Michael R. Warburg

# Evolutionary Biology of Land Isopods

Springer-Verlag Berlin Heidelberg GmbH


ALLE · ZEIT · WACH
1842
SP

M.R. Warburg

# *Evolutionary Biology of Land Isopods*

With 96 Figures

Springer-Verlag Berlin Heidelberg GmbH

Prof. Dr. MICHAEL R. WARBURG
Technion, Department of Biology
Technion City
Haifa 32000, Israel

ISBN 978-3-662-21891-4

Library of Congress Cataloging-in-Publication Data. Warburg, Michael, 1931- Evolutionary biology of land isopods / Michael Warburg. p. cm. Includes bibliographical references and index.

ISBN 978-3-662-21891-4 ISBN 978-3-662-21889-1 (eBook)
DOI 10.1007/978-3-662-21889-1

1. Isopoda — Anatomy.
2. Isopoda — Ecology. I. Title. QL444.M34W37 1993 595.3'72—dc20 92-42564

Originally published by Springer-Verlag Berlin Heidelberg New York in 1993
Softcover reprint of the hardcover 1st edition 1993

31/3145/SPS-5 4 3 2 1 0 - Printed on acid-free paper

*In memory of my*
*late father*, Sigmund, *and uncle*, Edgar,
*who both influenced in different ways*
*my approach to nature*

**Fig. 1.** *Bathytropa wahrmani*, a rare isopod inhabiting leaf litter in forests of the Mediterranean region in Israel ( × 35)

# Preface

Already as a young boy, I used to walk with my late father, an ardent naturalist at heart, though to his regret not by profession, in the fields and woods on Mt. Carmel where we lived. My father, being largely an amateur ornithologist but also loving other vertebrates, was less interested in the little creatures (- the invertebrates) so abundant under stones. These were, more often then not, isopods which are particularly abundant in the Mediterranean region of northern Israel, and therefore not difficult to encounter (Fig. 1). Thus, my interest in the terrestrial isopods started at an early stage. Many years later, after graduating from the Hebrew University, Jerusalem, I worked as an assistant to my late friend and colleague, Professor Michael Costa, at the Teachers Seminary in Oranim. One day I found on my desk a copy of Edney's (1954) paper: *Woodlice and the land habitat*, which my friend left for me knowing of my interest in this group. Therefore, due to the stimulus of Edney's paper, and the many interesting questions it raised in my mind, I developed a lifelong interest in this amazing crustacean group. My research in the ecophysiology of this group followed to a large extent the directions formulated by Edney and Cloudsley-Thompson whose name will be mentioned throughout this book. I am also indebted to the many stimulating discussions with my friends and colleagues C.S. Crawford, K.E. Linsenmair, and E. Hornung and to the kind hospitality extended to me by M.A. Alikhan while writing parts of this book during my stay in his laboratory. This research interest continued to occupy me and proved to be most rewarding to me and to my students. I would like to express my gratitude to my students, technicians and collaborators for sharing the joys of isopod research. Foremost I would like to thank my assistant, Ms. Mira Rosenberg, for her great help over many years, especially for her expertise in EM and SEM techniques. Dr. Klara Bercovitz, Ms. Nili Cohen, and Ms. Dorit Weinstein contributed greatly to our understanding of the Mediterranean isopods while working on their M.Sc. theses. Likewise, Ms. Dina Rankevitch assisted in the study of the diversity in the Mediterranean ecosystem, and Ms. Shoshi Goldenberg was largely involved in the physiological studies. To all I wish to express my appreciation. Last, but not least, I would like to thank my family, in particular my wife, who for many years travelled with me throughout the country examining the life under stones. We were later joined also by our children who shared their father's enthusiasm.

Haifa, Israel
January 1993

MICHAEL R. WARBURG

# Contents

# 1 Taxonomy

The taxonomic status even of families seems to be continuously changing, but it is still largely based on Vandel's concepts (Vandel 1943, 1960). The taxonomic criterion used most often is the shape of the male's genital apparatus (Fig. 1.1). Vandel recognized two main evolutionary lines (series): the Tylienne and the Ligienne. The first series includes only the Tylidae. All the remaining 20 families belong to the second series. These were arranged into 4 superfamilies: Styloniscoidea, Trichoniscoidea, Atracheata and Pseudotracheata (see Table 1.1). From an evolutionary point of view the most advanced forms seem to be the conglobating forms found in the Eubelidae, Armadillidae and Armadillidiidae (Table 2 in Vandel 1943).

**Fig. 1.1.** Male genital apparatus of *Porcellio barroisi* (×50)

**Table 1.1.** Vandel's taxonomic system of the Oniscoidea

| Series Tylienne | Superfamily | Family |
|---|---|---|
| | | Tylidae |
| | | Ligiidae |
| | | Mesoniscidae |
| | Styloniscoidae | Styloniscidae |
| | | Schöbliidae |
| | Trichoniscoidae | Trichoniscidae |
| | | Buddelundieliidae |
| | | Stenoniscidae |
| | | Tendosphaeridae |
| | Atracheata | Spelaaeoniscidae |
| | | Squamiferidae |
| | | Oniscidae |
| | | Cylisticidae |
| | | Porcellionidae |
| | | Atlantidiidae |
| | Pseudotracheata | Armadillidiidae |
| | | Eubelidae |
| | | Actoeciidae |
| | | Armadillidae |

**Table 1.2.** A taxonomic system for the Suborder Oniscidea (Changes and additions by Holdich et al. 1984)

| | | | |
|---|---|---|---|
| Infraorder – Tylomorpha | | | |
| Infraorder – Ligiamorpha | | | |
| | Superfamily | Trichoniscidea | |
| | Superfamily | Styloniscidea | Turanoniscidae |
| | Superfamily | Oniscidea | Bathytropidae |
| | | | Berytoniscidae |
| | | | Halophilosciidae |
| | | | Hekelidae |
| | | | Olibrinidae |
| | | | Philosciidae |
| | | | Pudeoniscidae |
| | | | Scleropactidae |
| | | Porcellionoidae | Balloniscidae |
| | | | Irmaosidae |
| | | | Pseudoarmadillidae |
| | | | Trachelipidae |

Schmölzer (1965) in his monograph mentioned only 17 families out of Vandel's 21. On the other hand, Grüner (1966) followed Vandel's system except for replacing the Platyarthridae instead of the Squamiferidae. Recently, Holdich et al. (1984) proposed a taxonomic list that includes 34 families in 4 superfamilies, thus adding 13 new families, 6 of which have been erected since 1960 (see Table 1.2).

For more details about the reasoning that provided guidelines to these taxonomic conclusions, the reader is referred to the three monographic works and to Holdich et al. (1984).

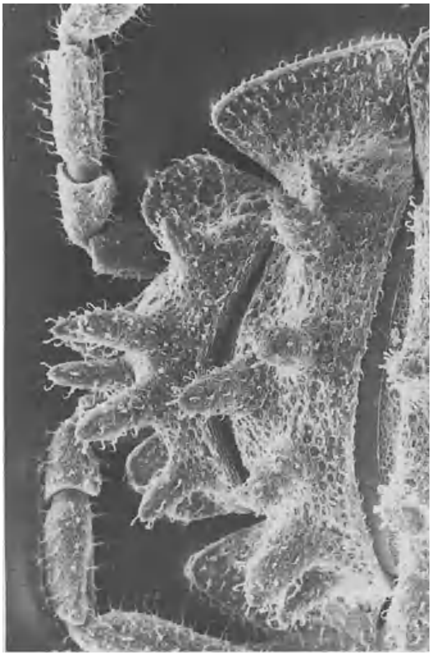
# 2 The Integument and Moult

## 2.1 Structure and Function

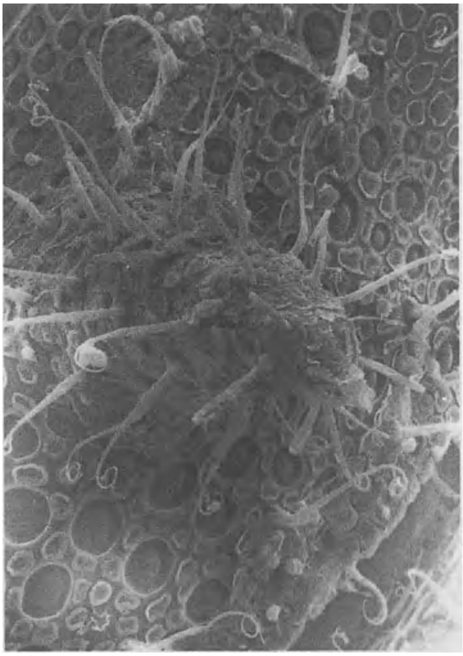
The integument covered by the cuticle has been studied in recent years in great detail thanks to the introduction of the scanning electron microscope (SEM). This has enabled the observation of the fine microstructure, and the various sensory structures associated with integumental covering (Figs. 2.1–2.14).

Larger tubercles (Figs. 2.1–2.6) could be seen, and various functions assigned to them such as protection and water conservation (Schmalfuss 1975, 1977). There is some relationship between morphological and environmental or behavioural adaptations of isopods (Schmalfuss 1984). Various plaques and pits (Figs. 2.7–2.10) as well as setae and sensillae (Figs. 2.11, 2.13) have been described (Holdich and Lincoln 1974). All terrestrial isopods examined have numerous tricorn-shaped sensillae on their tergites (Figs. 2.12, 2.13). These sensillae are dispersed among plaques of various forms and pits in between. The tricorns are scale-like structures, and the plaques partly overlap, similar to a tile roof. The pits are semicircular depressions. The tricorns seem to be innervated and could be hygroreceptors (Price and Holdich 1980a). The setae observed at the margins of the tergite plates could be proprioceptors (Fig. 2.14). Similar observations were made on several isopod species by Schmalfuss (1975, 1977, 1978a), Powell and Holcrow (1982) and Holdich (1984).

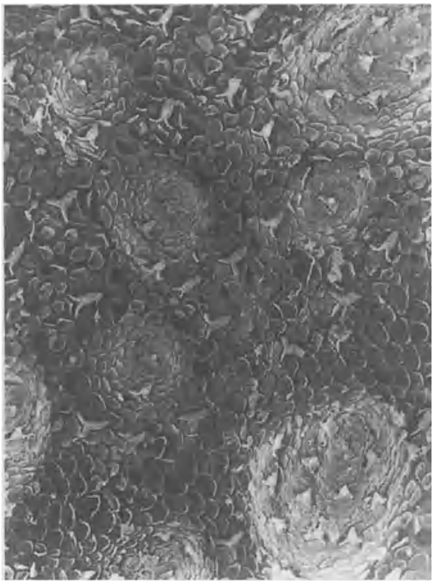
The integument consists of the epidermis, a lamellated procuticle (or endocuticule) and a two-layered epicuticle (Price and Holdich 1980a). Recently, Compere (1991) has described the fine structure of *Oniscus asellus* cuticle. The epicuticle is composed of five layers: (1) a cement layer with numerous dermal canal ducts; (2) a surface coat; (3) four laminated cuticulin layers; (4) a wax layer; and (5) the inner epicuticle. The outer layer of the epicuticule contains lipids in some isopod species (*Hemilepistus reaumuri*; see Hadley and Warburg 1986; Chap. 6). In *Porcellionides pruinosus* the epicuticule is covered by numerous spherical particles or balls of various diameter (Figs. 2.6–2.9). One possible function of these balls could be to reduce transpiration (Hadley and Hendricks 1985). All these cuticular structures contain $Ca^{2+}$. This calcium carbon-



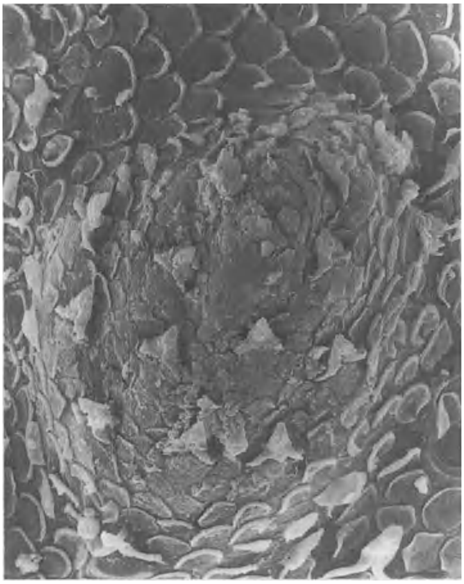
2.1



2.2



2.3



2.4

**Fig. 2.1.** Head region of *Bathytropa wahrmani* showing tubercles ( × 75)
**Fig. 2.2.** A single tubercle, enlarged ( × 350)
**Fig. 2.3.** Tubercles of *Porcellio barroisi* ( × 200)
**Fig. 2.4.** A single tubercle as in Fig. 2.3, enlarged ( × 500)

ate in the integument of *Oniscus asellus* is amorphous (Wood and Russell 1987).

In the integument, under the epidermal cell layer, lies the chromatophore layer, which contains spherical pigment granules that change during the isopod's development (Negishi and Hasegawa 1991).

### 2.1.1 The Tegumental Glands

Tegumental glands were observed in terrestrial isopods about 100 years ago ("Webers glands", see description in Ter-Poghossian 1909; for literature review, see Herold 1913). They are present in the head region, thorax and abdomen, lateral plates, legs and uropods (Gorvett 1946, 1956). There appear to be several (5–6) kinds of tegumental glands.

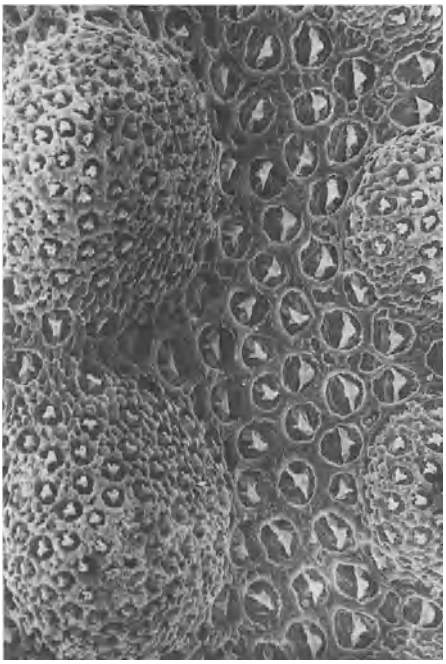
### 2.1.2 The Rosette Glands

Rosette glands are located on the head and mouth parts, lobed glands are found on the uropods and lateral plates and, furthermore, there are several compound and unicellular glands (described already by Ter-Poghossian 1909 in several oniscids). Gorvett (1946) raised the possibility that at least the rosette glands are concerned with the formation of cuticule. This was later confirmed by Stevenson (1961, in *Armadillidium vulgare*), who demonstrated that they secreted polyphenol oxidase essential for sclerotization of the newly formed cuticule. The development of the rosette glands was followed throughout the moulting cycle (Stevenson 1964).

Moulting in isopods takes place in two stages: first, the posterior half (5th thoracic segment from the end), and only then the anterior half a few days later (Verhoeff 1940). During this period, the tegumental glands have sufficient time to develop. During the moulting cycle, the glands are fully developed and ready to secrete (Gorvett 1946).

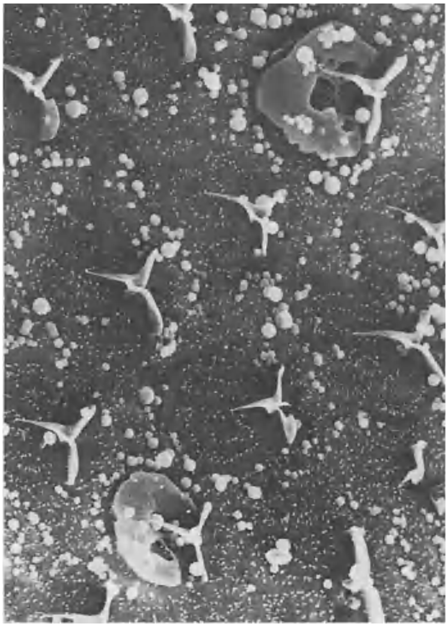
### 2.1.3 The Lobed Glands

These glands are located on the lateral plates and uropods. There are about 50–60 on each isopod, and about 18 on each lateral plate. They open to the outside through minute pores. The degree of development of the lobed glands varies greatly among different isopod species. They secrete a strongly acidic secretion with a repellent odour. Apparently, they are a defence mechanism against scorpions (Herold 1913) and spiders (Gorvett 1956).

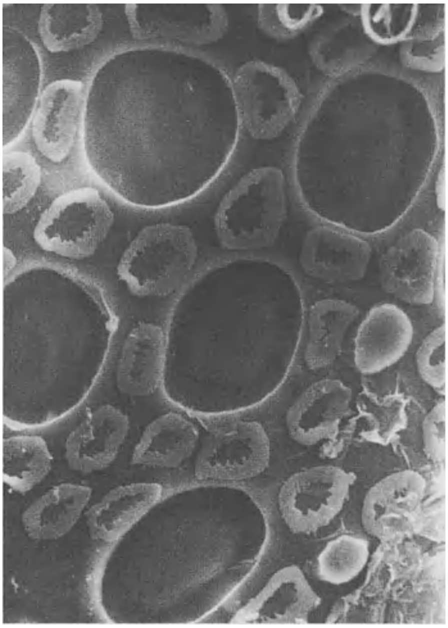


2.5

2.6



2.7



2.8

**Fig. 2.5.** Tubercles of *Armadillo tuberculatus* ( × 150)

**Fig. 2.6.** A single tubercle as in Fig. 2.5, enlarged ( × 350)

**Fig. 2.7.** Cuticle of *Porcellionides pruinosus*; note the tricorns ( × 500)

**Fig. 2.8.** Pits in cuticle of *Bathytropa wahrmani* ( × 1000)

## 2.2 Moulting

The moulting cycle in terrestrial isopods was described by Aubin (1914) and Tait (1917) and separated into various stages similar to those described in amphipods (Stevenson 1961). The stages were described in *Armadillidium vulgare*. These include stages A–E that represent the resting period up to actual ecdysis. The moulting takes place in two phases: first, the posterior half of the animal and after a few days, the anterior half (Verhoeff 1940).

*Stage A*: Post-moulting stage when the cuticule is still soft, shiny and sticky; the colour of the isopod is dark brown to grey. This stage lasts 1–2 h.

*Stage B*: The cuticule starts to harden, and half of the body expands to its maximal size. The animal normally eats the exuvium. This stage lasts several hours.

*Stage C*: Final colouration is achieved, and the cuticule hardens. This stage lasts 15–60 days.

*Stage D*: Preparation for moult. This stage can be subdivided into four substages D1–D4.

D1: A pair of white plates develops on each of the thoracic sterna (1–4).

D2: The white sternal plates disappear within 1 day.

D3: Not noticeable in isopods.

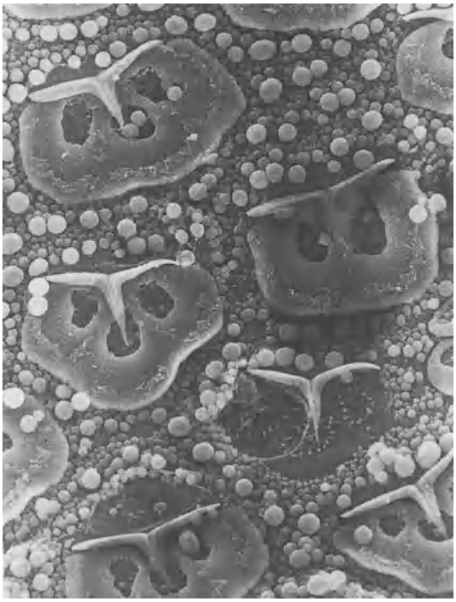
D4: Half the body is compressed for a few hours.

*Stage E*: Apolysis or moulting takes place at any hour of the day or night.

Correlated with these changes are changes in the B-cells of the hepatopancreas described by Wieser (1964a; see also Chap. 7). This cell enlargement, followed by cell secretion, takes place twice during the moulting cycle. The first time the cells secrete before the onset of the posterior moult. During this period, the blood pH drops as a result of the inflow of hepatopancreatic fluid at pH 5.5 (Numanoi 1939). The second time, cells secrete after the completion of the anterior moult (see Table 4 in Wieser 1964a; see also Chap. 7). During the whole period, the ingestion rate drops markedly (Strong and Daborn 1980).

During the moulting cycle, the epidermis cells become first vacuolated, and the subepidermis proliferates (Price and Holdich 1980b). The new epicuticule appears before the endocuticle (George and Sheard 1954). Apparently (in *Oniscus asellus*), the whole process of apolysis is not connected with water uptake and expansion but instead is brought about by internal hydrostatic pressure (Price and Holdich 1980b). Both acid and alkaline phosphatases are involved in the moulting cycle and the development of the tissues (Alikhan and Saleem 1977).

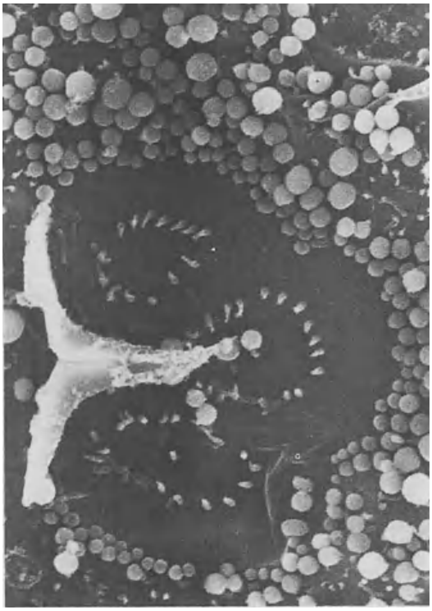
The white sternal plates indicate $Ca^{2+}$ deposits (Steel 1982). However, they are apparently not used as calcium reserves during moulting, and are sloughed off with the exuvium (Tomescu 1972).



2.9

2.10

2.11



2.12

**Fig. 2.9.** Cuticle of *Porcellionides pruinosus*; note the tricorns, typical 'enclosures' and minute ball-like structures ( × 750)

**Fig. 2.10.** Tricorns in depressions in cuticle of *Armadillo tuberculatus* ( × 750)

**Fig. 2.11.** Spines in cuticle of *Armadillidium fallax* ( × 1000)

**Fig. 2.12.** Tricorns in cuticle of *Porcellionides pruinosus* cleared with acetone. Ball-like structures remain, but enclosures have disappeared ( × 2000)

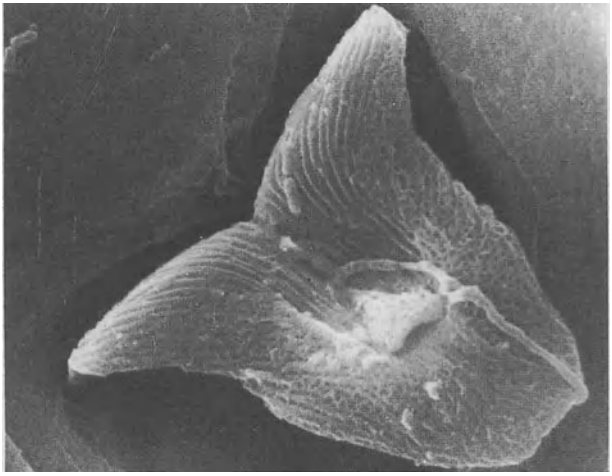
Steel (1982) recognized 15 stages in the moulting cycle relating the changes in the appearance of the sternites with concurrent microscopic changes. Numanoi (1937) described the migration of calcium from the carapace into the haemolymph and back again. The amount of calcium in the form of calcium carbonate within the white sternal plates is about 37% (Numanoi 1937). In the more terrestrial forms a high percentage of integumentary calcium accumulates (Lagarrigue 1968). In *Porcellio scaber* Auzou (1953) found about 31% calcium in the integument. It seems that while the calcium accumulates in the anterior half during premoult, the posterior half undergoes resorption. The reverse takes place within a few days up to weeks later. In *Armadillidium nasutum*, tegumental calcium levels dropped between stages C and D, and haemolymph $Ca^{2+}$ increased (Böhm and Eibisch (1976). Hadley and Hendricks (1987) demonstrated that $Ca^{2+}$ levels are lower in the moult. There is some evidence indicating that calcium levels in the haemolymph are correlated with magnesium levels (Gondko et al. 1984). The subject of calcium balance and moulting in Crustacea was reviewed by Greenaway (1985). Both the storage of calcium and the secretion of the exocuticule are controlled by ecdysteriods (see discussion in Steel 1982; Chiang and Steel 1984). The hormonal control of moulting will be discussed presently (see also Chap. 3).

The regular moulting cycles of the female isopod alternates between normal moulting and parturial moulting when the marsupium was formed. Between the parturial moults there is a period of gestation which ends when the mancas (this term is used for larval ohiscid isopods; Holdich et al. 1984) hatch from the marsupium (Mocquard et al. 1976a). The moulting cycle is affected also by ambient conditions. Thus, increased temperature accelerates and shortens the length of the moulting cycle by shortening the intermoult periods (Mocquard et al. 1978). Moreover, the photoperiod too has an effect on the length of the intermoult periods (Mocquard et al. 1976a). Madhavan and Shribbs (1981) found that a long photophase in *Armadillidium vulgare* caused a parturial moult in 72.5% of the population, whereas a short photophase caused 96% to moult. Apparently, the process of moulting is also affected by the season (due to the changes in day length), and the cyclic rhythms. Thus, in *Excirolana chiltoni* moulting is largely restricted to the weeks preceding full moon (Klapow 1972a).

