitably this is somewhat arbitrary and no doubt, reflects a bias towards the works with which I am more familiar. Both modern and old publications have been quoted, especially where the latter have useful illustrations.

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CHAPTER I

# WOODLICE

## Classification and distribution

Woodlice are included in the sub-order Oniscoidea of the crustacean order Isopoda. They form a reasonably homogeneous group and are of particular interest because there are several common species showing different degrees of adaptation to life on land. The majority are between one and two centimetres in length, and the small size of certain genera such as *Platyarthrus*, *Trichoniscus* and *Sphaerobathytropa* is almost certainly a secondary feature correlated with various regressive characters such as a simplification in the structure of the eyes and appendices, reduction in the number of body segments and loss of pigmentation. An analogous phenomenon is found in the Acari.

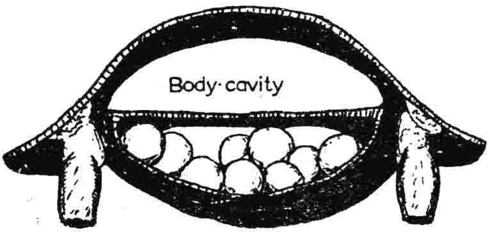


FIG. 3. Fifth thoracic segment of a female *Oniscus asellus* cut across to show the brood pouch with eggs. (After Webb and Sillem, 1906.)

The Oniscoidea are somewhat oval in form and their bodies are arched, the curve varying in different genera and species. The head bears two large antennae and a smaller pair of antennules anterior to them. The thorax consists of seven segments which are often considerably broader than the six succeeding ones that form the abdomen. Each of the thoracic segments carries a pair of walking legs and in the female, at the time when the eggs are laid, a pair of plates arises on segments two to five. These plates together form a brood pouch in which the eggs are carried until they hatch and in which the young remain for some time afterwards. The appendages of the abdomen are also plate-like, with the exception of the last pair or uropods. The endopodites or pleopods are homologous with the gills of aquatic Isopods and have a respiratory function, while the outer exopodites act as a protective cover. In the male the first two pairs of abdominal appendages are specially modified, their endopodites being long and pointed, while the uropods are often considerably larger than in the female and their shape is sometimes of value in classification.

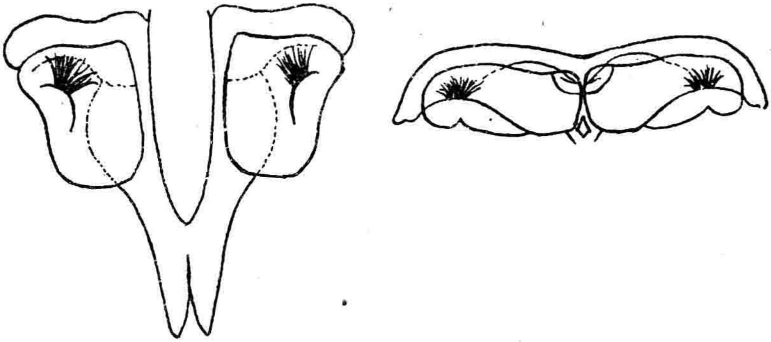

FIG. 4. Pleopods of first thoracic segment of *Porcellio scaber* showing pseudotracheae. Male on the left, female on the right. (Diagrammatic.)

In a comprehensive survey of the Oniscoidea, Vandel (1943) recognises some 18 families, of which five are included in the British fauna. These are the Ligiidae, Trichoniscidae, Oniscidae, Porcellionidae and Armadillidiidae. The geological history of the Crustacea is a long one and fossils occur in the Old Red Sandstone of the Devonian period and in the Carboniferous Coal Measures. Fossil woodlice, however, have not been found below the Upper Eocene which might suggest that colonisation of the land has been achieved somewhat late in the history of the group. When they do appear, however, they are generically indistinct from living forms, and Vandel believes that the ancestors of woodlice became terrestrial during the second half of the Palaeozoic era. He bases this conclusion on the fact that all the main types of organisation within the Oniscoidea have a world-wide distribution and consequently must have a very ancient origin.