### 2.2.1 Endocrine Control of the Moulting Cycle

Carlisle (1956) found that eyestalk extracts or an extract of X-organs (of *Leander*) accelerated premoult in *Ligia oceanica*, whereas sinus gland extracts had no effect on moulting.

Later, Maissiat and Graf (1973) found that indeed ecdysterone induced apolysis when isopods (*Ligia oceanica*, among other species studied) were in stage C of the moulting cycle. However, it delayed apolysis when


2.13

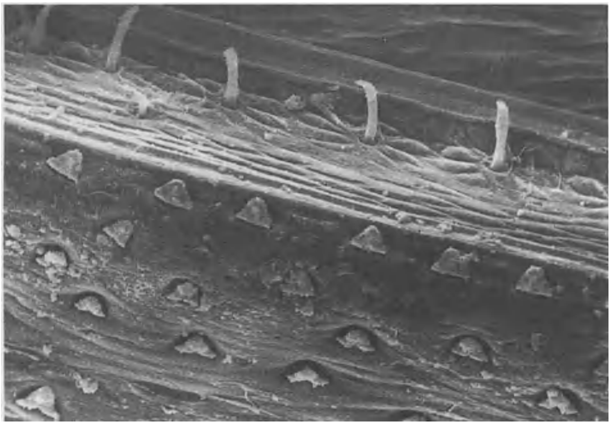

2.14

**Fig. 2.13.** Tricorn in cuticle of *Porcellio obsoletus ficulneus* cleared with acetone (×5000)

**Fig. 2.14.** Putative proprioceptors between tergites of *Porcellio obsoletus ficulneus* (×500)

applied during that stage. It seemed as if ecdysterone controls the release of an ecdysis factor. On the other hand, when injected during later moulting stages (up to stage D2), the isopods (*Sphaeroma serratum*) entered proecdysis but did not moult (Charmantier and Trilles 1976). Extirpation of the sinus gland or cauterization of the protocerebrum (in *Armadillidium vulgare*) shortened the intermoult phase (Böhm and Gersch 1976). It was found that the exuviation factor produced by the Y-organ controls the shedding of the cuticule (see Charmentier and Trilles 1976).

Analysis of the haemolymph of *Helleria brevicornis* has shown that ecdysteriods are present in very small amounts during stage C, but the hormone titre increased at stage D, the beginning of apolysis, dropping again after moult (Hoarau and Hirn 1978). Thus, it seems at present that moulting in isopods is controlled by the Y-organ, the brain and to some extent also the antennary gland. The Y-organ initiates proecdysis by participating in the production of ecdysterone and by secreting the ecdysis factor (Charmantier 1980). After the puberty moult, the ecdysterone level is reduced.

The brain induces proecdysis by secreting the Y-organ stimulating hormone. Removal of the central protocerebrum caused anecdysis (Martin et al. 1980). Increased ecdysteroid levels of the haemolymph intensify cell activity in the Y-organ (Girard and Maissiat 1983). In *Ligia oceanica* and other terrestrial isopods the neurosecretory cells (NSC) showed an increase in RER (rough endoplasmic reticulum) and in neurosecretory material (Martin and Maissiat 1973; Maissiat and Maissiat 1976).

More recently, five distinct types of terminals found in the sinus gland of several isopods have been found to lead to the brain (three of them) and to the optic tract (the remaining two; see Chiang and Steel 1984, 1986, 1989). Apparently, in this way the beta, gamma and B-cells have axons connecting to the sinus gland (see Chap. 3). It was shown that potentials measured from the sinus gland changed during the moulting cycle by dropping when the haemolymph ecdysteroid titre reached its peak (in *Oniscus asellus*; see Chiang and Steel 1987). Moreover, it was shown that neurosecretory cells of the optic tract were active after both the posterior and anterior moults. Thus, they may secrete the hormone involved in calcification of the exoskeleton (Chiang and Steel 1984, 1989). Finally, the antennary gland controls the mineral and water metabolism essential for exuviation (Bocquet-Vedrine 1979; see discussion in Chap. 5).

# 3 The Brain, Endocrine Glands and Control of Physiological Functions

With regard to some of the earlier literature on the endocrine control in crustaceans, one cannot but be surprised by the few (less than 20) papers dealing with isopods (cited by Knowles and Carlisle 1956; Carlisle and Knowles 1959). A number of general reviews on neurosecretion and neurohaemal organs have appeared since, but they include only limited information on isopod endocrines (Gabe 1966; Chaigneau 1985).

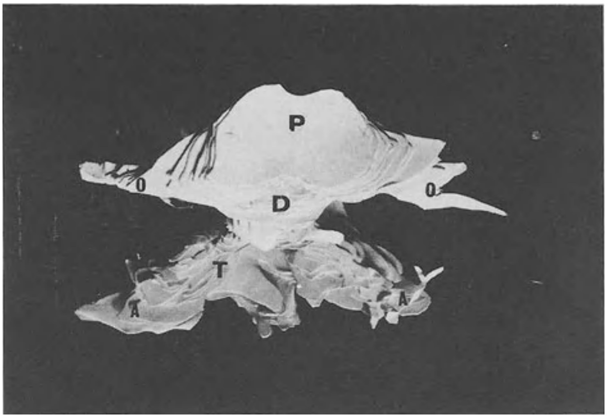
## 3.1 The Structure of the Isopod Brain

Němec (1895) described the brain in several isopod species belonging to the following genera: *Platyarthrus*, *Porcellio*, *Trichoniscus*, *Ligidium*. Hanström (1924) described in detail the brain parts of *Ligidium occidentalis*. Later, Gräber (1933) described various parts of the brain in *Armadillidium vulgare*, *Oniscus asellus* and *Porcellio scaber*. He distinguished between the protocerebrum, deutocerebrum and tritocerebrum (see Figs. 3.1, 3.2).

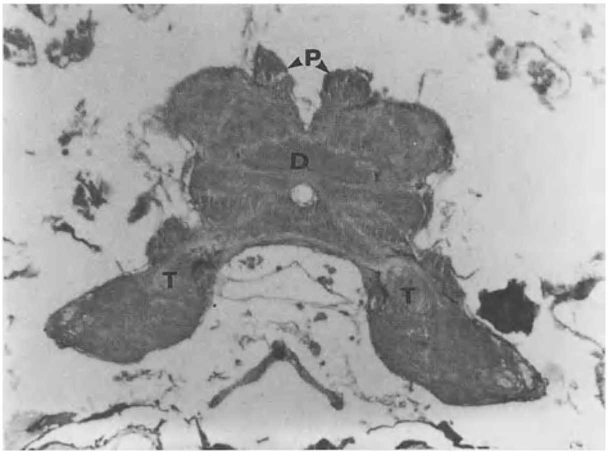
In both *Oniscus asellus* and *Armadillidium vulgare* the deutocerebrum, which consists of one neuropile lobe (Walker 1935; Schmitz 1989), is considerably reduced. The olfactory lobe is a small structure containing small cells. Sharma (1970), on the other hand, described in *Cubaris robusta* two antennal lobes in the deutocerebrum consisting of olfactory glomeruli and the olfactory tract and found that both the olfactory sensillum and the antennulae are reduced. A similar situation was described in *Porcellionides pruinosus* (Sharma 1979a), where a single medullary mass was recognized (Satija et al. 1967). In *Ligia exotica* the deutocerebral lobe appears to have shifted to the anterior region of the tritocerebrum, forming the olfactory neuropile (Sharma 1979a).

The tritocerebrum of *Cubaris robusta* consists of three neuropiles: antennary, olfactory and tegumentary (Sharma 1977). Three lobes were recognized also in *Porcellionides pruinosus* (Satija et al. 1967). This basic structure has already been described by Walker (1935).

The protocerebrum consists of two optic lobes containing small cells of characteristic appearance next to some large cells (Walker 1935). In *Ligia* the optic lobes are especially well developed. *Ligia exotica* has large



3.1



3.2

**Fig. 3.1.** Reconstruction of the brain of *Porcellionides pruinosus* based on 6–8-μm-thick serial sections. *P*, Protocerebrum; *D*, deutocerebrum; *T*, tritocerebrum; *O*, optic lobes; *A*, antennary lobes

**Fig. 3.2.** Section through the brain of *Porcellionides pruinosus* (×600)

eyes and well-organized optic masses on a long optic lobe (Sharma 1982). In *Porcellionides pruinosus* the protocerebral lobes have been described by Satija et al. (1967).

The pseudofrontal organ, described in *Oniscus asellus* by Gräber (1933), is an oval mass 50–80 μm in size attached by a narrow stalk to the optic lobe (Walker 1935). In *Armadillidium vulgare* it is suspended ventrally to the main protocerebral lobes (Schmitz 1989). This was later recognized to be the Y-organ of the isopods (see later). Earlier literature on this subject can be found in Gräber (1933) and Walker (1935).

## 3.2 The Organ of Bellonci

This peculiar organ was first described in 1881 (see Bellonci 1886) in *Sphaeroma serratum*, and later in *Porcellio maculicornis* (Bellonci 1886). It is connected to the brain through an extension or a peduncle consisting of a nerve-like tract originating from the sensory cell-like bodies of this organ (Chaigneau 1971). The cell bodies consist of an outer segment connected by a "ciliary piece". These are bundles of very long microvilli. Inside the cells large electron-dense spheres were observed consisting of many granules (glycogen?; Chaigneau 1971; Chaigneau and Chataigner 1977; Barres and Chaigneau 1981).

These cells are not secretory cells as was previously believed by Gabe (1952b, 1966, see pp. 228–246 therein), who suggested that they were homologous with the X-organ of the malacostracans. They are possibly photoreceptors as one of the three nerve type connections distinguished there is similar to arthropod photoreceptors (Chaigneau and Chataigner 1977). It could be a multiple sensory complex organ typical to all crustacean groups (Chaigneau 1978).

## 3.3 Neurosecretion in Isopods

There appears to be general agreement that there are at least four different neurosecretory cell (NSC) types: A, B, beta and gamma (see Table 3.1; Figs. 3.3–3.6). These have been described by Matsumoto (1959) in *Armadillidium vulgare* and by Martin (1972a) in *Porcellio dilatatus*. Thus, A-cells (30–40 μm) are known from the ventral side of the mid-brain. B-cells (15–20 μm) were found at the base of the optic lobe. Both these cell types were found also in the segmental ganglia. On the other hand, beta-

**Table 3.1.** Dimensions of neurosecretory cell (NSC) types (in μm; data after various authors)

| | NSC type | | | | |
|---|---|---|---|---|---|
| Species | A | B | β | γ | Source |
| *Ligia oceanica* | — | 13–20 | 20–30 | 8–13 | Juchault and Kouigan (1975) |
| *Porcellio scaber* | 20–30 | 6–22 | 17–28 | 10–13 | Messner (1966) |
| *P. dilatatus* | 30 | 10–20 | 14–28 | 30 | Martin (1972a–c) |
| *P. obsoletus* | 14–24 | 9–27 | 13–42 | 4–14 | Warburg and Rosenberg (1978) |

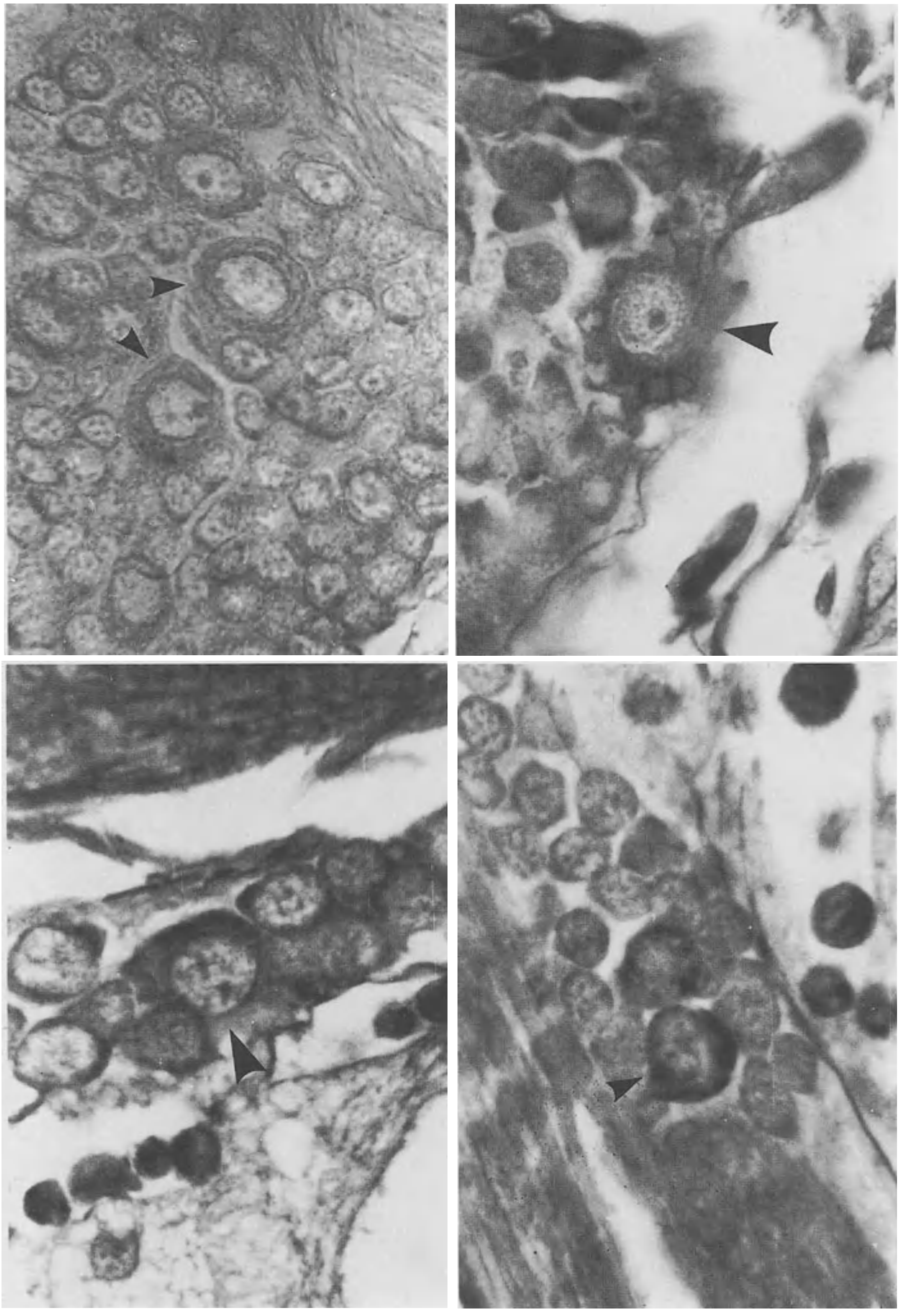


**Fig. 3.3.** Neurosecretory cells in the brain of *Porcellionides pruinosus* ( × 625). Type A-cell (*arrow*)

cells (34–40 μm), containing many secretory granules, and the smallest cells, gamma-cells (7–11 μm), were both described from the optic lobe peduncle. The latter cells were found to be acidophilic (Gabe 1952a; Matsumoto 1959). This optic lobe peduncle is also the location of the sinus gland (in *Idotea japonica*; see Miyawaki 1958). The axons of the γ-cells connect to the sinus gland and to the beta-cells of the protocerebrum (Vitéz 1970).

Vitéz described another cell type from the frontal part containing phloxinophilic colloid material. In *Ligia oceanica* the NSC are located in the median zone of the protocerebrum and in the optic lobe (Juchault and Kouigan 1975). Martin (1972a, b) found the beta-cells to be strongly AB; PF- and PAS-positive, whereas the B-cells were much less reactive to these dyes. On the other hand, the A-cells were largely phloxinophilic. The gamma-cells reacted strongly to either PF or AB.

In addition to the five NSC types described so far, Demassieux and Balesdent (1977) found additional cells in *Asellus aquaticus*. Two basophilic types of cells were investigated in the central nervous system, and two acidophilic types of cells were located in the optic lobe (Demassieux 1979).

In *Porcellio obsoletus* we described nine types of putative NSC (Warburg and Rosenberg 1978); of these, four were new ones. Some of them may or may not be subtypes of the B-cells that have been distinguished in *Sphaeroma serratum* by Chataigner et al. (1978).

Vitéz (1971) was the first to notice in a few terrestrial isopods a relationship between either light and temperature and the NSC activity. At high temperatures she found a larger amount of neurosecretion, and a few hours' illumination stimulated the NSC activity.

More specifically, the beta-cells of the protocerebrum show a cyclic activity related to the moulting cycle (Martin 1972b). The synthesis of the granules reached a peak at stage C of the moulting cycle (see Chap. 2). Damassieux and Balesdent (1978) assumed that the acidophilic secretion of the beta-cells was related to both moulting and reproduction. It could have an inhibitory effect on vitellogenesis. It is possible that some of the NSC described here are identical to some of the immunoreactive cells described by Takeda and Mizuno (1989).

The NSC are also affected by the season. Thus, Zahid et al. (1982) noted in *Porcellio evansi* that in summer the beta-cells store more material and the A-cells, less.

◄

**Fig. 3.4.** Neurosecretory cell in the brain of *Procellionides pruinosus* (×625). Type B-cell (*arrow*)

**Fig. 3.5.** Neurosecretory cell in the brain of *Procellionides pruinosus* (×625). Type beta-cell (*arrow*)

**Fig. 3.6.** Neurosecretory cell in the brain of *Porcellionides pruinosus* (×625). Type gamma-cell (*arrow*)

## 3.4 The Y-organ and the Neurohaemal Organs

Isopods have two cephalic neurohaemal organs: the lateral cephalic nervous plexus and the sinus gland (Martin et al. 1983). In addition, there is the Y-organ. This organ is comprised of cells about 200 μm in size and rich in mitochondria (in *Sphaeroma serratum*). This is the ecdysial or moulting gland. The Y-organ cells presumably absorb cholesterol from the haemolymph and convert it to the moulting hormone (Fingerman 1987).

Connected with it is the lateral cephalic nerve plexus (details in Delaleu and Giry 1967). Five different axon terminals have been described (Chiang and Steel 1985b), some of which connect to the Y-organ (in *Shaeroma serratum*, see Maissiatet et al. 1979b), and two connect to the protocerebrum (Chiang and Steel 1985b in *Oniscus asellus*).

Messner (1963, 1966) described the Y-organ in *Porcellio scaber* and *Oniscus asellus* and found that it shows a secretory cycle corresponding to the moulting cycle. Its size is about 200 μm large (Charmantier and Trilles 1979), and its cellular activity is synchronized with apolysis (Girard and Maissiat 1983). It contains proteinaceous material (Maissiat et al. 1979a) and regresses after the puberty moult when the ecdysterone levels are low (Charmantier and Trilles 1977a, 1979; Maissiat and Maissiat 1978).

The Y-organ initiates procedysis probably by producing the moulting hormone ecdysterone (Charmantier 1980) and the ecdysis factor (Charmantier and Trilles 1977a, b). Its destruction prevents regeneration, which can be restored by injecting the moulting hormone ecdysterone (Noulin and Maissiat 1974).

The sinus gland was first described by Gräber (1933) as the pseudofrontal organ in several isopods. It is located posterior to the optic lobe (see also Miyawaki 1958; Sharma 1979a, b). The sinus gland is connected to the lateral nervous plexus, another neurohaemal organ found in isopods, which is connected to both the tritocerebrum and the subesophageal ganglion (Juchault and Kouigan 1975). Its ultrastructure has been described in detail by Martin (1972c, 1982) in *Porcellio dilatatus*. In *Ligia oceanica* it contains 4 types of terminals (Martin et al. 1983). Apparently, the sinus gland contains a group of neurosecretory cells (Chiang and Steel 1989). Three types of neurosecretory granules were recognized in the sinus gland of *Armadillidium vulgare* (Taketomi and Ban 1986). The number of granules changed during the moulting cycle. Chiang and Steel (1985a, b) recorded bursts of electrical activity in *Oniscus asellus* due to two neurosecretory cells in the sinus gland.

Gabe (1952b) noted a cyclic appearance of this gland in *Oniscus asellus*. Thus, during moulting the sinus gland fills in a cyclical manner

(Messner 1963). Apparently, it contains more secretion during winter (Zahid et al. 1982).

## 3.5 Endocrine Control of the Moulting Cycle

Carlisle (1956) found that eyestalk extract or extracts of X-organs (or *Leander*) accelerated premoult in *Ligia oceanica*, whereas sinus gland extracts had no effect on moulting.

Later, Maissiat and Graf (1973) and Maissiat and Maissiat (1976) found that indeed ecdysterone induced apolysis when the isopods (*Ligia oceanica* among other species studied) were in stage C of the moulting cycle (see also discussion of the subject in Chap. 2). However, it delayed ecdysis when applied during apolysis. It seems as if ecdysterone controls the release of an ecdysis factor. On the other hand, when injected at stages up to D2 the isopods (*Sphaeroma serratum*) entered proecdysis but did not moult (Charmantier and Trilles 1976).

Extirpation of the sinus gland, or the cauterization of the protocerebrum (in *Armadillidium vulgare*), started the intermoult phase (Böhm and Gersch 1976). It was found that the moulting factor was produced by the Y-organ and controlled the shedding of the cuticle (Charmantier and Trilles 1976).

Analysis of the haemolymph of *Helleria brevicornis* has shown that ecdysteroid is present in very small amounts during stage C, but the hormone titre increases at stage D, the beginning of apolysis, dropping again after the moult (Hoarau and Hirn 1978).

Thus, as it seems at present that moulting in isopod, is controlled by the Y-organ, the brain and, to some extent, the antennary glands.

The brain induced proecdysis by secreting the Y-stimulating hormone. In *Ligia oceanica* removal of the central part of the protocerebrum shortened the intermoult period (Mocquard et al. 1971). Removal of the sinus gland changed the intermoult period (Martin et al. 1980). The increased ecdysteroid levels of the haemolymph intensified cell activity of the Y-organ (Girard and Maissiat 1983).

Recently, five distinct types of terminals located in the sinus gland of several isopod species were found to lead to the brain (three of them) and to the optic tract (the remaining two) (see Chiang and Steel 1984, 1986). Apparently, in this way the beta-, gamma- and B-cells have axons connecting to the sinus gland (Chiang and Steel 1989). The beta-cells are most likely involved in moulting (Chiang and Steel 1985a). As is known, potentials measured from the sinus gland fluctuate during the moulting cycle, dropping when the haemolymph ecdysteroid titre reaches its peak. Moreover, it was shown that NSC of the optic tract are active following both the posterior and anterior moults; thus, they may secrete the hormone involved in calcification of the exoskeleton (Chiang and Steel 1984, 1989).

Finally, the antennary glands control the mineral and water metabolism essential for exuviation (Bocquet-Vedrine 1979); (see discussion in Chap. 5).

## 3.6 Colour Changes

Kleinholz (1937) and Enami (1941a, b) noted that *Ligia baudiniana* and *L. exotica*, respectively, change their body colour when on different backgrounds by the dispersion and concentration of pigment granules within the melanophores. This was later seen also in other marine isopods (Okay 1943). Apparently, the dimensions of the pigment granules change with the development of the isopod (Negishi and Hasegawa 1991). Kleinholz (1937) and Enami (1941a) also noted that there was a rhythmic activity in the pigment movement. In *Idotea japonica* melanophores expand in the daytime and concentrate at night (Oguro 1959). This has been observed also in *Ligia occidentalis*, where the pigment concentration reached its peak at 10.00 PM, and maximal dispersion at 08.00 AM (Armitage 1960). *Sphaeroma quadridentatum* shows a similar pattern (Leboeuf and Howe 1981).

Kleinholz (1937) injected aqueous extracts of whole heads of *Ligia* and found that they caused lightening of the colour. For a detailed discussion of this subject, see Armitage (1960). In *Ligia exotica* this was confirmed by Nagano (1949) and by Oguro (1959). The 'melanophore dispersing hormone' originated in the post-commissural and sinus organs (Fuse and Yamamoto 1985). Homogenates of the sinus glands of some terrestrial isopods caused pigment dispersion in melanophores when injected into *Ligia exotica* (Castrucci and Mendes 1975). Injection of *Trachelipus rathkei* sinus gland extracts caused a marked dispersion of red pigment in *Cambarus* (McWhinnie and Sweeney 1955).

Another phenomenon of the movement of retinal pigment is in response to light and darkness (in *Ligia olfersi*). This was found to be under the control of the sinus gland and the supraoesophageal ganglion, which contains the principle that causes dark adaptation of the reflecting pigment (Fingerman and Oguro 1963).

In the terrestrial isopods there is no colour change, but chromatophoric substances are produced by the neurosecretory cells of the protocerebrum (Castrucci and Mendes 1975).

## 3.7 The Aggregation Pheromone

This pheromone has been recently described in several isopod species by Takeda (1984). It is apparently secreted by the gut into the lumen and finally passed on to the faecal pellets. The nature of this factor and the ways it acts need further studies.