The most primitive and at the same time the least well adapted of the woodlice to terrestrial conditions are littoral species belonging to the family Ligiidae. There are two British species in this family, *Ligia oceanica*, the largest of the British woodlice—up to 30 mm in length and rather more than twice as long as broad—and the smaller *Ligidium hypnorum* which is sometimes found far inland, nearly always in the neighbourhood of water.

*Ligia oceanica* has a wide distribution around the shores of Great Britain and indeed of practically the whole north coast of Europe. It also occurs in France, Spain, Morocco and America. Although never found far from the sea, it is truly terrestrial and can withstand prolonged submersion in sea water only if this is well aerated. The normal habitat is in deep narrow crevices in the rocks just above high-tide level, under stones on sandy beaches or on the sides of quays: hence the name 'quay-louse' or 'quay-lowder'. In St. Kilda *Ligia* has been found in the crevices of boulders over 450 ft. above sea level, but on that exposed islet spray is often blown to this height (Nicholls, 1931). I have found specimens over a mile inland on the Isle of Man.

The family Trichoniscidae also occurs in very moist places, but the Porcellionidae and Armadillidiidae are found in progressively drier localities. Now this sequence is also one of increasing morphological specialisation within the group, the significance of which will be considered below.

Hatchett (1947) has found that in Michigan *Armadillidium nasatum* does not occur outside buildings, while *A. vulgare* is chiefly found around human habitations; *Cylisticus convexus* prefers rocky regions and *Ligidium longicaudatum* occurs only in very wet situations. *Metoponorthus pruinosus* is somewhat urban in its distribution. *Porcellio scaber* lives on beaches, river banks and other moist situations. *P. spinicornis* requires a habitat where plenty of lime is available and *P. rathkei* is generally distributed but more abundant in deciduous woodlands than elsewhere, while *P. demivirgo* definitely prefers moist woodland situations.

With regard to the British species, Heeley (1941) notes that *Trichoniscus pusillus* is abundant in very moist woodlands, though the animals are frequently overlooked owing to their small size and dark colouring. They can easily be mistaken for young *Philoscia*. They favour the thick sodden layers of decaying leaves which lie beneath the trees throughout the winter and during the summer they live amongst the resulting leaf mould beneath low bushes well shaded from the sun, or within rotting twigs.

*Philoscia muscorum* is fairly common in moist shady situations in moors and woodlands, particularly amongst the roots of grasses beneath bushes and brambles and at the base of tree trunks, where the soil receives the drippings from the trees and is shaded from the sun. This species is somewhat local and restricted in its distribution and is present mainly in woodland. *Oniscus asellus* on the other hand is the commonest of all woodlice and is found almost everywhere that damp conditions prevail, particularly beneath half buried stones and bark. It seems to prefer rather more moist situations than *Porcellio scaber* and may often be found with the latter in the same tree, but usually nearer the ground where the wood is old and rotting.

*Porcellio scaber* is also very common, particularly beneath the dry loose bark of vertical trunks of living trees. It sometimes inhabits damp houses and has been found in heaps of clinker and the nests of wood ants, *Formica rufa*.

Finally, *Armadillidium vulgare* is particularly common on chalk lands, on heaths and slopes covered with low scrub such as are found in railway cuttings and on roadsides. The species also occurs in the neighbourhood of houses and builders' yards where there is loose cement or lime, but is never very numerous in woodland. It can even survive under dry stones warmed by the sun.