## 3.8 Hyperglycaemic Neuropeptides

Gersch and Eibisch (1976) found that the blood sugar content of *Armadillidium vulgare* haemolymph increased during the intermoult and was subsequently followed later by a drop. Animals without the sinus gland or the median part of the protocerebrum showed a decreased blood glucose level at all periods.

The release of this hyperglycaemic hormone (CHH) is probably serotonin-dependent as injection in vivo of serotonin into male *Porcellio dilatatus* induced increased hyperglycaemia (Martin 1978). The same effect was noted when the sinus glands of the same species were injected (Martin et al. 1984a). The source of the CHH was traced to two NS cells (beta- and gamma-cells) in each of the brain's hemispheres within the protocerebrum (Martin et al. 1984b).

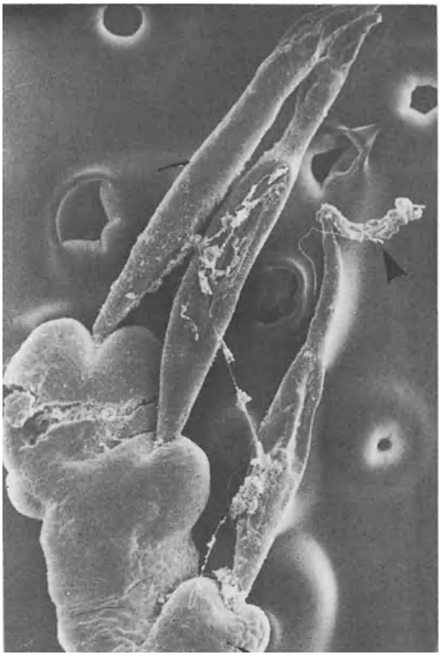
## 3.9 Endocrine Control of Water Balance

In recent years Takeda and co-workers have found evidence for arginine vasopressin (AVP), arginine vasotocin (AVT), and angiotensin II immunoreactive cells in the brain of terrestrial isopods (Takeda and Mizuno 1989). In vertebrates these hormones are largely associated with the control of water balance. AVP immunoreactive cells were localized in the central part of the optic nerve and the sinus gland (in *Ligia exotica*, but not in *Porcellio scaber*). AVT immunoreactive cells were localized in the central nervous system of *Ligia*. Water loss was inhibited by injecting AVP in *Porcellio*, but less so in *Armadillidium vulgare*. Angiotensin II immunoreactive cells were found in the optic lobe and the posterior protocerebrum of *Armadillidium vulgare*, *Porcellio scaber*, but not in *Ligia*.

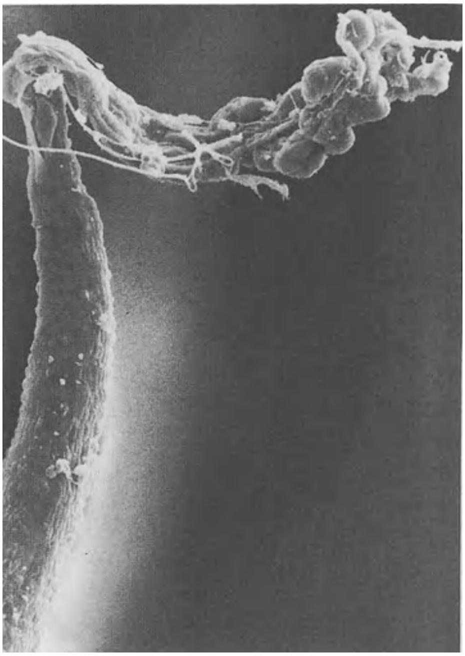
## 3.10 The Androgenic Gland

In the male isopod an androgenic gland is attached to the terminal part of the testes (Figs. 3.7, 3.8). Some details of ultrastructure are given in Malo and Juchault (1970). It was found that the implantation of an androgenic gland in a female *Armadillidium vulgare* caused the appearance of male sexual characters (Katakura 1960, 1961a for earlier literature; Hasegawa and Katakura 1981, 1983, 1985). Extracts of the androgenic gland induced masculinization of the sexual characters of the females, causing them to form testes, seminal vesicles and a vas defferens (Katakura and Hasegawa 1983). The subject of sex determination was reviewed by Legrand et al. (1987). It may be concluded that the androgenic gland hormone is the determining factor for sex differentiation (Katakura 1984). When the gonads of *Armadillidium vulgare* were partly removed, sex reversal took place (Suzuki and Yamasaki 1991).

On the other hand, the implantation of ovaries into males induced no change. Cross implantation was occasionally effective. Thus, *Armadillidium vulgare* females responded to implanted androgenic glands of *Porcellio dilatatus*, but not vice versa (Juchault and Legrand 1978). More-



3.7



3.8

**Fig. 3.7.** Androgenic gland at the tip of a testis lobe (*arrow*) ( × 50)

**Fig. 3.8.** Same as in Fig. 3.7, enlarged ( × 100)

over, in *Sphaeroma serratum*, Raimond and Juchault (1983) succeeded in converting an ovary into functional testes by implanting androgenic glands.

Recently, Katakura (1984) found that masculinized females of *Armadillidium vulgare* when mated with normal females produced offspring at a ratio of 1:3 male to female.

The androgenic hormone was found to be water soluble, of about 15–17 000 molecular weight and possibly a protein (Katakura et al. 1975; Hasegawa et al. 1987). However, there is no evidence of lipids, and it is still active up to 125°C (Juchault et al. 1978). In *Armadillidium vulgare* it does not contain cysteine (Martin et al. 1990).

Perhaps there are two specific neurohormones; one from the protocerebrum and the other from the Central Nervous System (CNS), the first controlling the development of the androgenic gland and the second the synthesis of the male hormone (Juchault and Legrand 1978).

There is apparently a cyclic discharge of the hormone from the holocrine glandular cells (Radu and Cracium 1976, see also earlier literature therein). The secretory activity of the androgenic gland increased with a rise in temperature (Malo 1970). The androgenic gland cells (of *Porcellio scaber*) are rich in mitochondria, vacuoles and secretory granules. They are arranged in compact clusters, and the cyclic discharge is shown by their clear or dense appearance.

## 3.11 Sex Inversion in Isopods

This subject has been studied in great detail by Legrand (1967) and in later publications with colleagues (Juchault et al. 1974; Legrand and Legrand-Hamelin 1975; Juchault and Legrand 1989). It appears that the feminizing factor responsible is a small, intracytoplasmic, symbiotic, bacterium-like organism. The microorganisms are adapted to live around the oocyte nucleus in various oniscid ovaries (*Ligia oceanica*, *Oniscus asellus*, *Porcellio scaber*, *P. laevis*, *P. dilatatus*, *Armadillidium vulgare* and others; see Juchault and Legrand 1974, 1989). They cause either feminization or masculinization of their hosts. The intersex male-like isopod is capable of producing vitellogenin in the fat body (Souty-Grosset and Juchault 1987).

## 3.12 Endocrine Effect on Reproduction

Four types of vitellogenins were identified in *Armadillidium vulgare* (Suzuki 1987). Their production is controlled by the 'vitellogenesis inhibiting hormone' (VIH) synthesized by the NSC in the median part of the protocerebrum. VIH acts to restrain the synthesis of vitellogenin by the fat body (Juchault et al. 1989).

There is also a gonad-inhibiting hormone produced by the protocerebrum (in *Ligia oceanica*), as was shown by various authors (reviewed in Legrand et al. 1982).

Souty et al. (1982) found that extirpation of the moulting gland (Y-organ) in *Porcellio dilatatus* females caused a lower rate of vitellogenin release into the haemolymph. When beta ecdysone was injected, the vitellogenin levels were restored to normal. Similarly, gonadotrophins could stimulate the synthesis of vitellogenin in the fat body of *Idotea balthica* (Souty and Picaud 1984). Apparently, a vitellogenin-inhibiting factor stored in the sinus glands of *Porcellio dilatatus* controls its synthesis in the fat body (Gohar et al. 1984).

Suzuki (1986) noted that in *Armadillidium vulgare* oocytes ceased to grow when the Y-organ was surgically removed (at stage C of the moulting cycle). Their rapid development (occurring at stage D of the moulting cycle) is related to the activity of the Y-organ. Thus, the presence of the Y-organ is required for normal oocyte growth. The subject of reproduction is more fully discussed in Chapter 11.

# 4 Respiratory Organs and Respiration

## 4.1 Structure of the Respiratory Organs

Whereas the aquatic and marine isopods breathe through gills, which are their 3rd, 4th and 5th pairs of endopodites, the terrestrial oniscids breathe through pseudotracheae or tree-lungs (Unwin 1931).

The gills have been described in great detail in the marine isopods *Mesidotea* (Babula and Bielawski 1981) and *Jaera* (Bubel and Jones 1974), as well as in the terrestrial oniscid *Porcellio scaber* (Bielawsky and Babula 1980). Their common feature is the many infoldings and the abundance of mitochondria in the gill cells.

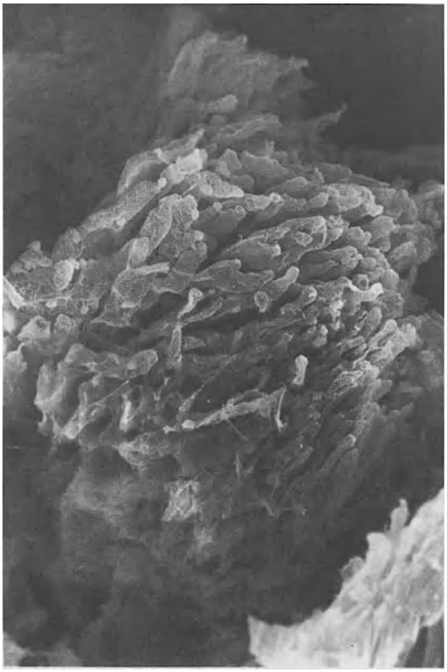
The study of the respiratory organs of terrestrial isopods began at the end of the last century (for earlier literature, see Stoller 1899; Bepler 1909). These studies were concerned with understanding the 'white bodied' or 'pseudotracheal fields' (Verhoeff 1917a, b, 1921; Mödlinger 1931; Unwin 1931; Maccagno 1939). Several isopod genera and a large number of species were compared (Mödlinger 1931). More recent work by Mahmoud (1956) described the structure of the pseudotracheal organ in *Porcellio laevis*. Both Unwin (1931) and Vandel (1943) tried to provide an evolutionary outlook based on the structure of these tree-lungs. The exopodites of the 3rd, 4th, and 5th abdominal appendages were modified to carry out respiratory function by having an extremely thin outer wall separating the haemolymph from the air (Unwin 1931). Invagination of the outer wall formed branching trees of air tubes (Figs. 4.1, 4.2).

The respiratory epithelium of *Porcellio scaber* consists of very flat cells forming a thin cytoplasmic layer (0.5 μm) (see Babula and Bielawski 1976; Bielawsky and Babula 1980). The mean distance between the air and haemolymph is about 0.67 μm. The surface of the cuticle at the opening of the pseudotrachea has remarkable ultrastructure, as can be seen under the scanning electron microscope (Figs. 4.3–4.6), reminding some of brushes whose purpose is to sieve the dust (Fig. 4.7). Babula (1981) suggested that the complex infolding structure in *Porcellio scaber* is connected with the resorption and diffusion of air inside.

Recently, the ultrastructure of these lung-like structures has been investigated in detail by Ebbe (1981) and Hoese (1982a, b, 1983). In *Tylos granulatus*, according to Ebbe, the interior of the pleon exopods shows


4.1


4.2


4.3

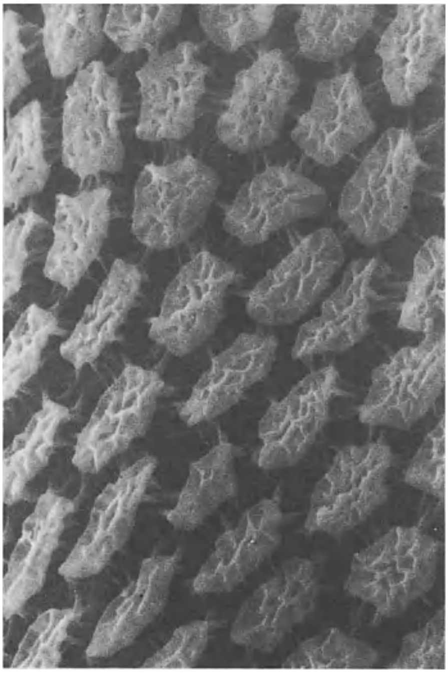

4.4

**Fig. 4.1.** Opening into the pseudotrachea of *Porcellio olivieri* (*arrow*; × 100)

**Fig. 4.2.** Pseudotrachea of *Porcellio olivieri* ( × 100). *Arrow* indicates opening for air entrance

well-developed tracheal organs rather reminiscent of the arachnid's lungbooks (see his Fig. 19). These lamellae are shown in Fig. 4.8. Hoese (1983) found differences between *Tylos spinulosus* with its single openings to the folded lungs and *T. granulatus, T. capensis* and *T. latreille*, whose openings (stigmata) are smaller. *Ligia* is still a gill-breathing animal, whereas all other terrestrial oniscids are lung-breathing (Hoese 1982a). The adaptation to terrestrial breathing is reflected in the structure of the lungs. [This brought Verhoeff (1949) to conclude that *Tylos* must have returned to the sea secondarily as the lung structure is of the terrestrial pattern]. Thus, *Oniscus* forms a single infolding lung which is not covered, whereas others (*Armadillo, Hemilepistus*), more terrestrial forms, have covered tubular lung openings into an atrium. In the mesic-inhabiting porcellionid, *Porcellio laevis*, there appears to be more air openings (Figs. 4.9, 4.10). A similar structure was described in *Periscyphis*, whose tubuliform lung terminates in an extremely narrow cleft whose branches penetrate into the body (Ferrara et al. 1991).

## 4.2 Respiration

Early researchers were curious to learn how the terrestrial isopods breathe. Thus, Bepler (1909), Verhoeff (1917c), Herold (1925) and Reinders (1933) all tried to measure the survival of the terrestrial species under water (among other simple experiments they performed). The information on oxygen consumption is based on data from only five species of isopods (Table 4.1).

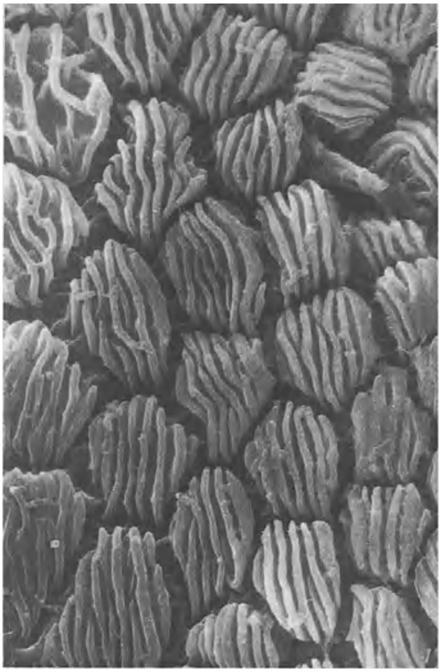
In *Ligia*, Ellenby (1951) observed that the rate of pleopodal beat was inversely related to size, as was the oxygen consumption. This animal has been extensively studied by Newell et al. (1976). Apparently, in aquatic isopods the gas exchange is carried out by the non-swimming pleopods (Alexander and Chen 1989).

Edney and Spencer (1955) found that oxygen uptake through the general integument amounted to 50%, possibly largely through the thin ventral cuticle of the leg of *Ligia* and the abdominal cuticle of *Oniscus* and *Porcellio*.

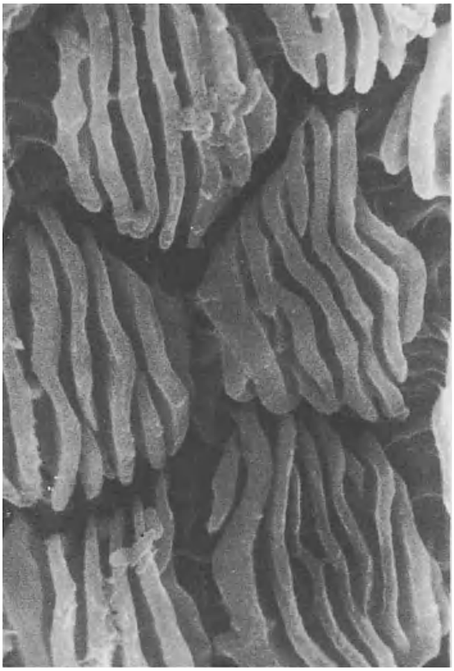
Wieser (1962) noted that the size (weight) of the isopods did not affect their respiration rate. Thus, the specific rate of oxygen consumption is independent of body mass (Wieser and Oberhauser 1984). However, both Carefoot (1989) and Husain and Alikhan (1979a, b) described a negative

**Fig. 4.3.** Tubular structure of pseudotrachea of *Porcellio olivieri* (× 350)

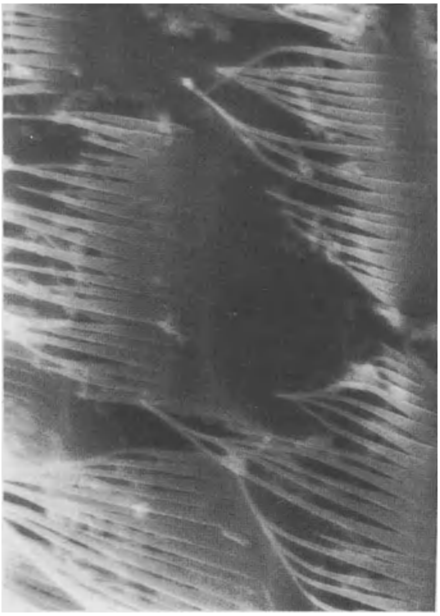
**Fig. 4.4.** Specialized cuticular structure at the entrance of the pseudotrachea of *Porcellio obsoletus ficulneus*, presumed to trap dust (× 2000)



4.5



4.6



4.7

4.8

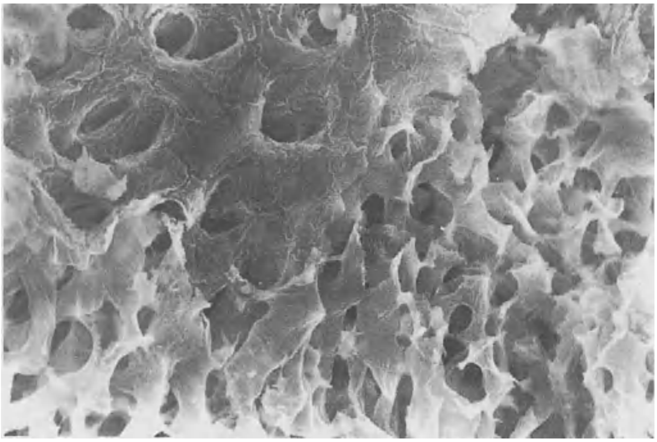
**Fig. 4.5.** Same structure as in Fig. 4.4 but in *Procellio barroisi* (× 2000)

**Fig. 4.6.** Same as in Fig. 4.5, enlarged (× 5000)

**Fig. 4.7.** Brushes at the entrance into pseudotrachea of *Armadillo officinalis* (× 3500)

**Fig. 4.8.** Respiratory lamellae of *Tylos* sp. (× 75)

4.9



4.10

**Fig. 4.9.** Air passage at the entrance into the pseudotrachea of *Porcellio laevis* (×500)

**Fig. 4.10.** Same as in Fig. 4.9, inside the pseudotrachea (×500)

relationship between the live weight of *Ligia* and *Porcellio laevis*, and their oxygen consumption. The smaller or younger specimens consumed more oxygen than larger or older ones (Bagatto and Alikhan 1986).

Temperature does not appear to affect the oxygen consumption in several isopods (Wieser 1972, 1984; Newell et al. 1974, 1976). Thus, little variation was found in oxygen consumption over a range of 5–15°C (Alikhan 1983b; Husain and Alikhan 1979a, b). On the other hand, temperature affected the oxygen uptake in *Porcellionides pruinosus* (Al-Dabbagh and Marina 1986; Table 4.2). Similarly, in *Tracheoniscus nodulosus* and *Porcellio scaber* respiration was temperature-dependent between 15 and

**Table 4.1.** Rate of oxygen consumption in terrestrial (in $\mu l\ O_2 \cdot g^{-1} \cdot h^{-1}$)

| Species | $O_2$ consumption | Source |
|---|---|---|
| *Porcellio laevis* | 112–213 | Edney (1964b) |
| *P. scaber* | 80–340 | Edney and Spencer (1955)<br>Wieser (1962)<br>Newell et al. (1974)<br>Wieser and Oberhauser (1984) |
| *Porcellionides pruinosus* | 148–772 | Al-Dabbagh and Marina (1986) |
| *Oniscus asellus* | 115–684 | Edney and Spencer (1955), Phillipson and Watson (1965) |
| *Armadillidium vulgare* | 38–300 | Allee (1926), Edney and Spencer (1955), Al-Dabbagh and Marina (1986) |

**Table 4.2.** Temperature effect on oxygen consumption

| Species | Temperature (°C) | $O_2$ consumption ($\mu l\,O_2 \cdot g^{-1} \cdot h^{-1}$) | Source |
|---|---|---|---|
| *Porcellio scaber* | 10 | 164 | Gromysz-Kalkowska and Szubartowska (1984) |
| | 25 | 295 | Gromysz-Kalkowska and Szubartowska (1984) |
| | 34 | 573 | Gromysz-Kalkowska and Szubartowska (1984) |
| *P. laevis* | 5–15 | 120–150 | Husain and Alikhan (1979b) |
| | 20–30 | 150–370 | Husain and Alikhan (1979b) |
| | 30–35 | 140–180 | Husain and Alikhan (1979b) |
| *Porcellionides pruinosus* | 10 | 148–240 | Al-Dabbagh and Marina (1986) |
| | 25 | 238–378 | Al-Dabbagh and Marina (1986) |
| | 35 | 510–772 | Al-Dabbagh and Marina (1986) |
| *Armadillidium vulgare* | 10 | 51–131 | Al-Dabbagh and Marina (1986) |
| | 25 | 121–301 | Al-Dabbagh and Marina (1986) |
| *A. nasutum* | 10 | 144 | Gromysz-Kalkowska and Szubartowska (1984) |
| | 25 | 337 | Gromysz-Kalkowska and Szubartowska (1984) |
| | 34 | 490 | Gromysz-Kalkowska and Szubartowska (1984) |

**Table 4.3.** Rate of $O_2$ consumption during different seasons (in $mm^3$ $O_2/mg \cdot h$)

| Species | Month | $O_2$ consumption | Source |
|---|---|---|---|
| *Porcellio scaber* | III–V | 0.09–0.16 | Wieser (1962) |
| | IX–I | 0.06–0.14 | Wieser (1962) |
| *Trichoniscus pusillus* | III | 0.12–0.13 | Meyer and Phillipson (1983) |
| | VI | 0.26–0.38 | Meyer and Phillipson (1983) |
| *Oniscus asellus* | VIII–IX | 0.10–0.20 | Phillipson and Watson (1965) |
| | V–VI | 0.50–0.60 | Phillipson and Watson (1965) |
| *Armadillidium vulgare* | III–V | 0.06–0.10 | Wieser (1962) |
| | IX–I | 0.07–0.11 | Wieser (1962) |

30°C (Hornung 1981). However, Alikhan (1983b) noted a significant decrease in oxygen uptake beyond 30°C (in *Porcellio laevis*). Studying *Trichoniscus pusillus*, Meyer and Phillipson (1983) noted that at 5°C the oxygen consumption was 0.13 $\mu l \cdot mg \cdot h$, increasing to 0.32 $\mu l \cdot mg \cdot h$ at 15°C. Dehydration appears to cause a drop in oxygen consumption in several isopod species (Carefoot et al. 1991). On the whole, isopods do not seem to be capable of compensating for temperature changes (Nash 1979).

There seems to be a difference in the patterns of respiratory metabolism between a "nocturnal" isopod (*Porcellio laevis*) and a "diurnal" isopod (*Armadillidium vulgare*) (Husain and Alikhan 1979b; Bagatto and Alikhan 1986). Thus, during daylight isopods require less food from the fields. Moreover, they respire less during the daytime (Alikhan 1983b). Likewise, *Tylos granulatus* maintained a low oxygen consumption during its diurnal resting hours (Marsh and Branch 1979). During activity, the isopods consumed double the amount of oxygen (Wieser 1962; York 1973). This could be related to the photoperiod (Wieser 1963b). There was also a difference in the response of isopods from different localities and under different ecological conditions (Hornung 1981). Thus, Phillipson and Watson (1965) noticed a seasonal difference in respiration in both sexes of *Oniscus asellus*, with a peak in the spring (Table 4.3).

Oxygen consumption seems to increase during the moulting cycle, reaching its peak at ecdysis (Edney 1964b). Similarly, Husain and Alikhan (1979b) noted a significantly increased oxygen consumption at the 10th instar of *Porcellio laevis*. In *Armadillidium vulgare*, Alikhan (1983a, b) found that the oxygen consumption ranged from 13 to 43 $\mu l$ $O_2/mg$ body wt · h in males as compared with 14–59 $\mu l$ $O_2/mg$ body wt · h in females and increased in both during ecdysis. There is evidence for a dependence of $VO_2$ on the food consumed by the isopods (Carefoot 1989). However, this was not seen in *Metoponorthus pruinosus*, as starvation did not cause a change in their respiration rate (Al-Dabbagh and Marina 1985).

# 5 Excretory Organs and Excretion

Under this heading we include organs involved in excretory or osmoregulatory functions as well as we discuss the excretory products in isopods.

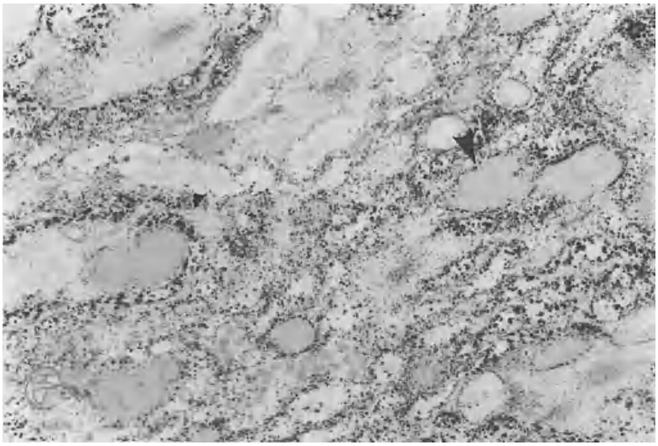
## 5.1 Excretory Organs

Various excretory organs have already been described in isopods by Němec (1896a, b), Ter-Poghossian (1909), Mehely (1931) and Needham (1942). In isopods the antennary glands are located at the base of the antennae above the oesophagus. They are homologous to the maxillary glands of the decapods (Maissiat 1989). These excretory organs were studied in detail by Ter-Poghossian (1909) in several isopod species (*Asellus*, *Platyarthrus*, *Porcellio*, *Oniscus*). They are large, ovoid, about 50–80 μm in size (in *Ligia oceanica*, Maissiat et al. 1980; Maissiat 1989) and vacuolated (Needham 1942). Ultrastructure study reveals an abundance of mitochondria-rich cells (Charmantier 1982). There is a difference among the isopods in the size of this organ. Thus, in *Ligidium* this organ is larger than in other oniscids (Němec 1896a, b).

It is thought that the main function of the antennary glands is involved in the absorption of water from the integument, thereby affecting moulting (Maissiat 1972). It causes the movement of $Ca^{2+}$ ions from the integument into the haemolymph (or hypocalcaemia). It is apparently only involved in a limited way with sodium ion regulation (Charmantier and Trilles 1977b).

The main excretory organs are believed to be the maxillary organs (Strömberg 1964; Charmantier 1982). These are located at the basal portion of the second maxillae (in *Ligia oceanica*, Hewitt 1907). The maxillary gland consists of an end sac, a looping duct and a bladder (Needham 1942).

There are, in addition, several pairs of nephrocyte cells located at the base of the branchiae of *Ligia* (Hewitt 1907). Němec (1896a, b) thought that the channels he observed at the base of the pseudotracheae (in *Porcellio*) were openings of the excretory organs.


5.1

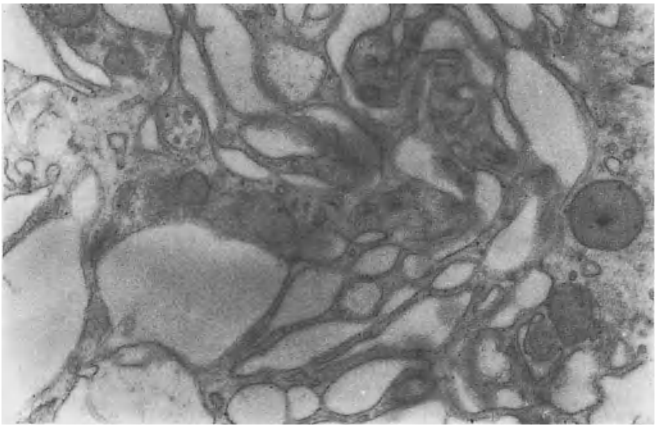

5.2

**Fig. 5.1.** Section through the rectal part of the hindgut of *Armadillo officinalis*, showing reaction product of ATPase activity (*arrows*) along the membranes and surrounding the mitochondria ( × 15000; details in Warburg and Rosenberg 1989)

**Fig. 5.2.** Same as in Fig. 5.1, showing a control section (with vanadate) ( × 15000)

In marine and aquatic isopods the osmoregulating function of the gills is well-known (Babula 1979). While the exopodites are the main respiratory organs, the endopodites are involved in ion transport (Wägele 1982). Apparently, they take part also in the elimination of heavy metal ions (Cu, Hg, Cd) in the marine isopod *Jaera* (Bubel 1976).

Based on ultrastructural features, Kümmel (1981, 1984) described in various terrestrial isopods (*Armadillidium*, *Hemilepistus*, *Porcellio*) pleopodal features pointing to putative osmoregulatory features.

Another organ apparently involved in osmoregulation is the rectal epithelium. This conclusion was based on ultrastructural grounds in some marine and aquatic isopods by Hryniewiecka-Szyfter and Tyczewska (1975). Holdich and Mayes (1975) have suggested that the hindgut of *Porcellio* was the site of osmoregulation of ions and water.

We were recently able to confirm this suggestion by locating ATPase activity in the hindgut cells of *Armadillo officinalis* (Figs. 5.1, 5.2; see Warburg and Rosenberg 1989). This would possibly indicate that the transport of ions takes place there.

## 5.2 Excretion

The terrestrial oniscid isopods excrete much less nitrogen than the fresh water isopods (Wieser and Schweizer 1970). They are largely ammonotelic (Dresel and Moyle, 1950, in *Ligia oceanica*, *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*). Ammonia production varies with age and was lower in juveniles than in older isopods. It showed a diurnal rhythm reaching its peak between 1600 and 2300 hours (Bagatto and Alikhan 1986). Ammonia excretion in *Porcellio spinicornis* was found to be higher in males than in females (Alikhan and Pani 1988). In *Hemilepistus reaumuri* it changed with the food source, from 0.063 mg/isop · day when fed on soil crust and plant material to 0.048 mg/isop · day when fed on soil alone (Steinberger 1989).

Ammonia excretion amounts to over 50% of the total nitrogen excretion: in *Ligia* 83%, in *Oniscus* 47%, in *Porcellio* 57% and in *Armadillidium* 55%. Traces of urea (1%) were found in *Porcellio spinicornis* and of uric acid as well (6% in *Ligia*, 5% in *Oniscus*, 4% in *Porcellio* and 8% in *Armadillidium*). This analysis by Dresel and Moyle (1950) was done on the faecal pellets. When the entire animal was studied, *Armadillidium* was shown to contain ten times more uric acid than *Oniscus*, but still relatively insignificant amounts. Patane and Giuffrida (1962) found uric acid in the tissues of *Armadillidium vulgare*, especially in the organs of Zenker near the antennal gland.

Studying *Oniscus asellus*, Hartenstein (1968, 1970) found that the total diffusible content of ammonia was 1.2 mg% in the body fluid, whereas uric acid made up 11.3 mg% body wt, and most of that (93%) in the body wall. Urea was found in insignificant amounts. Sloan (reported by Hartenstein 1968) found that 10–30% of the ammonia was excreted as gas. It is suggested that ammonia is excreted into the ventral water duct system, becoming volatile (Wieser 1984). The average content of $NH_3$ released via the faeces was 0.84 ng/mg body wt · h, or 200 $\mu$g/10 g during a 24 h period (Wieser and Schweizer 1970). The faecal ammonia content was up to 10% of the total nitrogen release in *Porcellio scaber*. The rest was in gaseous form. Thus, between 0.46 and 1.12 ng ammonia/mg body wt · h was traced in the faecal pellets compared with 2.3–3.25 ng in gaseous form (Wieser and Schweizer 1970). On the whole, the ammonia release of terrestrial isopods was low (Wieser and Oberhauser 1984).

Wieser et al. (1969) found that both *Porcellio scaber* and *Oniscus asellus* released gaseous ammonium twice as much during the spring as in the autumn. The pattern of release was rhythmical, possibly related to their locomotory activity (Wieser 1984). In *Ligia beaudiana*, the ammonia excretion was three to eight times higher in September compared with October (Wieser 1972a), but only when the animals were kept on a moist substrate. The ammonia production rate depended (in *Porcellio scaber*) on the diet (leaf litter). In the body wall, 1.13–17.3 mM ammonia per litre tissue water was detected (Wieser and Schweizer 1972).

# 6 Water and Thermal Balances of Terrestrial Isopods

## 6.1 The Water Balance

The subject has been reviewed by Edney (1957, 1967, 1968, 1977), Cloudsley-Thompson (1975, 1977) and Warburg (1989). Our knowledge is based on studies of about 40 species.

### 6.1.1 Water Content and Water Uptake

The water content of isopods ranges between 60 and 70% (Gere 1962; Ghabbour and Rizk 1979; Warburg 1987a), depending on the physiological state, season, etc. Needless to say, water is essential for life for a crustacean living on land (Edney 1968; Cloudsley-Thompson 1975). Water is taken up mostly via the food (Kuenen 1959). Studying *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*, he found that the latter species was most effective in extracting water from its food. Previously, Spencer and Edney (1954) had shown that these species are capable of an active imbibition of water through both the mouth and anus. Moreover, *Ligia oceanica* was incapable of drinking water. Den-Boer (1961) believed that water uptake seemed to be generated by the physical processes of the osmotic pressure of the haemolymph. The site of water uptake was thought to be through the cuticle, a view supported by Coenen-Stass (1981, 1984a). This is based on his observations on *Hemilepistus reaumuri* cutaneous absorption from saturated air.

There is also a limited amount of water taken up through coprophagy of the faecal pellets (unpubl. observ. on *Hemilepistus reaumuri*). The structure of the hindgut suggests that it is involved in the transport of ions and water (Smith et al. 1969). We were able to show that hindgut cells in *Armadillo officinalis* contain an active $Na^+$, $K^+$/ATPase, thereby indicating its role in the transport of ions and in water uptake (Warburg and Rosenberg 1989). The percentage of water in the pellets was between 43 and 63% (Kuenen 1959). In the burrowing species, *Hemilepistus*, soil moisture within the burrow could provide a source of moisture (Coenen-Stass 1981). A recent report by Wright and Machin (1990) has shown that water uptake takes place across the ventral pleon and the rectum (in *Armadillidium vulgare*, *Porcellio scaber* and *Oniscus asellus*). In *Idotea* the branchial tissue was shown to be the main site of $Na^+$, $K^+$/ATPase activity (Holliday 1988). This agrees well with the ultrastructure of the pleopods (Wägele 1982).

### 6.1.2 The Distribution of Water in Body Compartments

The water content of *Hemilepistus reaumuri* and *Armadillo officinalis* was measured in three different body compartments: cuticle, haemolymph and gut plus gonads (Warburg 1987a). A large part of the body water content was in the cuticle. In *Porcellio scaber* the water content of the cuticle was about 54% (Salminen and Lindqvist 1972). There were also differences between the sexes. The haemolymph water content was higher in female *Hemilepistus* than in male.

### 6.1.3 Loss of Water

The evaporation rate was studied in several isopod species (see Davis 1989; reviewed in Warburg 1989). One of the earliest experiments on the loss of water via the cuticle was carried out on *Porcellio* by Colosi (1933). Later, Miller (1938) studied the survival time of various isopod species under desiccating conditions at different relative humidities. He found that *Armadillidium vulgare* survived longest among the terrestrial species, followed by *Porcellio scaber* and *P. laevis*. It was Edneys' (1951a) study that showed that the evaporation rate of *Armadillidium vulgare, Porcellio scaber* and *Ligia oceanica* increases with temperature. The site of the main water loss was through the pleopodal area. Bursell (1955) suggested that the permeability of the isopod's cuticle was limited by lipids. This subject will be discussed later in this chapter. On the other hand, Mead-Briggs (1956) found no temperature effect up to 55°C on the cuticular permeability of *Oniscus asellus*.

In another isopod, *Venezillo arizonicus*, I was able to show an abrupt increase in evaporation from the whole animal when exposed to 38–40°C (Warburg 1965a). These animals lost very little water compared with all other isopods studied until then. Other desert isopods, *Periscyphis jannonei and Porcellio evansi* (Cloudsley-Thompson 1969; Constantinou and Cloudsley-Thompson 1987), and both *Porcellio olivieri and Armadillo albomarginatus* (Warburg 1989) were all good water-conservers.

The continuous records of water (weight) loss were studied in some Australian isopod species (*Buddelundia* spp.; Warburg 1965b). Bursts of water loss coincided with evaporative cooling of the body temperature. Using a similar principle but a different technique, Quinlan and Hadley (1983) examined *Porcellio laevis* and *Porcellionides pruinosus*. They found that the temperature affected the cuticlar permeability.

Lindqvist (1968) in *Armadillidium vulgare* reached the conclusion that some of the evaporation is due to the activity of the animals and is necessary to counteract the hydration. Moreover, about 34% of the isopod's body water was lost via the mouth (in *Porcellio scaber*, Lindqvist 1972b). Therefore, he concluded that the animal discharges some of its surplus water through the alimentary canal onto the integument (Lindqvist 1971). The rate of water loss is affected not only by temperature, but also by the humidity of the air surrounding it, as was previously shown by Edney (1951a, b). Later, Bursell (1955) and others including my own investigations (Warburg 1965a, b, 1968a) confirmed this observation. The general belief was that the water loss curve followed the curve for the saturation deficit of the air (see also Coenen-Stass 1981). I was unable to confirm this; perhaps in some isopods this is the case, whereas in other species it is not so.

### 6.1.4 The Water-Conducting System of the Isopods

Verhoeff (1917c) described the existence of a channelling system around the tergites of the isopods (see Figs. 6.1–6.5). The function of this was to keep moisture on the surface of the animal. Hoese (1981, 1982a) described this system in several species. The first and more common one was the '*Porcellio*-type'. This is a closed recycling system in which the urine is excreted by the maxillary 'nephridium', spreads through the ventral and dorsal water-conducting systems along the pleopods and is eventually reabsorbed by the gut. Along its path the ammonium in the urine evaporates and, thus, only the water is reabsorbed by the gut.

The second type, the '*Ligia* type', is different in that it is an open system of both urine and water; the mixture flows into grooves on the 6th and 7th pereiopods. Its functions are the same as the '*Porcellio*-type', but it is more wasteful of water. Thus, the water running through the conducting system is conserved.

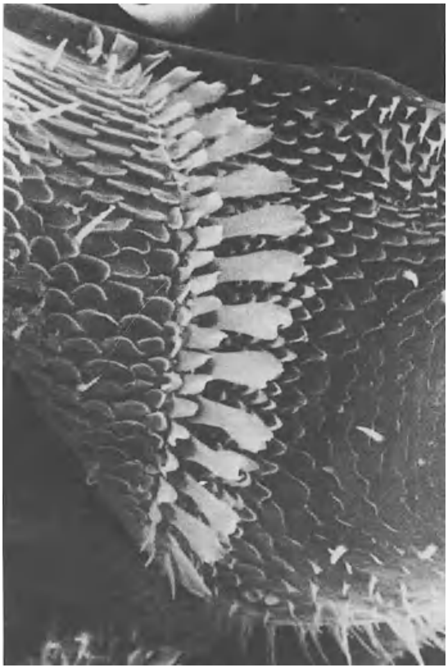
### 6.1.5 The Cuticular Lipids

The presence of cuticular lipids could explain to some extent the remarkably low evaporative water loss of some terrestrial isopods. Although the suggestion that cuticular lipids might be present in the isopodan cuticle has been present in the literature for many years (see Warburg 1965a), they have never actually been located. However, Hadley and Quinlan (1984) were able to establish the presence of traces of wax, hydrocarbons, cholesterol esters and triaglycerols in *Porcellio laevis*. These authors concluded that the lipids, although present in the cuticle of

→

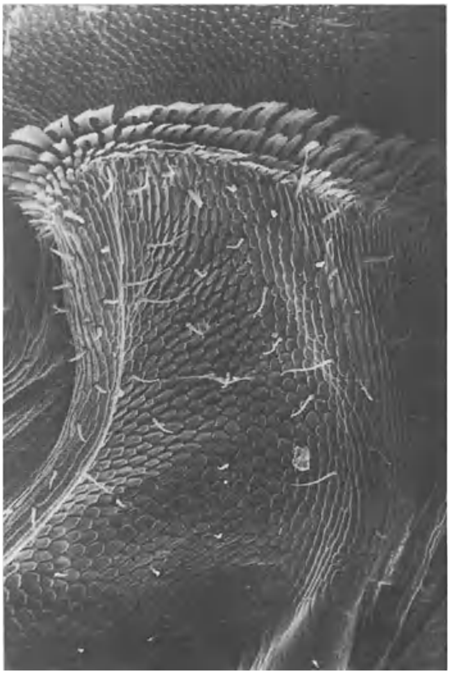
**Fig. 6.1.** Part of the water-conducting system located at the sternites of *Porcellio barroisi* (× 350)

**Fig. 6.2.** Same as in Fig. 6.1 at the tergites of *Porcellio laevis* (× 100)

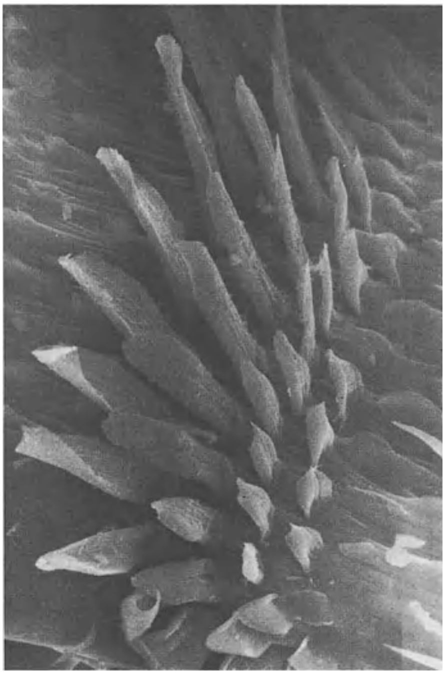


6.1

6.2



6.3



6.4

**Fig. 6.3.** Same as in Fig. 6.1 at the legs of *Porcellio obsoletus ficulneus* (× 150)
**Fig. 6.4.** The water-conducting system between two legs in *Armadillidium fallax* (× 1500)

*Porcellio laevis*, do not provide an effective barrier to water flux. More recently, two desert isopods, *Hemilepistus reaumuri* and *Armadillo albomarginatus*, were analysed (Hadley and Warburg 1986). Numerous components, as well as long-chain, branched molecules were found in the cuticle of *Hemilepistus reaumuri.* These cuticular lipids/hydrocarbons help reduce water loss in these species, and they are very similar in structure to those found in scorpions! Histochemical studies have demonstrated lipids in the cuticle (Figs. 6.6–6.9; Warburg 1989). The treatment of cuticles with acetone has produced differences that could be seen with scanning electron microscopy (Figs. 6.10–6.13; Warburg 1989).

It is of interest to note here that Lindqvist (1972b), on examining *Porcellio scaber* and *Armadillidium vulgare*, found no change in the cuticular permeability during desiccation. The water content of the cuticle in these two species was 53–54% (Lindqvist et al. 1972). In *Oniscus asellus* the cuticle showed a 'rhythm' and 'oscillated' around a 20% water content (Mayes and Holdich 1976). The water content of the cuticle was maintained throughout desiccation. I have observed differences in the water content of the cuticle between two isopod species and between the sexes (Warburg 1987a). Thus, in *Hemilepistus reaumuri*, the male's cuticular water content was 51% compared with 25% in females. In *Armadillo officinalis* males the cuticular water content was 44% compared with 47% of the females. This subject needs further investigation.

### 6.1.6 Haemolymph Osmotic Concentration

The ion concentration in the haemolymph of terrestrial isopods is high (for review see Table 6.1; Table 4, Warburg 1989).

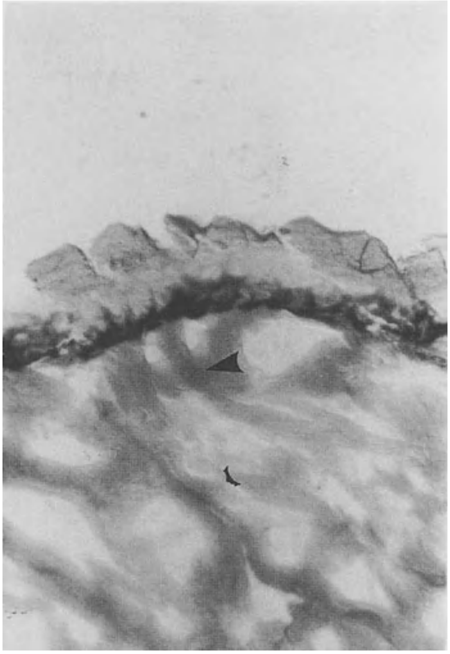
Bateman (1933) studied the haemolymph concentration of *Ligia oceanica* under moist conditions and different concentrations of seawater and found evidence for osmotic regulation. *L. oceanica* was a most efficient osmoregulator at 25°C in seawater (Todd 1963). Widmann (1936) observed in *L. oceanica* differences in the osmotic values between the sexes (slightly higher in females). On the whole, *L. oceanica* has a considerably higher haemolymph osmotic pressure than terrestrial oniscids (Parry 1953). There were also differences in the osmotic pressure during the various seasons (Todd 1963). *Oniscus asellus* and *Porcellio scaber* have shown higher values in winter compared with summer (Widmann 1936). I have recorded seasonal variations in osmolality in *Hemilepistus reaumuri* and *Armadillo officinalis* (Warburg 1987a). The differences in haemo-

→

**Fig. 6.5.** The water-conducting system of *Porcellio obsoletus ficulneus* (×350)

**Fig. 6.6.** Histochemical reaction to lipids (*arrow*) in the cuticle of *Porcellio obsoletus ficulneus*, using Sudan black (×125)


6.5


6.6


6.7

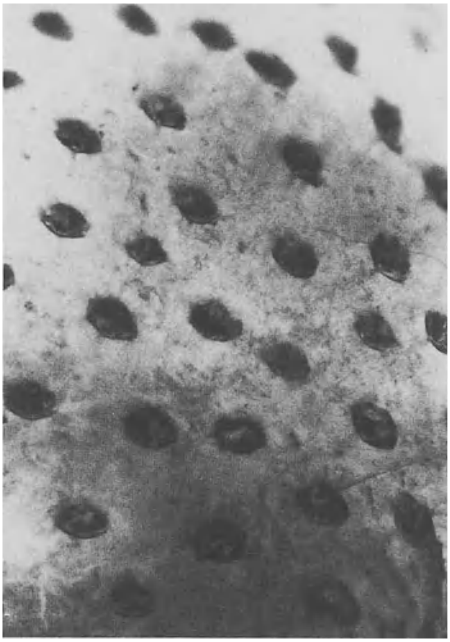

6.8

**Fig. 6.7.** Histochemical reaction to lipids (*arrow*) in the cuticle of *Porcellio obsoletus ficulneus*, using oil-red-o ( × 125)

**Fig. 6.8.** Histochemical reaction to lipids (*arrow*) in the cuticle of *Armadillo albomarginatus* using Sudan black ( × 125)

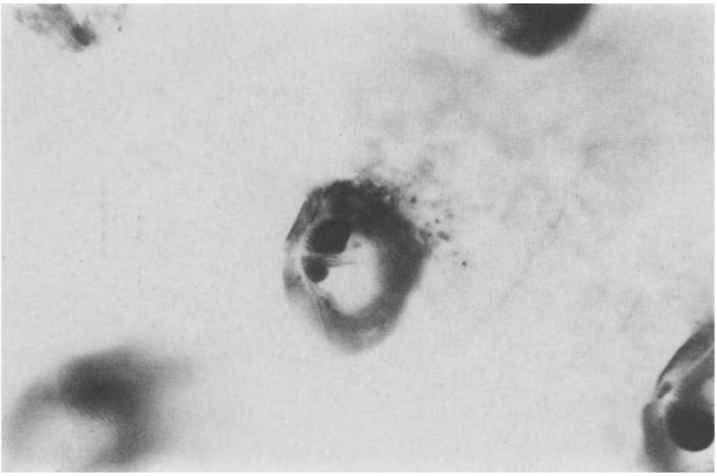


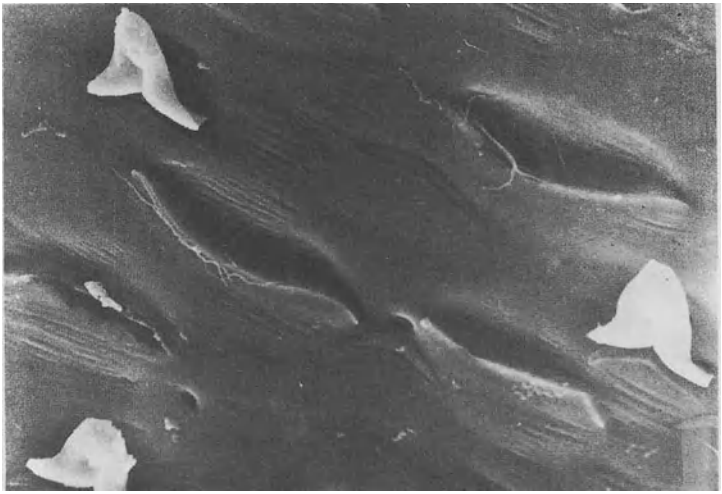
**Fig. 6.9.** Same as in Fig. 6.8 enlarged (×600)

lymph osmolality were more than 20%, and those in ions ($Na^+$ and $Cl^-$) over 30%.