Now Heeley claims that it is possible to predict which species of woodlouse will be present in a given habitat by its water-content. In his experiments, however, he provided a moist surface for the animals in the form of a carrot as food. It has since been shown that woodlice of the same species, if desiccated and subsequently kept in unsaturated air, but with access to moist plaster of Paris surfaces, regain their weight by absorption of water through the mouth. These experiments explain how woodlice which are known to lose water in all but saturated air, can nevertheless survive indefinitely in unsaturated air provided that a moist surface is available (Edney, 1954).

## General behaviour

In different parts of the country there are many curious superstitions about woodlice. For example, in some places their presence indoors is regarded as unlucky and any food on which they may happen to wander is considered poisoned. On the other hand, in certain other districts until very recently a few live woodlice thrust down the throat of a cow were believed to have beneficial effects and 'to promote the restoration of the cud'. No doubt this is why in Shropshire and neighbouring counties woodlice or slaters are sometimes referred to as 'cud-worms'. At one time too, woodlice were prescribed to be swallowed alive as a remedy for scrofulous symptoms and for diseases of the liver and digestive organs. It is surprising too how many local names have been given to woodlice: Collinge (1935) listed no less than 65 ranging from 'Bibble bugs' (Stafford), 'Cheese-pigs' (Berkshire) and 'Coffin-cutters' (Ireland) to 'Monkey peas' (Kent), 'Penny-pigs' (Wales), 'Sink-lice' (Lancashire and Stafford) and 'Tiggy-hogs' (Northamptonshire). In America they are known as 'Sow-bugs'.

Humidity is an environmental factor of prime importance, both to woodlice and to myriapods, as they all lack a waterproof integument. Woodlice are very sensitive to humidity gradients and aggregate in areas of high humidity. The mechanism by which this occurs is two-fold: firstly, the animals show a decrease in activity and speed in moist air and secondly they change direction more frequently in damp places so that once they have arrived in a moist situation they tend to remain there. This reaction to the relative humidity of the air is also combined with avoidance of light and a reaction that causes them to make contact with as much of their surroundings as possible. The result of this is that not only do the animals enter narrow crevices, but they bunch together and consequently protect each other from evaporation.

However, a reversal of the response to light occurs when woodlice become somewhat desiccated, so that if their daytime habitat should dry up they are not restrained there until they die, but become attracted to light and are then able to wander in the open until they find some other damp dark hiding place where they again become photo-negative (Cloudsley-Thompson, 1952).

The clearest adaptation to terrestrial life is to be found in the pleopods. These are variously modified and in the more advanced forms bear tufts of invaginated tubules forming 'lung-trees' or 'pseudotracheae'. Each tree opens to the exterior by a slit-like aperture near the edge of the pleopod, and the minute ramifying tracheae are thin-walled tubes surrounded by blood which carries oxygen to the tissues of the body. When the air is dry, the pleopods are probably kept moist by water that diffuses from the body fluids of the animal.

Like most other woodlice, *Ligia oceanica* is nocturnal in habit and emerges during the night at low tide to feed on seaweeds such as *Fucus* and other algae. The species is strongly photo-negative and tends to remain under cover on moonlight nights. Edney (1954) has recently pointed out that *Ligia* can live on land as a result of wide osmotic tolerance rather than by developing osmotic independence. Since other species of woodlouse can lose much water by evaporation without dying, it seems likely that such osmotic independence is characteristic of the group as a whole. The colour of *Ligia* ranges from a dark greyish-green to a light, dirty brown, while young specimens have two light-coloured patches on the middle of the dorsal side. The British *Ligia oceanica*, as well as the American *L. baudiniana* and *L. exotica*, have been found to show well marked colour responses due to the expansion and contraction of colour pigment cells or chromatophores, so that they become light when placed on a white background and turn dark on a black background. In addition there is a diurnal rhythm of colour change and they tend to be dark by day and pale by night.

The family Trichoniscidae includes a number of small, elongated woodlice that are fairly widely distributed in damp places under moss, bark, fallen leaves, logs and so on. The Oniscidae are less dependent on moisture, but the common *Philoscia muscorum*