When desiccated, both the haemolymph osmolality and sodium concentration increased in *Hemilepistus reaumuri.* This was observed also by Coenen-Stass (1985) as well as by Price and Holdich (1980c) in *Porcellio scaber*, *Oniscus asellus*, *Ligia oceanica* and *Armadillidium depressum* (Bursell 1955; Holdich and Mayes 1976). Lindqvist and Fitzgerald (1976) suggested that the increased haemolymph concentration was due to a withdrawal of gut fluid. On the other hand, Horowitz (1970) thought that although some water was lost from the muscles, the haemolymph concentration did not rise in *Porcellio scaber.*

Apparently, the nature of the diet affected the haemolymph concentration. The decrease in amino acid concentration in the haemolymph appears to be related to the degree of terrestrialism in isopods (Sevilla and Lagarrigue 1974, 1975; Sevilla 1975). A salt-rich diet increased the blood osmolality and $Na^+$ concentration (Alikhan 1973). Moulting also affected the haemolymph osmolality in *Porcellio scaber* and *Oniscus asellus*, by lowering it (Lindqvist 1970), whereas Parry (1953) found the opposite: it increased the osmolality.

Some isopods have very high osmotic values. Thus, both *Ligia occidentalis* and *L. pallasii* survive in over 100% seawater and are therefore hypo osmotic, whereas in less than 100% seawater they are hyperosmotic (Wilson 1970). The remarkable aquatic-terrestrial isopod, *Haloniscus searlei*, inhabiting brackish water (Williams 1983), equals the brine shrimp, *Atremia salina*, in its osmoregulatory abilities (Bayly and Ellis



6.10

6.11

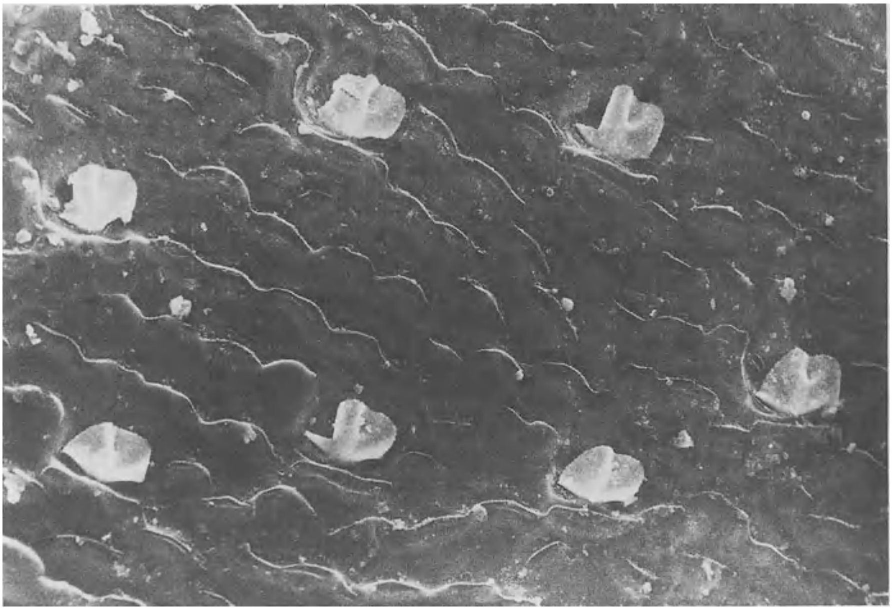
**Fig. 6.10.** Tergite of *Porcellio obsoletus ficulneus* washed in acetone (×1000)

**Fig. 6.11.** Same as in Fig. 6.10, untreated control (×1500)

1969). Vader and De Wolf (1988) described the tolerance of *Armadillidium album* to seawater.

The ions found in the blood of the terrestrial isopod are less concentrated than in *Ligia*, but still higher than in most other terrestrial arthropods. Thus, Lagarrigue (1969) found in *Ligia italica* 849 mEq/l of $Na^+$ (981 mEq/l of $Cl^-$), in *Tylos latreille* 577 mEq/l of $Na^+$ (636 mEq/l of $Cl^-$), in *Porcellio laevis* 267 mEq/l of $Na^+$ (316 mEq/l of $Cl^-$), in *Armadillo officinalis* 239 mEq/l of $Na^+$ (310 mEq/l of $Cl^-$). Similar values were reported for *Armadillo officinalis* and *Hemilepistus reaumuri* (Warburg 1987a, b).

6.12



6.13

**Fig. 6.12.** Tergite of *Armadillo albomarginatus* washed in acetone (×500)

**Fig. 6.13.** Same as in Fig. 6.12, untreated control (500)

## 6.2 Thermal Balance

Edney's (1951a, b, 1953) study was the first to draw our attention to the link between water balance and the body temperature of isopods. Thus, after 30 min at 20°C *Ligia oceanica* was capable of depressing its body

**Table 6.1.** Ionic concentration in the haemolymph of some isopods

| Species | $Na^+$ | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Cl^-$ | Source |
|---|---|---|---|---|---|---|
| *Tylos latreillei* | 577 | 24 | 51 | 110 | 636 | Lagarrigue (1969) |
| *Ligia italica* | 613 | 16 | 70 | 38 | 704 | Lagarrigue (1969) |
| *Porcellio laevis* | 267 | 7 | 33 | 25 | 317 | Lagarrigue (1969) |
| *Hemilepistus reaumuri* | 348–370[a] | | | | 326–444[a] | Warburg (1987a) |
| *Armadillo officinalis* | 239 | 7 | 39 | 32 | 311 | Lagarrigue (1969) |
| | 204–313[a] | | | | 265–380[a] | Warburg (1987a) |

[a]In mM/l, otherwise in mEq/l.

temperature by 2.6°C as compared with 1.5°C by *Oniscus asellus*, 0.4°C by *Porcellio scaber*, and 0.5°C by *Armadillidium vulgare*. At 27°C (for 30 min), *Ligia* had a body temperature 6.8°C lower than the ambient temperature as compared with 2.7°C lower temperature in *Oniscus*, 1.3°C in *Porcellio* and 1.8°C in *Armadillidium*. When a similar experiment was repeated in the sun, *Ligia* depressed its body temperature by 8°C *Oniscus* by 4–5°C, *Porcellio* 2–3°C and *Armadillidium* by 4°C (Edney 1953). *Ligia* had the lowest temperature tolerance and *Armadillidium* the highest. The latter could tolerate 46.5°C for 15 min at 15% relative humidity (RH). On the other hand, *Armadillidium* had the lowest evaporation rate and *Ligia* the highest (Edney 1951a). The upper lethal temperatures tolerated for longer periods (30 min) were 41.6°C for *Armadillidium* and for *Porcellio laevis* (Edney 1964a). These temperatures are considerably higher than those recorded by Tomescu and Radu (1971) for six isopod species. In nature, *Hemilepistus reaumuri* can survive longest at a burrow temperature of 10°C (Dubinsky and Steinberger 1979).

In an attempt to show the direct connection between evaporation and body temperature in isopods, I have studied *Porcellio scaber* and *Buddelundia albinogrisescencs*. The apparatus measuring the weight changes was a Cahn gram-electrobalance accurate to ±0.01 mg, connected to a thermocouple (Warburg 1968a). Thus, simultaneous measurements could be obtained. The relationship between water loss and thermoregulation was more pronounced in *Porcellio*, which nevertheless died sooner and at a lower temperature than *Buddelundia*.

For further discussion on this subject, see Cloudsley-Thompson (1977).

# 7 The Gut, Hepatopancreas and Digestion

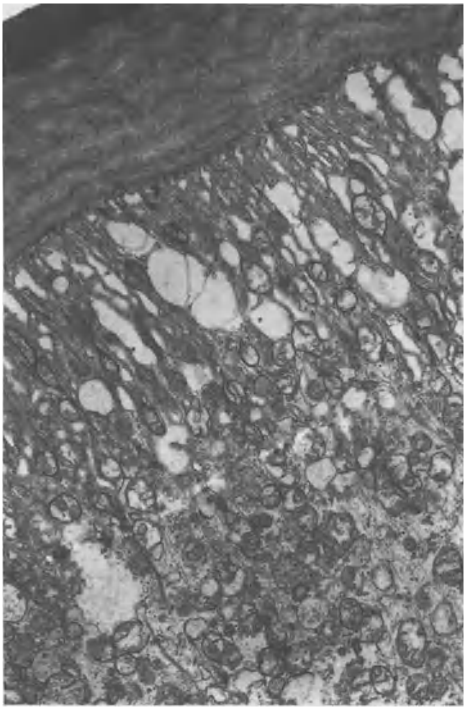
## 7.1 Structure and Function of the Digestive System

The isopodan alimentary canal consists of a straight tube and two pairs of digestive glands or hepatopancreas on each side. The subject received attention in early research (see McMurrich 1898; Schönichen 1899; Murlin 1902 for early literature). Later, studies by Schmitz and Schultz (1969), Alikhan (1968, 1969a, 1971) and Hassall and Jennings (1975) confirmed the general structure outlined. The digestive tract consists of a foregut, midgut and hindgut (Hassall 1977). A detailed account has been given by Hames and Hopkin (1989). The oesophagus contains acid polysaccharides (AB-positive at pH 2.5, see Lane 1988). The typhlosole runs along the dorsal part of the anterior gut (Hames and Hopkin 1989). This was not noticeable in *Ligia* (Nicholls 1931b). A peritrophic membrane (intima) lines the interior of the gut's anterior side as well as its posterior end, but not its middle part (Lane 1980, 1988; Bettica et al. 1987; Brecko et al. 1991). In *Cylisticus convexus* there is no evidence for a midgut (Brecko et al. 1991). The gut undergoes moulting simultaneously with the whole animal (Palackal et al. 1984).

Liquid and food particles are drawn back into the foregut via the typhlosole. There they are filtered and passed on to the lumen of the hepatopancreas. The hindgut cells are rich in mitochondria, and an elaborate RER lies inbetween numerous infoldings (Vernon et al. 1974; Palackal et al. 1984; Figs, 7.1, 7.2). These cells were presumed to have an osmoregulatory function (Coruzzi et al. 1982; Palackal et al. 1984). We have recently produced indirect evidence of ATPase activity in the basolateral membranes of these cells (Warburg and Rosenberg 1989).

The stomach was described in detail by Flasarova (1967) in several isopod species. Storch (1987) and Storch and Štrus (1989) described the double filtering system of bristles in *Procellio scaber*, and in other isopods as well. The ingested food is filtered twice through both primary and secondary filters (Storch 1987).

Various parts of the gut show different enzymatic activities (Hassall and Jennings 1975). Thus, esterases are produced in the ceca and pass into the anterior hindgut. This difference is also reflected in different pH values (noted by Nicholls 1931b) in *Ligia oceanica*. Thus, alkaline phopsphatase activity was shown in the stomach (Lane 1988), whereas maltase


7.1

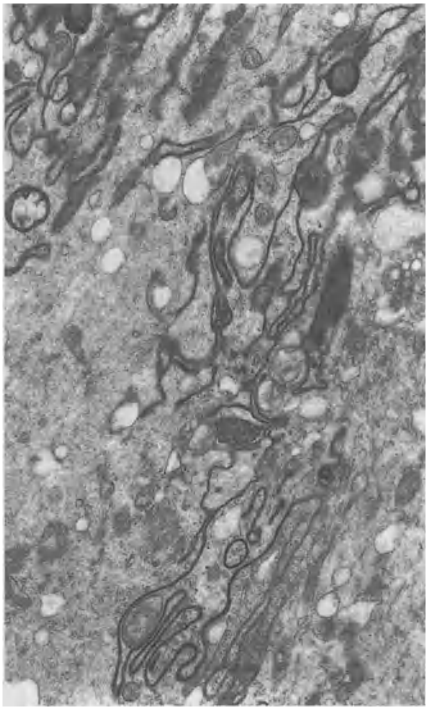

7.2

**Fig. 7.1.** Part of the hindgut of *Armadillo officinalis* showing the intima (*upper left*) and the numerous infoldings and mitochondria (×4000)

**Fig. 7.2.** Same as in Fig. 7.1, enlarged, note the infoldings and mitochondria (×7000)

activity appears to be confined to the hindgut (Alikhan 1969a). On the other hand, lipids are absorbed by the large midgut cells (Hryniewiecka-Szyfter and Storch 1986; Storch 1987). They are not found in the hindgut but reach the midgut cells from the haemolymph of the hepatopancreas (Hrnywieczka-Szyfter and Storch 1986; Storch 1987).

## 7.2 The Hepatopancreas

The four digestive glands of the hepatopancreas were described by Frenzel (1884) in *Oniscus murarius*. The subject was discussed and reviewed by Nusbaum-Hilarowicz (1921). The hepatopancreas is in fact a pair of bilobed glands connected to the gut between the fore- and hindgut (Bettica et al. 1984). It contains two cell types, S and B (Patrick 1926). These have recently received much attention (Szyfter 1966; Storch and Lehnert-Moritz 1980; Storch 1982, 1984; Prosi et al. 1983; Bettica et al.

1984; Fogarty and Witkus 1989). The hepatopancreas secretes digestive fluids and thus functions as a midgut (Clifford and Witkus 1971; Storch and Štrus 1989).

The large cells (B-type) contain abundant microvilli, RER, dictyosomes and secretion bodies. They secrete enzymes and absorb nutrients (Bettica et al. 1984). These enzymes are largely phosphatases. They also contain lipid droplets that provide an energy reserve (Morgan et al. 1990). They undergo a certain ultrastructural change during starvation (Storch and Lehnert-Moritz 1980; Storch 1984) and alter also when the isopods are fed on different diets. They reduce in size, their mitochondria become enlarged, while their matrix decreases. The lysosome size and number increase (see Štrus et al. 1985). All these changes are reversible once the animal feeds (for a detailed discussion, see Storch 1984). The B-cells change also during the moulting cycle (Wieser 1964a). They secrete the first time before the posterior moult has started and a second time after the anterior moult has ended (see Table 4, Wieser 1964a).

Most of the hydrolytic enzymatic activity was localized in the hepatopancreas (in *Oniscus asellus*, see Hartenstein 1964b). Glycogen was found there as well as in the gut (and integument). The glycogen levels dropped in starved isopods (*Procellio laevis*, Alikhan 1972b). Four kinds of carbohydrates were found in the hepatopancreas: amylase, $\alpha$-glucosidase, $\alpha$-galactosidase and $\beta$-glucosidase. Alikhan (1969b) located phosphomonoesterase in the hepatopancreas and the gut (63% acid phosphatase and 71% alkaline phosphatase). The acid phosphatase level was highest (37%) in the hindgut, and the alkaline phosphatase level was highest (45%) in the midgut (of *Porcellio laevis*, see Saleem and Alikhan 1974).

The activities of acid and alkaline phosphatase changed during the development and moulting cycle of *Procellio laevis* (Alikhan and Saleem 1977; Bettica et al. 1984). They were found to be involved in the degradation of the nymphal tissue and the synthesis and differentiation of the adult tissue.

On the other hand the dehydrogenase activity of *Oniscus asellus* was confined to the typhlosole region of the gut (Hartenstein 1964a). In *Tracheoniscus rathkei* some enzymatic activity of 1,4-$\alpha$-glucans and 1,3-glucans was evident in the digestive tract as was activity of xylene and carboxymethyl-cellulose (Kukor and Martin 1986).

## 7.3 Metal Storage

The smaller cells (S-type) which are located inbetween the B-cells lack this enzymatic capability but are capable of storing material, mostly heavy metals (see Prosi et al. 1983). The metals are mostly stored in membrane-bound organelles (Storch 1984; Prosi and Dallinger 1988).

Thus, $Cu^{2+}$ (1.8–89%) was stored in vesicles in the S-cells, whereas $Ni^{2+}$ (73–89%) was stored in the cytoplasmic lumen of these cells (Alikhan and Storch 1990). Recently, Dallinger and Prosi found heavy metals in the lysosomal fraction of the cells. *Oniscus asellus* appears to tolerate high amounts of $Ni^{2+}$ (Alikhan 1990) but will eventually die of $Zn^{2+}$ poisoning (Hopkin 1990). The concentration of $Zn^{2+}$ was twice as much in *Porcellio scaber* than in *Oniscus asellus* at the same site (Hopkin et al. 1989). Starvation leads to a high accumulation of $Cu^{2+}$ (Alikhan 1972b). Similarly, pollution caused an increase in metal levels in isopods (Joose and Van Vliet 1984). Several metals are stored extracellularly (Prosi et al. 1983). For example, $Fe^{2+}$ is stored in the gut (Hopkin 1990). It accumulates twice as fast in *Procellio scaber* as in *Oniscus asellus*. Both $Mg^{2+}$ and $Mn^{2+}$ are stored in the hepatopancreas. The magnesium concentration was 10–44%, and that of manganese was 46–76% (Alikhan and Pani 1989). These two metals were also found in the exoskeleton (Alikhan 1989). Apparently, there is a negative relationship between the amount of heavy metal stored and the energy reserve which becomes reduced (Morgan et al. 1990). The cells are also involved in the uptake and storage of catabolites (uric acid, copper sulphate); thus, they are similar to insectan nephrocytes (Marcaillou et al. 1986).

# 8 Resource Utilization and Energy Expenditure

## 8.1 Food Preferences and Feeding Habits

In general, most isopods are omnivorous, feeding on detritus (Gere 1956), fungi, live or dead plants or animals (Paris and Sikora 1967; Edney et al. 1974; Nair 1976a), as well as their own faecal pellets (Paris 1963; Hassall and Rushton 1982). Thus, *Metoponorthus pruinosus* is omnivorous in the wild, feeding on decomposing litter, and is occasionally cannibalistic (Nair et al. 1989). The gut of *Ligidium hypnorum* contained 23% plant material, 27% fungal material and 38% detritus (Strüve-Kusenberg 1989). Feeding on decomposed leaves is made possible by bacteria in both the gut and hepatopancreas of the isopod (studies on *Oniscus asellus*, Griffith and Wood 1985; Wood and Griffith 1988). *Protracheoniscus amoenus* is of major importance as a decomposer in the forests of Hungary (Pobozsny 1978). The subject of feeding behaviour has been reviewed by Hassall and Rushton (1984).

Isopods are also very efficient grazers (Blinn et al. 1989). Although most isopod species studied so far (about 20 species, see Warburg 1987b) have a wide range of food items available to them, some may be more restricted. This, however, could cause a serious handicap in competition for 'choice' items.

Most studies on food preference have been conducted on two common isopod species: *Procellio scaber* and *Armadillidium vulgare* (Watanabe 1978). These studies have shown that the palatability of plants increased if broken down by microorganisms (Hassall and Sutton 1984). It seems that isopods increase decomposition by stimulating microbial growth while processing leaves through their alimentary canal (Hassall et al. 1987). It was recently shown that *Porcellio scaber* 'preferred' leaves with fungi (Stöckli 1990).

Some isopods seem to 'prefer' certain kinds of leaves. This was clearly shown in two armadilidiid and two philosciid species (Dudgeon et al. 1990; Ma et al. 1991b). Thus, the leaf litter of dicotyledonous plants was 'preferred' over grasses (Rushton and Hassall 1983a). It has been shown that monocotyledonous leaves cause mortality in *Armadillidium vulgare* for an unkown reason (Rushton and Hassall 1983a, b). No particular preference for any kind of food could be found in *Procellionides pruinosus* (Nair et al. 1989).

On the other hand, Szlavecz and Maiorana (1991) found that green leaves (with a high nitrogen content) were 'preferred' over decayed leaves or 5-week-old leaf litter. In *Oniscus asellus* most litter was acceptable (Piearce 1989); however, Gunnarson (1987) demonstrated selective feeding on different parts of maple leaves depending on the bacterial growth. One species, *Hemilepistus reaumuri*, was shown to be a soil feeder (Shachak et al. 1976). Isopods ate larger quantities when offered a mixture of various kinds of leaves (Ma et al, 1991a). The ability of isopods to break down organic acids is a very important function in the soil formation process (Neuhauser et al. 1974; Neuhauser and Hartenstein 1976).

Apparently, there is also a tendency to shift from one type of food to another. Thus, during drought some isopods cease being vegetarians and become scavengers. This was observed in *Armadillidium vulgare* (Paris and Sikora 1967). The food preference can take the form of feeding more often on one plant species than on another (Biwer 1961). *Porcellio scaber* 'preferred' poplar leaves, and *P. laevis*, *Morus indica* leaves (Nair 1976a). Similarly, *Hemilepistus reaumuri* 'prefers' *Hammada* sp. and *Artemisia* sp. leaves and branches (Shachak et al. 1976), among the 48 different food items that they can recognize (Shachak and Newton 1985). *Hemilepistus* feeds on many plant species, fresh and dry, as well as on lichens and algae. It is also a scavenger feeding on insect and isopod corpses and faeces from various sources (Warburg et al. 1984). Similarly, the marine isopod, *Idothea baltica*, shifts from feeding on algae (*Fucus*) to feeding on live or dead animals (Cruz 1963). Adult *Tylos granulatus* 'preferred' dry algae to fresh (Kensley 1974), whereas *Armadillidium vulgare* fed on both dry and fresh leaves of *Sylibum marianum* and *Vicia sativa* (Paris and Sikora 1967). These changes in diet are to some extent seasonal and are therefore reflected in the fatty acid composition of the isopods (Zar and White 1969).

In the various plant species that composed the diet of *Metoponorthus pruinosus*, the carbohydrate contents of the leaves did not differ, but the protein and nitrogen values varied (Nair et al. 1989). Apparently, the degree of palatability of some leaves depends on their phenol content. This was shown by preference tests on 25 plant species by Neuhauser and Hartenstein (1978). Such experiments were conducted also on the preference of *Ligia* for various red and brown algae (Carefoot 1973a, 1979). *Porcellio scaber* demonstrated a preference for feeding on decayed pine needles (Soma and Saito 1983).

A special kind of feeding habit was shown in *Platyarthrus*, where the isopods were nutritionally linked to their ant host (*Lasius flavus*; Williams and Franks 1988). They fed on the ant's faeces or on regurgitated infrabuccal pellets.

Growth is greatly affected by the food quality (Merriam 1971). Fresh leaves undoubtedly have a positive effect on the growth of *Oniscus asellus* (Beck and Brestowsky 1980). Growth and fecundity were higher when isopods were fed on dicotyledonous leaves than when fed on monocotyledonous leaves (Rushton and Hassall 1983b). On the other hand, no difference was shown in the growth rate of *Porcellionides pruinosus* when fed on different food items (Nair et al. 1989).

## 8.2 Coprophagy

Isopods seem to prefer fresh pellets to decayed or dried ones. Apparently, they gain some moisture from these pellets (unpublished observation on *Hemilepistus reaumuri*). The enhanced microbial activity in the faeces increased their nutritive value (Hassall and Rushton 1982). Recently, Gunnarsson and Tunlid (1986) fed *Oniscus asellus* on its faecal pellets after having fed them on wood pieces. Immediately after this, the gut microorganism counts were lower than before, as both lysis and growth of bacteria took place in the isopodan gut. However, the amount of nitrogen did not change. Thus, feeding on its own faecal pellets did not fulfill the isopod's own nitrogen requirements.

It is possible that by feeding isopods on faecal pellets they gain nutritive materials, enzymes as well as minerals. Preventing coprophagy caused retarded growth in *Porcellio scaber* (Hassall and Rushton 1982) and in *Philoscia muscorum* (Hassall and Rushton 1985). This could be corrected by feeding the isopods on fresh carrots (Hassall and Rushton 1982). Coprophagy is of importance especially when the isopods were fed on fresh rather than fallen leaves (Hassall and Rushton 1982, 1985).

## 8.3 Food Requirements

Food requirements of *Ligia pallasii* were studied by Carefoot (1984a, b). He found that they require, among other food items, carbohydrates (starch, cellulose), $Ca^{2+}$, $Mg^{2+}$, phosphorus, $Cu^{2+}$, $Ni^{2+}$, $Zn^{2+}$ and $Fe^{2+}$ but did not require vitamins (Carefoot 1984a). No growth took place on amino acids alone (Carefoot 1984b); however, histidine and theramine were indispensible amino acids (Carefoot 1984a, b). Sodium was assimilated at high rates in juveniles of *Philoscia muscorum* compared with adults, whereas potassium was assimilated at a lower rate (Hassall and Sutton 1985). *Tracheoniscus balticus* assimilates 79–84% of Ca radioisotope from its food (Radu et al. 1971).

Copper was one of the constituents frequently named as a trace mineral of importance (Wieser 1965, 1966, 1968, 1978; Dallinger and Wieser 1977). However, the isopod's copper balance can be maintained without resorting to coprophagy (White 1968). Moreover, both $Ca^{2+}$ and $Zn^{2+}$ are assimilated irrespective of coprophagy (Coughtrey et al. 1980).

The lack of copper may cause retarded growth in *Porcellio scaber* (Hassall and Rushton 1982). The copper content of the isopod varies with that of the environment (Wieser et al. 1976; Dallinger 1977), as well as during the seasons of the year (Oguro and Sakai 1971; Wieser et al. 1977). In general, the copper content of adult isopods was higher than that of younger ones (Alikhan 1972a). In *Porcellio laevis* most of the copper was contained in the hepatopancreas (32–78 g/g dry wt. compared with 3–42 g/g dry wt. in the haemolymph).

In the hepatopancreas copper is localized in special cells (Alikhan 1972; Hryniewiecka-Szyfter 1972). These are small cells (described by Wieser 1968, and then in detail by Prosi et al. 1983) or 's'-cell which contain three types of inclusions: (1) special spherical inclusions with a heavy metal precipitate, (2) electron-dense inclusions and (3) very small granules containing heavy metals ($Cu^{2+}$, $Pb^{2+}$, $Zn^{2+}$). The subject has been summarized by Hopkin and Martin (1982, 1984) and was discussed in Chap. 7. It appears that these cells are a sink for heavy metals ($Zn^{2+}$, $Cd^{2+}$, $Pb^{2+}$) in general, and not only for $Cu^{2+}$ (Hopkin et al. 1986). The amount of these heavy metals found in isopod tissue is related to the amount found in their environment.

## 8.4 Food Consumption, Assimilation and Energy Expenditure

Food consumption increased with temperature (Gere 1956; Schneider and Krczal 1984). Also, the kind of food utilized may have an influence on the total food consumption (see Table 8.1). Isopods consumed more when the leaf litter was more extensively decayed (Gere 1956). *Armadillidium vulgare* consumes more of low quality food (Hassall and Rushton 1984). *Hemilepistus reaumuri* was shown to feed on loess crust and on various organic matter substrates (Shachak and Yair 1984; Shachak and Newton 1985). When feeding on plants alone, it utilizes up to 3.4 mg per individual per day, as compared with 25 mg when feeding on soil (Shachak et al. (1976). *Hemilepistus* consumed most when fed on soil crust and the desert plant *Hammada scorpia* (Steinberger 1989). On the other hand, isopods consume more food when fed on a mixture of leaves (Dudgeon et al. 1990).

Species vary in their food consumption (Table 8.1). This may be due to different metabolic rates, energy expenditure or ambient conditions. In *Cirolana harfordi*, Johnson (1976) found that 65% of the assimilated energy was used on activity (respiration) and on maintenance.

It is of great importance to run these experiments on animals of the same weight and sex feeding on a single food item at the same time of day and during the same season. The rate at which isopods absorb or assimilate varies with the food items (see Table 8.2). Moreover, there is a great

**Table 8.1.** Consumption efficiency (mg consumed/mg body wt · day) of various isopod species under varying conditions

| Species | Conditions | Food items | Consumption efficiency | Source |
|---|---|---|---|---|
| *Idotea baltica* | M | *Fucus vesiculosus* | 1.1 | Salemaa (1987) |
| | F | *Fucus vesiculosus* | 2.6 | Salemaa (1987) |
| *I. chelipes* | M | *Fucus vesiculosus* | 0.5 | Salemaa (1987) |
| | F | *Fucus vesiculosus* | 0.7 | Salemaa (1987) |
| *I. granulosa* | M | *Fucus vesiculosus* | 1.0 | Salemaa (1987) |
| | F | *Fucus veisculosus* | 1.6 | Salemaa (1987) |
| *Tylos punctatus* | | *Macrocystis pyrifera* | 4–5 | Hayes (1974) |
| *Protracheoniscus politus* | | *Ouercus* | 1.9–4 | Gere (1956) |
| *Oniscus asellus* | | *Ouercus rubra* | 0.11 | Neuhauser and Hartenstein (1978) |
| | | *Betula alleghaniensis* | 15.04 | |
| *Porcellio scaber* | | *Thuja occidentalis* | 0.75 | Neuhauser and Hartenstein (1978) |
| | | *Ailanthus altissima* | 24.45 | |
| | | *Pinus thunbergii* | 2.0 | Soma and Saito (1983) |
| | Decayed | *P. thunbergii* | 19.2 | |
| *Armadillidium vulgare* | | *Acer saccharum* | 0.08 | Neuhauser and Hartenstein (1978) |
| | | *Salix nigra* | 11.08 | |
| | 23°C | *Sylibum marianum* | 23.3 | Hubbell et al. (1965) |
| | 10°C | *S. marianum* | 9.6 | |

M, Male; F, Female

difference between data obtained in the lab and those obtained from the field. The latter are about seven times higher (Hubbel et al. 1965). *Ligia pallasii* was found to assimilate 78% of the algae *Ulva* sp. and 55–76% of brown algae *Hereocystes* sp. (Carefoot 1973a). Was this due to the different nourishing values of these plants? In *Philoscia muscorum*, assimilation was about 99.4% (Hassall and Sutton 1977). On the other hand, Bize and Célérier (1986) found that assimilation rate varied between 25.9 and

**Table 8.2.** Assimilation efficiency (assimilation/consumption) of various isopod species (in %)

| Species | Food item | Assimilation efficiency | Source |
|---|---|---|---|
| *Tylos punctatus* | *Macrocystis* | 64 | Hayes (1974) |
| *Ligia dilatata* | *Macrocystis* | 5.5 | Koop and Field (1981) |
| *L. pallasii* | *Ulva* | 78 | Carefoot (1973a) |
|  | *Hereocystes* | 55–76 | Carefoot (1973a) |
| *Protracheoniscus politus* | *Ouercus* (20°C) | 4.9 | Gere (1956) |
|  | Decomposed | 17.7 | Gere (1956) |
| *Oniscus asellus* | *Acer* (20°C) | 16.2 | Hartenstein (1964b) |
|  | Birch (22°C) | 15–48 | Dallinger and Wieser (1977) |
| *Porcellio spinicornis* (males) | Carrot (20°C) | 81.2 | Bukhari and Alikhan (1984) |
| (females) |  | 98.7 | Bukhari and Alikhan (1984) |
| *P. laevis* | Birch (22 °C) | 7–76 | Dallinger and Wieser (1977) |
| *P. scaber* | *Pinus* | 41 | Soma and Saito (1983) |
|  | Decomposed | 4.2 | Soma and Saito (1983) |
|  | Birch (22°C) | 15–43 | Dallinger and Wieser (1977) |
| *Hemilepistus reaumuri* | *Hammada* | 51–82 | Shachak et al. 1976) |
|  | Soil | 25–35 | Shachak et al. (1976) |
| *Cylisticus convexus* | Lettuce (20°C) | 60 | Reichle (1967) |
| *Armadillidium vulgare* | *Sylibum*(23°C) | 6–13 | Hubbell et al. (1965) |
|  | In the field (10°C) | 53–75 | Hubbell et al. (1965) |
|  | Lettuce (20°C) | 64 | Reichle (1967) |

42.5%. In *Armadillidium vulgare* and *Cylisticus convexus* the assimilation value was 73% (Reichle 1967, 1968). On the other hand, Striganova et al. (1981) noted that in *Armadillidium vulgare* the assimilation efficiency was 48.5% (Striganova et al. 1981). Apparently, isopods utilized about 5–8% of this for growth (Striganova and Kondeva 1980). However, all these various data depend on the varying food items. Thus in *Hemilepistus reaumuri*, assimilation efficiency dropped from 51–82% when fed on *Hammada* spp. branches to 25–35% when fed also on loess soil (Shachak et al. 1976). Similar results are seen in other desert isopods (see Kozlovskaja and Striganova 1977).

Apparently, the efficiency of assimilation increased also with the concentration of copper in the food. This was proven for *Porcellio scaber*, *P. laevis* and *Oniscus asellus* (Dallinger and Wieser 1977; Debry and Lebrun 1979). With the increased assimilation rate of copper-enriched leaf litter, there was an increase in weight gain in *Oniscus asellus* (Debry and Muyango 1979). Thus, in *Ligia oceanica* 46.4 KJ/$m^{-2}y^{-1}$ was devoted to growth, but only 3.8 $kJ \cdot m^{-2} \cdot y^{-1}$ to reproduction (Willows 1987c).

Energy expenditure by isopods is largely devoted to growth. It increased with rising temperatures (in *Porcellio scaber*, see Wieser 1964b). Thus, the energy proportion allocated to growth in *Hemilepistus reaumuri* was 54% in males and 52% in females (Shachak 1980). However, as was shown in *Hemilepistus reaumuri*, during the reproductive period females spend about the same amount of energy on growth and reproduction (Shachak 1980). On the other hand, *Armadillidium vulgare* females spend over 8% more energy on reproduction than on growth (Lawlor 1976a, b), whereas Reichle (1967) found the opposite pattern: the same isopod species spent 13 Cal/g more on growth than on reproduction. In *Philoscia muscorum* the respiratory rate increased during the breeding season (Hassall 1983). This conflicting evidence is difficult to resolve. What may be needed is comparative studies on females of the same cohort, both virgins and mated ones, studied over a period of time with samples taken periodically for energetic studies. This should give an answer on the energy expenditure of non-reproducing (virgin) females, assuming most of it is on growth. This figure can then be compared with one for males (presumably very similar). It can also be compared with the figures obtained for females at different reproductive stages. The difference between the two values should indicate the net difference in energy expended on growth as compared with reproduction.

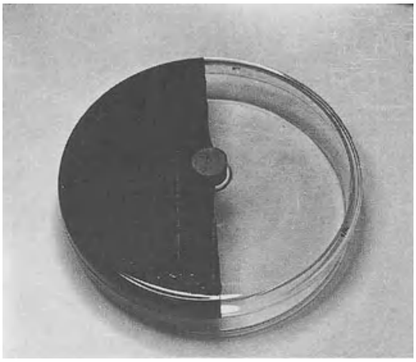
# 9 Behavioural Responses

## 9.1 Experimental Procedure

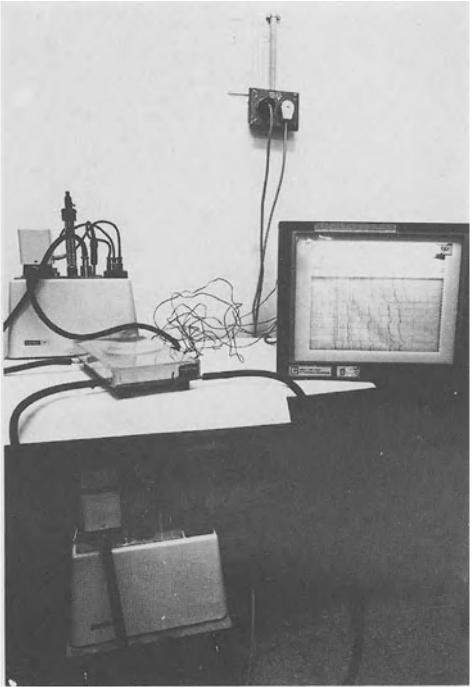
The behavioural responses of isopods have been studied since the turn of the century. The experimental conditions need to be held constant strictly enough to merit comparison in spite of the differences in technique. The procedure involved in my own studies consisted principally of two criteria (Warburg 1964), firstly, the behaviour of an individual and secondly, the behaviour of a small group of animals (up to 10). With the first criterion I used two procedures: measurement of the actual time spent in one place (condition) and counting the number of times (*n*) the animal shifted from one alternative to the other. Thus, I could calculate the percentage of time spent at each 'place' (or 'residence time'), as well as the speed at which an animal travelled from one place to another. These analytical indices could be used whether one used a choice-chamber apparatus (Fig. 9.1) or a temperature gradient apparatus (Fig. 9.2). In addition, it was possible to calculate the intensity of response (I); for details of these procedures, see Warburg 1964; Warburg and Berkovitz 1978a, b). With the experiments on groups of animals, another criterion was used of counting once every minute the positions held by each member of the group, without taking actual time measurements of their whereabouts.

## 9.2 Chemoreception

Earlier work was reviewed by Wenig (1903). Abraham and Wolsky (1930a) described putative chemoreceptors on the 2nd maxilla of *Porcellio scaber* and *Armadillidium vulgare*. They studied in detail 15 species of isopods and noted chemoreceptors on the terminal segment of their antennae (Abraham and Wolsky 1930b). The fact that isopods respond to their own specific odours was shown by Kuenen and Nooteboom (1963) in *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*. These species also respond to the odours of other species. Fischbach (1954) demonstrated that isopods react to odours produced by members of their own species. In that way, they are helped in locating suitable shelter. The



9.1



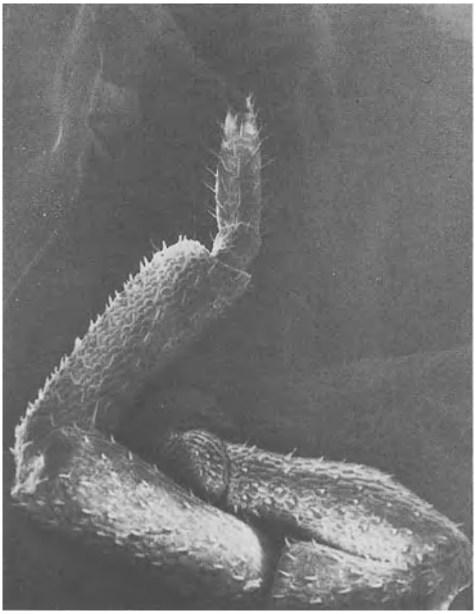
9.2

**Fig. 9.1.** Choice-chamber apparatus for studying photoreaction; animal is introduced from the top

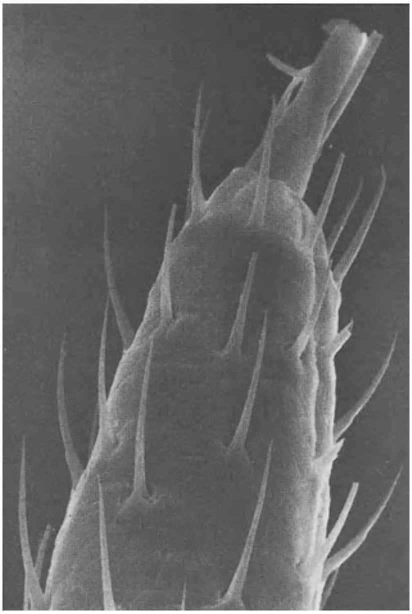
**Fig. 9.2.** Thermopreferendum apparatus connected to a potentiometer (*top, right*) recording temperature at several points on the metal plate of the apparatus. Cold water (*front*) from a refrigeration unit (*below*) and warm water from a thermal heater (*top, left*) are circulated under the plates

myrmecophilous isopod, *Platyarthrus*, responded positively to formic acid (Brooks 1942) but was found also in the nests of ants that do not secrete formic acid (O'Rourke 1950). A peculiar pattern of behaviour was recently described by Williams and Franks (1988), when *Platyarthrus* specimens were observed to climb on top of ants.

Contact chemoreceptors are located on the terminal segments of the flagellum of *Oniscus asellus* and *Porcellio scaber* (Figs. 9.3–9.6). Two types of sensillae were described by Gupta (1962): basiconic and trichoid. About 100 putative chemoreceptors were described on the antennae of *Ligia oceanica* (Alexander 1977). These sensory hairs, presumed to be chemoreceptors, open through a subterminal orifice or the apex, leading to a distal shaft and a canal to the cell body (see Figs. 9.7, 9.8). Similar chemoreceptors were located in *Metoponorthus sexfasciatus* (Mead et al. 1976) and on the antennae of *Ligidium hypnorum* and *Porcellio scaber*



9.3



9.4

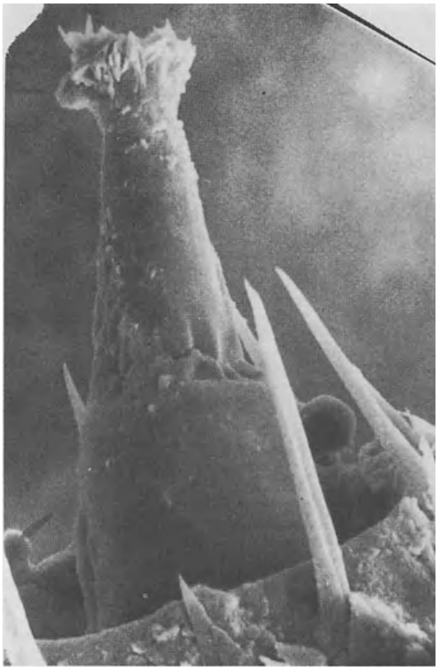
**Fig. 9.3.** Antenna of *Armadillo tuberculatus* (×100)

**Fig. 9.4.** Tip of the flagellum of the antenna of *Porcellio chuldaensis* (×1000)

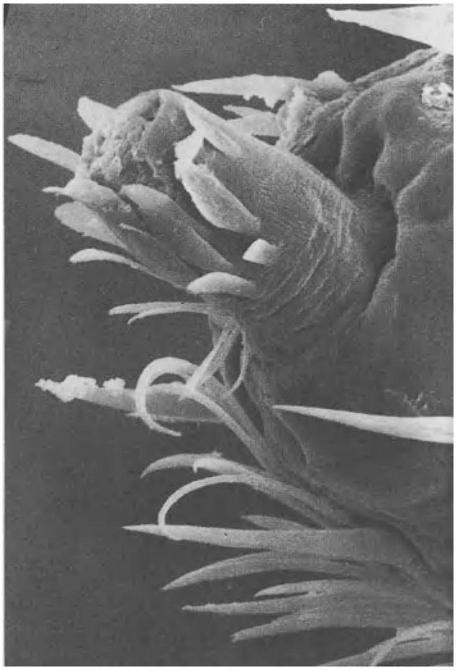
(Risler 1977, 1978). The antennular aesthetasc hairs of the marine isopod *Saduria entomon* have the structure of a chemoreceptor (Pynnönen 1985).

Their detailed ultrastructure has been described in *Asellus aquaticus* (Heimann 1984). It was shown that dissolved substances penetrate the poreless cuticle instantaneously. The chemoreceptors on the last segment of the second antennae of *Hemilepistus reaumuri* and other species was first described by Schneider (1973) and Schneider and Tschakaroff-Schuster (1978). These were later studied in detail by Seelinger (1977, 1983; see also Fig. 9.6). Two receptor types enable the isopods to distinguish between butyric acid and amines. Other receptors are gustatory in nature, some of them capable of tasting sugars and amino acids. There is evidence that some of the tricorn sensillae (Figs. 2.7–2.9) are contact chemoreceptors in *Ligia exotica* (Hatanaka 1989).

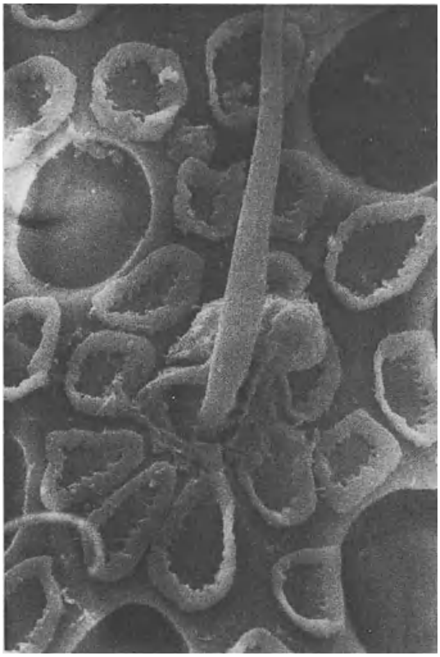
Hoese (1989) has presented evidence that the apical organ of the second antenna can perceive chemical and taste stimuli. The antennae move continuously in particular ways (Hoese and Schneider 1990, 1991). Three different kinds of movements were recognized: parallel, antiparallel and displaced phase. The chemoreception is mediated by the fluid excreted through the channels.



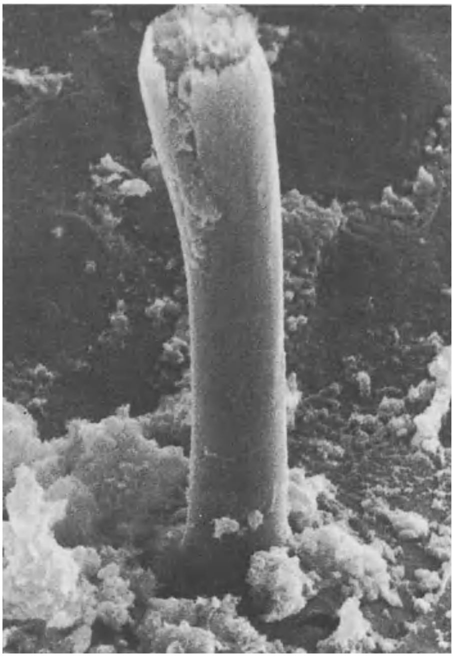
9.5



9.6



9.7



9.8

**Fig. 9.5.** Tip of the flagellum of the antenna of *Hemilepistus reaumuri* (×750)

**Fig. 9.6.** Tip of the flagellum of the antenna of *Porcellio laevis* (×1500)

## 9.3 Hygroreaction

Gunn (1937) found that *Porcellio scaber* responded to the humidity of the air. The isopod was more active in dry air and came to rest in saturated air. *Ligia italica* is sensitive to differences of 3% RH, in the high humidity range (Perttunen 1961). This sensitivity could possibly be due to special hydroreceptors on the thorax (Jans and Ross 1963).

Later, Waloff (1941) found that the activity of the isopod while moving, their speed of movement, and the duration of their resting periods in between were all related to humidity (up to 68% RH). This was shown in the three common species *Porcellio scaber*, *Oniscus asellus* and *Armadillidium vulgare*. Gunn (1937) and Waloff (1941) have shown that the change in the number of turns per unit time is the main mechanism of hygroreaction. The increase of this value in dry humidities caused the animal to move until it located a high humidity where it could come to rest. On the other hand, the orientation response of *Armadillidium vulgare* is stronger at the boundary region between the dry and the humid (Sörensen and Bell 1986). Increased desiccation caused a rise in the intensity of hygroreaction (Cloudsley-Thompson 1956a).

As the response to humidity is also affected by temperature (Cloudsley-Thompson 1956b), several workers suggested that perhaps the saturation deficit of the air could be the main stimulus (in *Oniscus* and *Porcellio*, see Miller 1938; Cloudsley-Thompson 1956a). However, this point has not been resolved, and at least in some isopods the response appears to be towards relative humidity and not saturation deficit (Warburg 1964).

Putative hygroreceptors leading to the hygroreaction were supposedly located on the tip of the antennae of *Porcellio* (Risler 1977). It was later suggested that a receptor functioning as a proprioceptor acts as an indicator for changes in haemolymph pressure (Haug and Altner 1984a), thereby indicating changes in water content. However, mechanoreception could also be responsible in mediating such a stimulus (Haug and Altner 1984b).

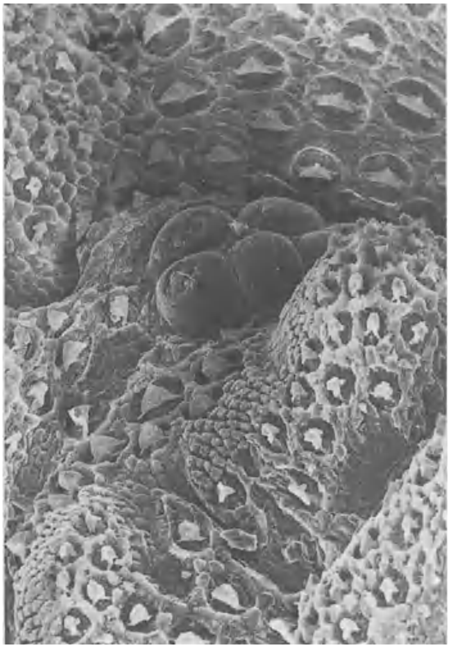
In *Platyarthrus* the response to humidity is stronger than the negative photoreaction (Mathes and Strouhal 1954). It may also be affected by other ambient conditions (Warburg and Berkovitz 1978a in *Armadillo officinalis*). The humidity response is less pronounced in darkness (Cloudsley-Thompson 1952, 1956b). In the oak-wookland pillbug, *Armadillo officinalis*, light plays a major role in stimulating the isopod and thus affects the normal hygroreaction (Warburg and Berkovitz 1978a). Another pillbug, *Armadillidium vulgare*, is normally positively hygrokinetic, and only rarely, when temperatures are high (above 35 °C), does it

◄———

**Fig. 9.7.** Chemoreceptor (?) of *Bathytropa wahrmani* (×1000)

**Fig. 9.8.** Same as in Fig. 9.7, (×1500)

9.9



9.10

**Fig. 9.9.** Eye of *Hemilepistus reaumuri* (×35)

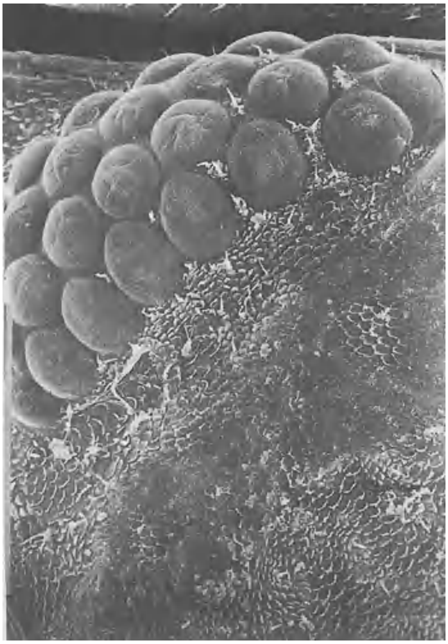
**Fig. 9.10.** Eye of *Armadillo tuberculatus* (×200)

become restless and thus appears to act negatively hygrokinetic (Warburg 1964). This is apparently the general behavioural pattern of mesic-inhabiting isopods. The more xeric ones (e.g. *Venezillo arizonicus*) are more influenced by light conditions than by humidity (Warburg 1964).

To conclude, isopods from the littoral zone and from mesic habitats are in general positively hygrokinetic, whereas isopod species from xeric or arid habitats are less responsive to humidity conditions except when the humidities become very low (Warburg 1968b).

The physiological condition of the isopods also has some effect on their hygroreaction. Thus, in the spheromatid, *Gnorimosphaeroma oregonensis*, the humidity response depends on the isopod's osmotic condition (Standing and Beatty 1978). Similarly, the state of dehydration of the isopod affects its hygroreaction. In *Ligia italica*, its moisture condition largely affects its hygroreaction (Perttunen 1963). Desiccated animals are known to reverse their normal humidity response (Cloudsley-Thompson 1952, 1956b; Lindqvist 1868, 1972a). This was also shown in *Armadillo officinalis* (see Warburg and Berkovitz 1978a).

9.11



9.12

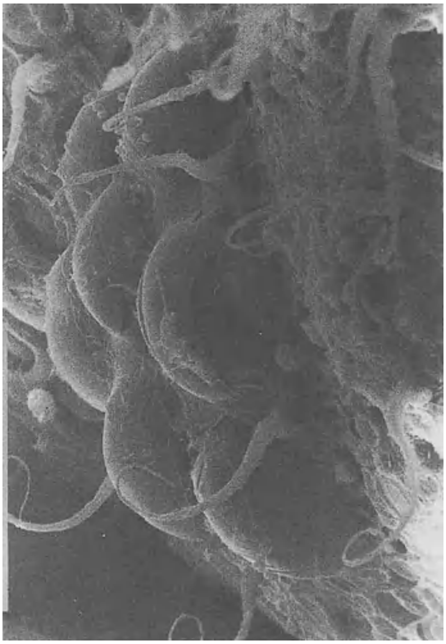


**Fig. 9.11.** Eye of *Porcellio olivieri* ( × 150)

**Fig. 9.12.** Eye of *Bathytropa wahrmani* ( × 750)

## 9.4 Photoreaction

The ommatidia of *Ligia exotica* contain seven retinular cells, of which one is sensitive to blue light, another to UV and the remainder to green wavelengths (Hariyama and Tsukahara 1985; Figs. 9.9–9.12). Apparently, the sensitivity to green light increases at night, whereas the UV sensitivity increases during the day (Hariyama et al. 1986). In addition, there are median ocelli whose function is unclear (Martin 1976). The Isopod's response to light is presumably a cue to where appropriate microclimatic conditions prevail. Recently, isopods were shown to perceive well the low light intensities (Nilsson and Nilsson 1981).

Isopods are by nature nocturnal (Cloudsley-Thompson 1974). Cole (1907) noted the negative photic response in *Oniscus*, as did Torrey and Hays (1914) in *Porcellio* and Müller (1925) in a number of other species. Henke (1930) was the first to describe how temperature affected the photoreaction. Bauers (1953), following the experiments with *Porcellio scaber*, *Oniscus assellus* and *Armadillidium vulgare*, found that they became increasingly negatively phototatic with rising temperature, as did *Ligia italica* (Perttunen 1961). The desert pillbug, *Venezillo arizonicus*, was under normal conditions negatively photokinetic regardless of temperature and humidity conditions. The xeric pillbug *Armadillo officinalis* is negatively photokinetic. Animals reversed their response to become positively photokinetic when temperature rose. (Figs. 9.13, 9.14; Warburg and Berkovitz 1978b). *A. officinalis* became somewhat less negative in its response to light at temperatures over 30 °C. This was reflected in its residence time in the shade (Figs. 9.15, 9.16) and in the number of shifts (Fig. 9.17). Other isopod species are normally photonegative, becoming somewhat less so when the temperature rises (Warburg 1987a, b).

Moisture conditions appear to affect the response to light. Thus, *Tylos latreille* became less negatively photoreactive when out of water (Warburg 1987b). In *Ligia italica* the photonegative reaction was reduced after desiccation (Perttunen 1961).

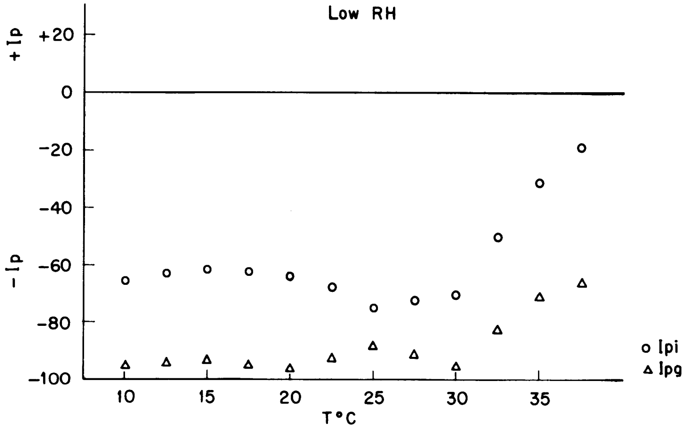


**Fig. 9.13.** Response of *Armadillo officinalis* to light (at low relative humidity, RH). *Ipi* is the intensity index of an individual and *Ipg*, of a group of 10 animals. Animals became less negatively phototactic in their response when the temperature rose (details in Warburg and Berkovitz 1978b)

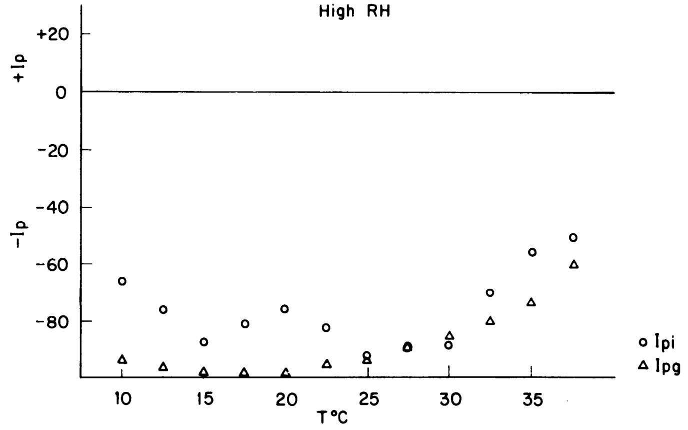


**Fig. 9.14.** Same as in Fig. 9.13 at high RH

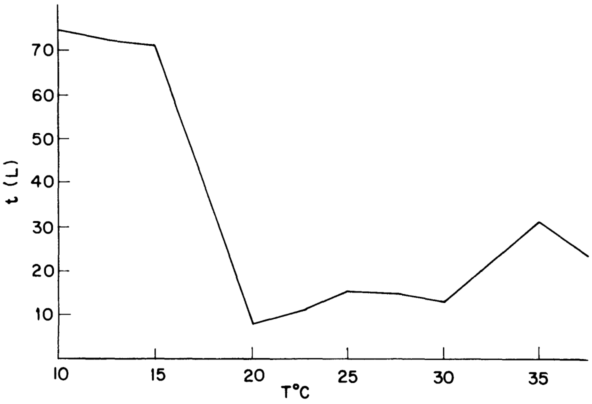


**Fig. 9.15.** The period of time *Armadillo officinalis* pillbugs stay in light ['t(L)'; *Residence Time*] when at different temperatures. This period is greatest at low temperatures

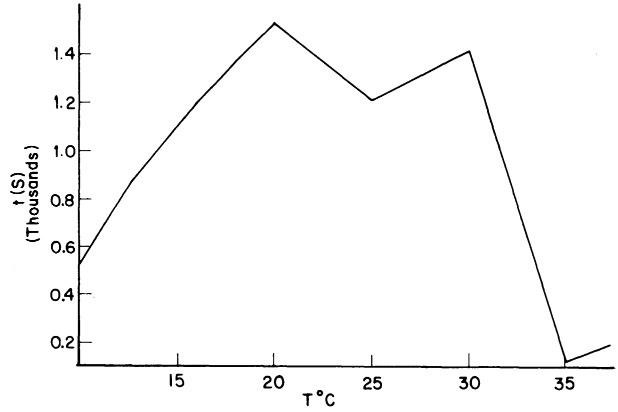


**Fig. 9.16.** Same as in Fig. 9.15, but in the dark ['t(S)']. This period is longest between 20 and 30 °C

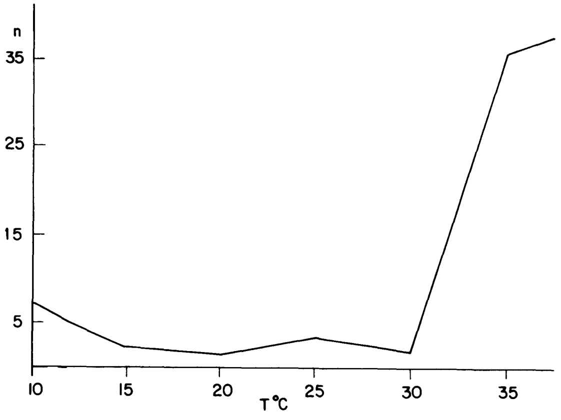


**Fig. 9.17.** The number of times an individual *Armadillo officinalis* pillbug shifted from light to dark. The number of shifts increased greatly at high temperatures

## 9.5 Thermoreaction

The response to temperature is largely a measure of activity changing with temperature. The result is that isopods are less active (or mobile) at a certain optimal temperature range (Refinetti 1984). Some isopods are more active regardless of the temperature (*Oniscus asellus* and *Armadillidium vulgare*, Warburg 1964). Others were less stimulated by the temperature increase (*Venezillo arizonicus*, Warburg 1964).

*Porcellio*, *Oniscus* and *Armadillidium* aggregated at the lowest temperature available to them (Barlow and Kuenen 1957) but *Sphaeroma*, at the highest temperature available (Elkaim et al. 1980). In a study of the marine isopod *Saduria*, the temperature selected was 15 °C (Kivivuori and Lagerspetz 1990). The mechanism for this response involved shifting less when moving inside the apparatus and lowering the speed of movement when temperatures were low. *Venezillo*, on the other hand, behaved in the opposite way, lowering its response when the temperature was high (Warburg 1964). I have described some differences between the males and females of *Hemilepistus reaumuri* in their thermal response (Warburg 1987b).

## 9.6 Mechanoreception

The proprioceptors located in the pereiopods of *Ligia oceanica* (measuring 20–40 μm each) are responsible for mechanoreception (Alexander 1969). They are capable of responding to the pereiopods or limb movement velocity and position (see Alexander 1970; Fig. 2.14). They are found also on the uropods (Alexander 1971; Stutt and Laverack 1979). Recently, Niida et al. (1990) described stretch receptors on the thorax of *Armadillidium vulgare*. Risler (1976) located chordotonal organs which are also proprioceptors on the 2nd antennae of *Armadillidium nasutum*. The response to mechanical stimuli is mediated by tricorn sensillae located on the dorsal tergite (of *Ligia exotica*, Hatanaka 1989).

## 9.7 Orientation

When isopods are made to move inside a passage ending in an abrupt turn, they are capable of correcting the direction in which they move (Schäfer 1986). This 'reverse turning response' apparently helps them in their orientation (Schäfer 1982). This turn alternation is brought about by differences in the leg movement rhythm on each side of the body (Hughes 1989).

A number of isopod species have been studied in respect of their orientation capabilities. Thus, *Tylos granulatus* was shown to avoid the breaking waves (Ondo 1958), and *T. latreille* is capable of orienting itself towards the sea (Mead and Mead 1972/73) and towards a slope away from the sea (Hamner et al. 1968). Both *Tylos granulatus* and *T. capensis* burrow around the tide mark and move up and down the tidal waves (Kensley 1974).

*Porcellio scaber* can orient itself and even detour large objects (10 cm) while moving to its objective (Ludwig 1978). *Armadillidium vulgare* travels on average 13 m during a summer day's foraging activity (Paris 1965), whereas *Hemilepistus reaumuri* can move very long distances (over 1 km). *Hemilepistus* navigates successfully towards its burrow (Hoffmann 1984a; Linsenmair 1984). It spends some time in locating suitable sites for excavation, in which the isopod pair can grow and reproduce. It locates its burrow by a combination of the sun's position, polarized light and landmarks (Hoffman 1983a, 1984a, b), in particular the faeces embankment surrounding the burrow (Hoffman 1985a). Its movement pattern is spiral-shaped (Hoffman 1983a). The final identification of its burrow is by perceiving the specific odour through chemoreceptors located on the terminal segment of the antennae (Hoffman 1983b). The 'family badge', a specific pheromone, enables each member of the family to be identified (Linsemair 1985, 1987; Schildknecht et al. 1988). This genus (*Hemilepistus*) is the only isopod species in which a family pattern of life form is maintained (Linsenmair and Linsenmair 1971; Schneider 1971) and where each member of the family 'recognizes' the other members through specific odours (Linsenmair 1984, 1985). It is possible that this social association among isopods is a result of their aggregation trait (Schneider and Jakobs 1977).

## 9.8 Rhythmic Activity

Rhythmic activity related to tidal or lunar rhythms was observed in a number of intertidal isopods: *Excirolana chiltoni* (Enright 1972, 1976; Klapow 1972b), *Idotea baltica* and *I. granulosa* (Hørlyck 1973), *Eurydice pulchra* (Jones and Naylor 1970; Hastings and Naylor 1980; Hastings 1981; Reid and Naylor 1985), and *Pseudaega punctata* (Fincham 1973, 1974). The rhythm was affected by lunar cycles of 26–33 days as well as by temperature. Similar lunar rhythms were observed in *Tylos granulatus* (Kensley 1972, 1974), where emergence was at night at low tide only (Ondo 1958, 1959; Tongiorgi 1968/69; Marsh and Branch 1979). During the daytime the animals dug into the sand where the moisture was about 1% (Holanov and Hendrickson 1980), returning to the sea at 0400 hours (Tongiorgi 1968/69). This animal is strictly nocturnal (Iga and Kitamura 1975), and this way it conserves water (Imafuku 1976).

Among the terrestrial isopods only in *Hemilepistus*, the desert isopod, is there a description of a rhythmic activity pattern changing with the seasons (Bodenheimer 1935; Cloudsley-Thompson 1956a; Schneider 1975). Previous studies have shown that the rhythmic activity of *Oniscus asellus* is not related to the moisture conditions (Cloudsley-Thompson 1952). Further studies are needed to see whether the phenomenon is more general and occurs in other isopods as well.

## 9.9 Thigmokinesis and Aggregation

The response to contact with a substrate or with another animal is termed the thigomotactic response. If an animal seeks such response actively, it displays thigmokinesis by orienting itself to come into contact with another animal or an inanimate body. In isopods the response was identified in the studies by Allee (1926). The contact between isopods appears to be a form of grooming. I have observed this in *Armadillo officinalis*; it could be related to moulting. The grooming phenomenon was described in terrestrial amphipods (Holmquist 1985).

Friedländer (1964) showed that thigmokinetic behaviour in isopods (*Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare*) varies with the species and is more pronounced in the more mesic species. Furthermore, when the humidity is low, thigmokinesis increases. As a result isopods aggregate in the more humid place (Allee 1926; Farr 1978). In *Porcellio scaber* no aggregation was observed in the dry alternative (Cloudsley-Thompson and Constantinou 1987). This phenomenon of aggregation is initiated by dry air and maintained by both hygrokinesis (Friedländer 1965) and the presence of a suitable microhabitat (Farr 1978).

There is some evidence that excretion products cause aggregation in isopods. Thus, Schliebe (1991) suggests that ammonia is an aggregating stimulus for *Oniscus asellus*. On the other hand, the faeces as well as regions of the hindgut contain the aggregation factor (Takeda 1980, 1984). This was shown in a series of experiments with *Tylos granulatus*, *Ligia exotica*, *Ligidium japonicum*, *Porcellio scaber* and *Armadillidium vulgare*. Aggregation was shown by Takeda (1984) to reduce oxygen consumption and metabolic rate. The pheromone is not a protein (in *Porcellionides pruinosus*) and is apparently not smaller than several ten thousands of Daltons (Ebisuno et al. 1982).

## 9.10 Social Interactions

In one isopod species, *Hemilepistus reaumuri*, a higher form of social interaction was observed (Linsenmair and Linsenmair 1971; Schneider 1971; see review in Linsenmair 1987). This desert isopod forms monogamous pairs that construct a burrow in which they raise their family. The pair provides food particles which are carried into the burrow. They also clean the burrow from faecal pellets, which are carried outside and dropped in a circle surrounding the entrance of the burrow. The male guards the burrow's entrance from intruders. In February the family is dissolved, and the juveniles disperse to a distance between 10 and 100 m from their burrow. They will then form new pairs and excavate a new burrow where they will raise a family. The entire life cycle lasts 18 months (details in Linsenmair 1989).

# 10 Distribution Patterns of Isopod Species in Different Habitats

## 10.1 The Distribution of Isopods

One of the most striking aspects of isopod biology is their wide distribution pattern. They are most commonly found in cryptozoic microhabitats under stones or bark of trees or in the upper layer of soil within mesic habitats (Fig. 10.1). Rather rarely, they are abroad on the ground's surface during the daytime (exceptions to this will be discussed later). Thus, most of the earlier studies (Herold 1925; Verhoeff 1931; Miller 1938; Meinertz 1944) were largely concerned with the different patterns of distribution exhibited by various isopod species. Herold (1925) tried to arrange the various isopod species found in different habitats and relate their distribution to moisture conditions or other climatic factors. This was followed by Verhoeff's (1931) attempt to demonstrate an ecological

**Fig. 10.1.** *Armadillo officinalis* under a stone in a pine forest (a julid millipede is shown, too)

**Fig. 10.2.** The seashore and dune habitats of *Tylos* sp. and *Armadillidium fallax*

**Fig. 10.3.** Hills along the coastal plains habitat of *Armadillidium fallax. A. marmoratus*, *Agabiformius* spp., *Metoponorthus pruinosus* and *Porcellio laevis*

meaning to the isopod distribution pattern in Germany and the Mediterranean lands. Thus, *Porcellio laevis* was found under warmer conditions than *P. dilatatus*, or *Armadillidium vulgare* was found in more stony habitats than *A. zenckeri*, inhabiting mostly meadows.

Miller (1938) arranged the isopod species found in the California Bay region in a series starting at the seashore and running all the way up to the hills (Figs. 10.2, 10.3). Thus, he found four species on the sandy beaches, whereas two *Ligia* species inhabited the rocky shores, and two *Philoscia* species were found in the grass fields. Several additional isopod species could be found higher up in the hills. A similar zonation of isopods was described in the coast of Somali (Chelazzi and Ferrara 1978). Schmalfuss (1978b) noted how *Ligia simoni* extending its distribution from the sea shore to the forest, as if recapitulating an evolutionary step.

Another pattern of microhabitat dispersion was described by Brereton (1957) for an isopod population within an Oxford garden. Thus, among eight species found there, *Porcellio scaber* was noted during the winter at the tree base, whereas *Oniscus asellus* took refuge under stones. On the other hand, *Philoscia muscorum* 'favoured' leaf litter, whereas *Trichoniscus pusilus* 'preferred' dead pieces of wood.

Similar preference patterns were described by Beyer (1957/58, 1964) for isopods in the forests of Germany. The wettest parts of the deciduous forest were inhabited by *Armadillidium pulchellum*, *A. vulgare* and *Porcellio conspersum*, whereas in the oak forests, *Protracheoniscus saxonicus* was present. In the meadows Beyer found *Porcellio scaber*, whereas *Oniscus asellus* was found in the forests together with *Ligidium hypnorum* and *Trichoniscus pusillus.*

Radu and Tomescu (1976) studied an isopod community in Rumania, and Davis and Sutton (1977a) described the isopod community of a dune habitat in England. There *Philoscia muscorum* 'preferred' the more stable dunes in contrast to *Porcellio scaber* and *Armadillidium vulgare*, who were found in moving dunes. This pattern could be related to their burrowing ability. The habitat moisture condition affects other isopods. In Japan Tsukamoto (1977) demonstrated a separation pattern between two *Ligidium* species, one of which was found at the bottom of a hilly slope where it was moister. A similar effect of microclimate was described in *Trachelipus nodulosus* in the windy grassland of southern Hungary (Hornung 1984). These isopods were clumped in depressions in the soil which had a more humid microclimate.

Soil moisture is probably the main factor affecting the distribution and abundance of isopods (Heeley 1941/42; Warburg et al. 1984). In *Hemilepistus* the spatial distribution of burrows is related to soil moisture (Shachak and Yair 1984). Both the geological formation and precipitation were of significance here (Kheirallah 1980a; Brown and Steinberger 1983; Coenen-Stass 1984b).

Recently, the microdistribution of isopods was studied in different microhabitats within one habitat (Dangerfield and Telford 1991). It was found that microsite heterogeneity was of great significance, accounting for the distribution pattern of *Aphiloscia* in a tropical forest. Hassall and Dangerfield (1989) found differences in the distribution of isopods within the grassland. These could be related to the intensity of grazing that took place there. Thus, *Porcellio scaber* was more abundant on heavily grazed plots, whereas *Philoscia muscorum* was found on lightly grazed ones, and *Armadillidium vulgare* on both. In the Hungarian grassland, *Trachelipus nodulosus* and *Armadillidium vulgare* were found in depressions, showing an unique pattern of patchy distribution. Isopods seem to aggregate in the more humid microsites within these depressions (Hornung 1989, 1991).

Three species typical of the Mediterranean region were most abundant in all the areas studied within that region. These isopods, *Armadillo*

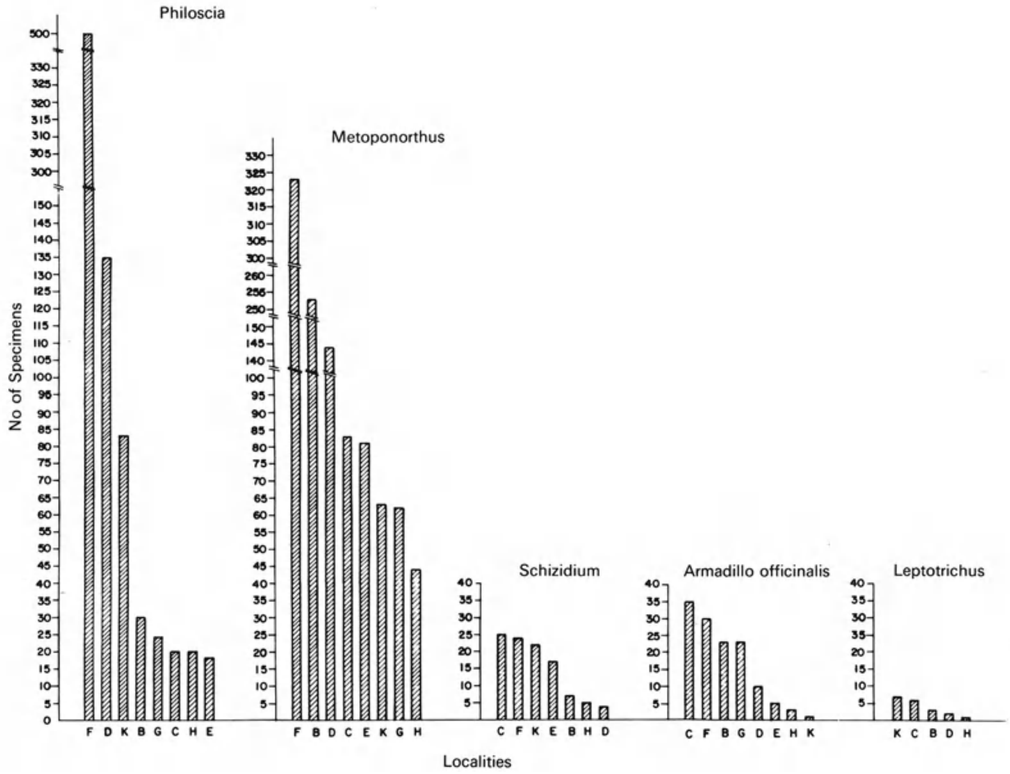


**Fig. 10.4.** The abundant isopod species in the Mediterranean region of northern Isreal: *B*, *E*, *H*, different habitats on Mt. Carmel; *C*, *D*, *F*, different habitats in the oak woodland of the Lower Galil; *G*, dense woodland in the Upper Galil; *K*, grassland in semi-arid habitat on Mt. Gilboa

**Table 10.1.** Number of specimens of the 6 most abundant species within 1000 $m^2$ plots in 4 different areas of the Mediterranean regions in northern Isreal

| Species | Gilboa Mt. (500) | L. Galil (650) | Mt. Carmel (750) | U. Galil (1000) | Total |
|---|---|---|---|---|---|
| *Armadillo officinalis* | 4 | 126 | 87 | 23 | 240 |
| *Metoponorthus pruinosus* | 87 | 580 | 552 | 62 | 1281 |
| *Chaetophiloscia* sp. | 170 | 696 | 190 | 24 | 1080 |
| *Schizidium tiberianum* | 30 | 88 | 57 | — | 175 |
| *Agabiformius* sp. | 8 | 12 | 5 | — | 25 |
| *Porcellio obsoletus ficulneus* | 3 | 32 | 11 | 19 | 65 |
| Total No. of specimens | 302 | 1534 | 902 | 128 | 2866 |
| Total No. of isopods per visit | 21.3 | 24.3 | 25.2 | 14.3 | 22.7 |

No. in brackets = annual rainfall in mm
L. Galil, Lower Galil; U. Gallil, Upper Galil
Details in Warburg et al. (1984)

**Fig. 10.5.** Grassland habitat on Mt. Gilboa. Habitat of a large number of isopod species (see Warburg et al. 1978)

**Fig. 10.6.** Oak woodland habitat in the Lower Galil. Habitat of 15 isopod species (see Warburg et al. 1978)

**Fig. 10.7.** Dense Garigue type of Mediterranean habitat inhabited by very few isopod species

*officinalis*, *Metoponorthus pruinosus* and *Chaetophiloscia spp*, comprised the bulk of the isopod population (see also Table 10.1, Figs. 10.4–10.7). It is of interest to note that the total number of isopod species was highest (14 species) in areas with comparatively low rainfall, the lower Galil Mts. and Mt. Gilboa with 650 and 500 mm rainfall, respectively. It was lowest (five species) in areas with very high (1000 mm) rainfall (Mt. Meron in the Upper Galil; see Table 10.2, Fig. 10.8).

This is an outcome of a 2-year-long study in the Mediterranean region of northern Israel (details in Warburg et al. 1978). Within this region eight sites were studied, ranging from grassland habitats in the xeric Gilboa Mts. (with 500 mm rainfall; Fig. 10.5) to woodland in the Upper Galil (Mt. Meron with 1000 mm rainfall). In between these two extremes additional sites were studied within the oakwoodland and the dense garigue bush vegatation of Mt. Carmel (750 mm rainfall; Fig. 10.6), and the Lower Galil hills (650 mm rainfall; Fig. 10.7). In these areas a total of about 3000 isopod specimens belonging to 16 species were collected. The species diversity ($H' = -\sum Pi \log e Pi$) ranged between 0.73 and 1.48 (details in Warburg et al. 1978). Pi is the probability that a certain species is found in a population of species within a certain habitat; in other words, the proportional share of this species in the species assemblages within a given habitat. It was highest in the areas with the lower rainfall. This of course does not mean that the same pattern exists in more xeric habitats or in arid regions. There, the number of isopod species is much smaller, although some of them are rather abundant (Table 10.2).

The phenology of the Mediterranean region isopods has also been recently studied in a pine forest in the Lower Galil (Cohen 1988; Fig. 10.8). *Armadillo officinalis* was the most abundant isopod species found there. Both *Chaetophiloscia* sp. and *Agabiformius* spp. were largely abundant in spring, whereas *Metoponorthus pruinosus* was found throughout most of the year except in the summer.

**Table 10.2.** The number of known isopod species[a] in different regions in Isreal

| Zoo-botanical region | Geographical region | Precipitation (mm) | Species |
|---|---|---|---|
| Mediterranean region | Coastal plain | 700 | ~5 |
| | Mt. Carmel | 800 | ~10 |
| | L. Galil Mts. | 650 | ~14 |
| | Upper Galil Mts. | 1000 | ~5 |
| | Mt. Gilboa | 500 | ~14 |
| Arid region | Jordan Valley | 250 | ~7 |
| | Negev Desert | 50–100 | ~7 |

[a] The species number is a conservative estimate

**Fig. 10.8.** Planted pine forest in the Mediterranean region, inhabited by 5 isopod species, with *Armadillo officinalis* the most dominant one

## 10.2 Dispersion Patterns of Isopods within the Same Habitat

Both moisture conditions of the soil and humidity conditions of the air are of great significance to the isopods and affect their dispersion. Thus, the amount of precipitation affects the distribution as well as the abundance of isopods due to its effect on soil moisture and air humidity. Temperature and light conditions are two additional environmental factors affecting the dispersal of isopods. The vertical movement up and down trees and inside the soil was first described by Cole (1946), Brereton (1957) and Den Boer (1961). In the deciduous forests of Europe, isopods (*Porcellio scaber*) moved up the trees in summer and down into the soil in autumn. This phenomenon is known in a number of isopod species, but all from the temperate region, none from the more arid regions. It is affected by both temperature and humidity conditions as well as sand dune habitat (Davis et al. 1977).

There is, in addition, a horizontal type of movement (in *Porcellio*) on the soil surface taking place in spring and autumn (Den Boer 1961) and during the summer (in *Armadillidium*, see Paris 1963). During that period, *Armadillidium vulgare* can move 13 m within 12 h, whereas during winter it moves less than 2 m/day.

**Fig. 10.9.** Wandering porcellionids (probably *Porcellio* sp.) during an outbreak, in the Upper Galil in early summer

We have recently observed a mass movement of a porcellionid (species not identified as yet, but probably of the *Porcellio ficulneus* group during early summer in the Upper Galil region (Fig. 10.9). This movement takes place during the daytime, a rather unusual phenomenon for isopods in that region, and has a directional pattern. This mass movement could be the outcome of a population explosion and will be discussed later (see Chap. 12).

In *Hemilepistus reaumuri*, the desert isopod (Figs. 10.10–10.11), individual members of the family disperse in February and travel great distances of several hundred metres (details in Hoffmann 1985a, b). Much of their surface activity (up to 86%) is devoted to collecting soil crust and plants for their offspring inside their burrows (Shachak and Newton 1985).

The vertical movement down the soil was described in several isopod species (Cole 1946). During winter, *Armadillidium vulgare* moves down the soil to a depth of 25 cm (Paris 1963), where the isopods aggregate at the base of bushes. In Japan, *Ligidium japonicum* was found to move deeper in the soil during winter as compared with summer. (Saito 1965). Similarly, the desert isopod, *Hemilepistus reaumuri*, burrows become

**Fig. 10.10.** Excavated burrow (*arrow*) of *Hemilepistus reaumuri* in the Negev desert

**Fig. 10.11.** *Hemilepistus reaumuri*

deeper as summer progresses (Shachak 1980), down to a depth of about 1 m (Fig. 10.10).

The burrowing inside the soil was shown to be influenced by three factors: temperature, relative humidity and burrowing capability of the isopod species (Davis et al. 1977). No correlation was found with soil moisture in *Armadillidium vulgare* (Al-Dabbagh and Block, 1981).

## 10.3 Isopods from Different Habitats

### 10.3.1 The Littoral Zone and Seashore Isopods

In the littoral zone we find two main kinds of isopods: the one more typical of rocky shores is *Ligia*, the other, *Tylos*, is found in coarse sand or gravel shores. Whereas the first isopod is a typically shaped woodlouse, the other is a conglobating form. *Ligia*, is largely a diurnal isopod (Edney 1951a, b; Barnes 1932), foraging on the vertical rocks or among the stones on the sea shore mostly out of reach of the waves. *Tylos* (Figs. 10.12, 10.13) is usually nocturnal in its behaviour (Tongiorgi 1968/69; Imafuku 1976)

**Fig. 10.12.** *Tylos* sp.

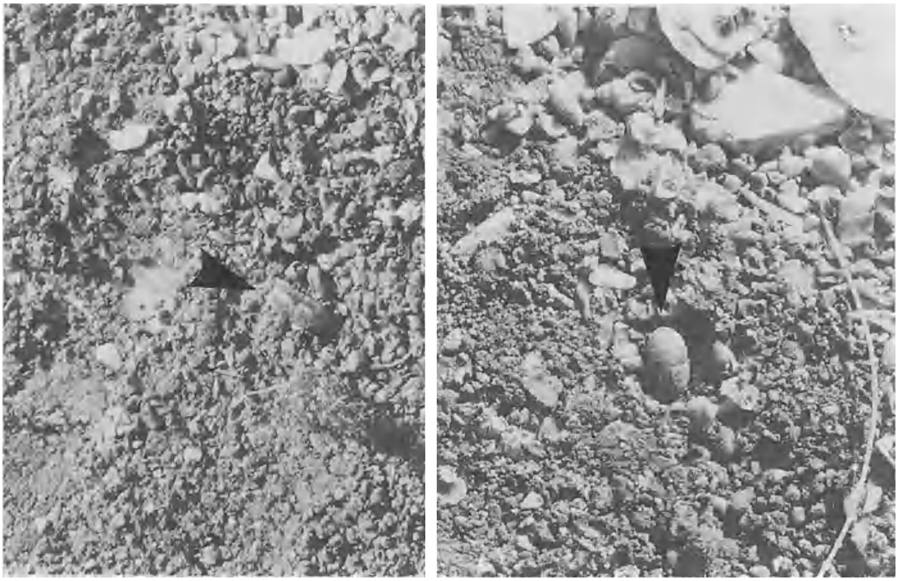


**Fig. 10.13.** *Tylos* sp. (*arrow*) on the seashore

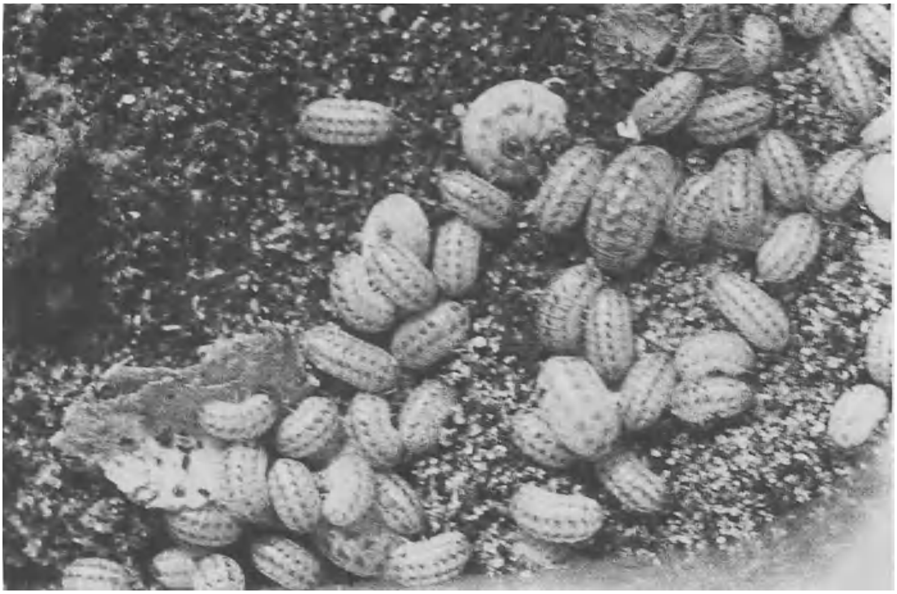


**Fig. 10.14.** *Armadillidium fallax* under stone on hills near the seashore

and is found during the daytime buried in the sand under stones. They feed on algae but also on animal remains (Mead 1968; Hayes 1977). Some *Tylos* species attain a very large size of several centimetres (*T. granulatus* in southwest Africa).

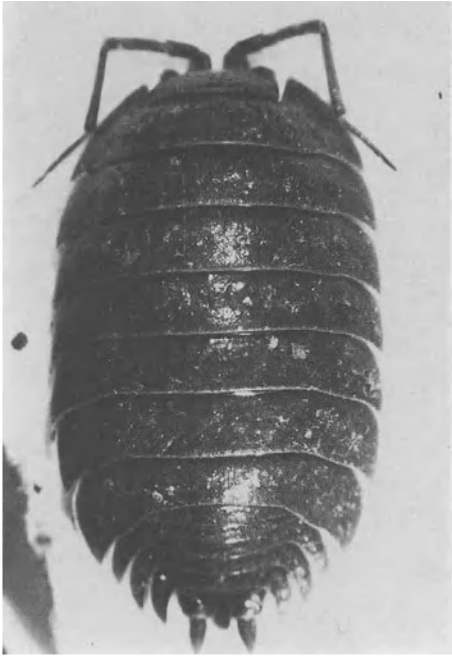
Under logs and other debris along the sea shore, we may find very small porcellionid isopods such as *Stenonyscus* sp., which are tolerant of seawater.

Higher up along the Mediterranean seashore banks of firm sand-soil, we may find several porcellionids and armadillids. Thus, both *Leptotrichus* spp. as well as *Porcellionides* spp. can be found together with *Armadillidium fallax* (see Fig. 10.14). The latter is found in large numbers aggregating under sand stones.

### 10.3.2 Isopods of the Grassland and Macqui Habitats

In grassland we find largely porcellionids of various types. *Porcellio ficulneus*, the large black woodlouse, as well as *P. laevis* (Fig. 10.15) and *P. chuldaensis*, are all found in large numbers in open habitats of grassland or macqui types of habitats (Fig. 10.16). In addition, some typical lithophylous isopods can be found. These may extend their distribution into the garique types of habitats. Some armadillidiids and armadillids (*Schizidium tiberianum* and *Armadillo officinalis*) inhabit the open area and penetrate into the garique and woodland.

10.15



10.16

**Fig. 10.15.** *Porcellio laevis* (× 120)

**Fig. 10.16.** *Porcellio chuldaensis* (× 120)

### 10.3.3 Garigue and Woodland Isopods

In habitats where the vegetation coverage is much denser, we find several species of isopods, both woodlice and pillbugs. Most typical of these habitats in the Mediterranean regions are *Philoscia* sp. and *Armadillo officinalis*. Also present are *Porcellionides* spp. and *Leptotrichus* spp. as well as other species, some of which are rare (*Bathytropa wahrmani*; see Fig. 1, Preface; Warburg et al. 1978). Isopods appear to be an important macroinvertebrate component of that fauna.

### 10.3.4 The Desert Isopods

Isopods have penetrated into the deserts as well. We can find a large porcellionid type of isopod in the Palearctic deserts of North Africa through the Middle East. This isopod, *Hemilepistus reaumuri*, is typically diurnal with a cyclic activity pattern changing throughout the year (Warburg et al. 1984). In some areas it is the most abundant macroinvertebrate found in loess types of soil as well as in rocky habitats (Figs. 10.17–10.19). It can be found in areas well under 100 mm average annual rainfall. It is unique in its way of life in that it stays in families where

**Fig. 10.17.** Negev desert habitat of *Hemilepistus reaumuri*, *Armadillo albomarginatus* and *Porcellio barroisi*

**Fig. 10.18.** Jordan Valley habitat of *Hemilepistus* and *Porcellio barroisi*

**Fig. 10.19.** *Armadillo albomarginatus* under stone

parents nurse their juveniles in a burrow throughout the hot and dry months. By its burrowing behaviour it accelerates soil erosion, and its faeces contain high concentration of salts, which affects the soil salinity (Shachak and Yair 1984). Sharing the habitat of sandy loess in the Negev desert are two additional isopods: *Porcellio olivieri* and *Agabiformius* sp. Very little is known about their ecology or behaviour due to their secretive, fossorial habits. They can be seen under stones only after the early winter rains.

A second isopod, a pillbug (*Armadillo albomarginatus*) is typical of rocky habitats in the desert (Fig. 10.19). This small pillbug is unique in its high resistance to desiccation (Warburg 1989), not unlike other desert isopods found in the southwestern USA (*Venezillo arizonicus*; see Warburg 1965b). Also typical of this habitat is a slender porcellionid, *Porcellio barroisi*, which is found only during spring time.

### 10.3.5 Other Habitats

There are a number of isopods species which are typical inhabitants of ant nests (O'Rourke 1950; Mathes and Strouhal 1954). Foremost among these is *Platyarthrus* sp., the slender, white and blind isopod, together with some *Agabiformius* sp., *Porcellionides* sp. and *Armadillo tuberculatus*, which are all found in nests of various ant species. In caves we find mostly isopod species which are also found outside and are not troglobitic or adapted to cave life; there are some exceptions to this. Finally, the isopod species that colonize refuse heaps differ from their neighbouring species (Koscielny 1983).

# 11 The Reproductive System and Reproduction

## 11.1 The Marsupium

The reproductive system of isopods was described in the early literature by various authors (see in Schöbl 1880; Friedrich 1883; Leichman 1891; Němec 1896a, b). The marsupium of the oniscid isopods is formed by five thoracic segments (Nos. 3–7). Four processes hang down from the thoracic epithelium; they are opaque or transparent, soft and surrounded by opaque mucus (Akahira 1956). There are three tubular evaginations per somite, called cotyledons, and the first somite bears only one (Patane 1940). When they shrink, the mancas ( = larvae) hatch out of the marsupium (Schöbl 1880 in *Porcellio scaber*). Verhoeff (1920) found that the cotyledons did not shrink within 42 days. There appears to be a relationship between the number of cotyledons and the habitat. More cotyledons were found in the more arid species (Lewis 1991).

There are apparently two types of marsupia. The first one, the *Ligia* type, is open at both its anterior and posterior ends, letting the water through. In all terrestrial forms the marsupium is completely closed (Hoese 1984). The subject was discussed therein and the older literature reviewed. The marsupia of *Helleria* and *Tylos* were described by Mead (1963, 1965). Apparently, the formation of the oostegites forming the marsupium is dependent on the maturing ovary (Suzuki and Yamasaki 1989).

The marsupial fluid was thought to be of limited nourishing value because, apparently, the mancas can develop even without it (Verhoeff 1917a). It was hypothesized that the marsupial fluid was needed mostly for gas exchange and to prevent dehydration (Verhoeff 1920). The marsupial fluid also contains some crystals, perhaps the product of catabolism of the embryos (Patane 1940). However, Hoese and Janssen (1989) found that the embryos are provided with water, oxygen and nutrients through the marsupial fluid.

## 11.2 The Male Gonad

The paired male gonads have been described by Friedrich (1883). They consist of a pair of three-lobed testes, each of which leads to a vas deferens and a vesiculum seminalis (Becker and Mann 1938, see Fig. 11.1). The vas deferens consists of giant cells in its anterior part, secreting mucoprotein (Newstead and Dornfeld 1965). The development of the male gonad is dependent on the androgenic gland (Becker-Carus 1966). Apparently, the three testes follicles are not synchronously active (Radu and Craciun 1969). The maximal intensity of spermatogenesis (in *Armadillidium vulgare*) was between May and June, although spermatogenesis occurred (in Rumania) most of the year except between November and February. Thus, it is true to consider this an annual cyclic event of spermatogenesis (Radu and Craciun 1971). The non-motile sperm is glued together by the mucoproteins to form a spermatophore (Mathur 1961). It was found to be viable for a year in *Armadillidum vulgare*, and in *Armadillo officinalis* for 2 years (Lueken 1963).

The females of *Armadillidium vulgare* and *A. nasutum* store functional sperm of a single mating until their death (Lueken 1963). In *A. perraccae* the females mate with several males (Lueken 1968). The offspring resemble the last male. The problem of multiple paternity and sperm mixing was studied in *Porcellio scaber* and was determined in over 80% of the broods (Sassaman 1978). He used as a marker the phosphoglucose isomerase (PGI) locus. Multiple insemination and sperm storage or

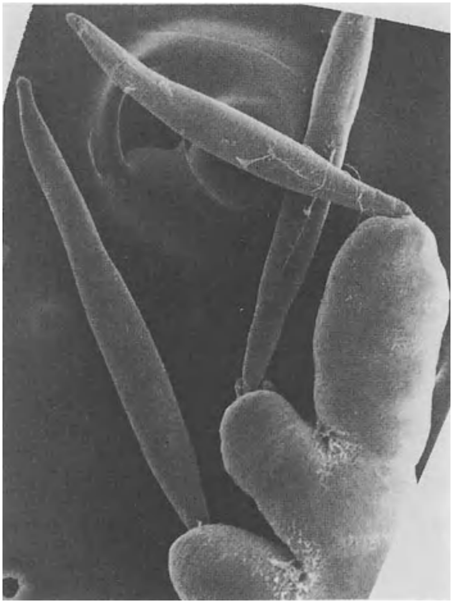


**Fig. 11.1.** Testis of *Armadillo officinalis* (×35)

sperm mixture was studied also in *Venezillo evergladensis* (Johnson 1982).

## 11.3 The Female Reproductive System

The pair of ovaria are situated laterally and open into a short oviduct (Figs. 11.2–11.4). Ovarian size will be discussed later in this chapter.

Ovarian protein shows a diurnal rhythm of synthesis, with the maximum at the beginning of the night (Gohar et al. 1985). There is a diurnal variation in both synthesis and release of haemolymph protein and in the synthesis of vitellogenin (Gohar et al. 1983). The vitellogenin is synthesized in the fat body (of ovariectomized female *Porcellio dilatatus*, Picaud 1980, and in *Idotea*, Souty and Picaud 1981). It is also stimulated by ecdysone (Gohar and Souty 1984). Immunohistochemical evidence for vitellogenin was shown in the hepatopancreas as well (Picaud and Souty 1980a, b). It accounts for most of the protein synthesized there (in *Idotea balthica*, see Souty and Picaud 1981). It is then stored in the hepatopancreas (Picaud 1980). The subject has been recently reviewed by Picaud et al. (1989).

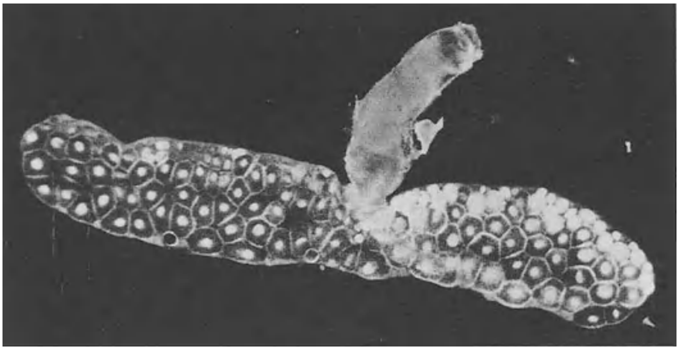
There is a difference in the amount of vitellogenin found in virgin, mated or ovariectomized females (Picaud and Souty 1981). There is evidence to suggest that the presence of males stimulates ovarian maturation (in *A. vulgare*, Jassem et al. 1982a).

King (1926) recognized two kinds of yolk: (1) the mitochondrial yolk which is diffuse but concentrates around the nucleus and (2) the Golgi yolk which is evenly distributed in the cell. Bilinski (1979) distinguished between the intra-oocytic yolk, which is formed by autosynthesis, and the extra-uterine yolk, which is formed through micropinocytosis. Disc-shaped bodies in the endoplasmic reticulum are the precursors of the intra-oocytic yolk, whereas the dictyosomes are involved in the yolk formation (Bilinski 1979).

The oocytes of *Idotea balthica* are 60–80 μm in diameter and surrounded by follicle cells (Souty 1980). In *Armadillidium vulgare* and *Porcellionides pruinosus* the oocytes are covered by spherules of glycogen and yolk (Lane 1980). The ovarian epithelium is rich in mucopolysaccharides, whereas the follicle cells are not nutritive.

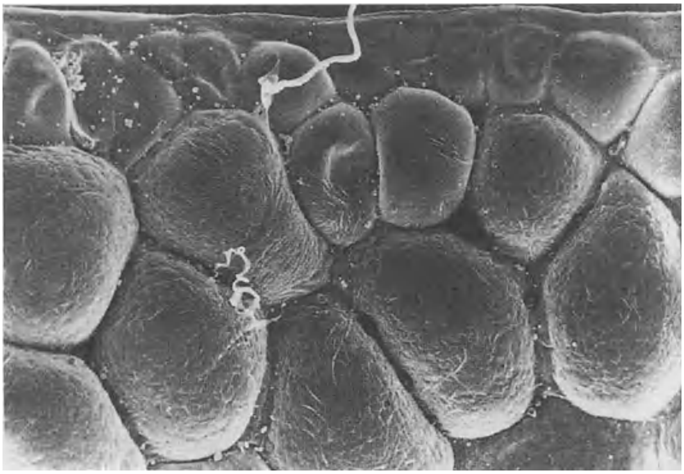
The fertilized egg (of *Hemionisus balani*) is wrapped by two envelopes (Goudeau 1976). The eggs leave the ovaria through thread-like tubes into the marsupium (Schöbl 1880). Once the eggs are extruded into the marsupium, they are covered by a chorion (Strömberg 1964). There is a close relationship between vitellogenesis and the parturial moult (Jassem et al. 1982b).

The embryonic development of the oniscid isopod *Oniscus murarius* has been studied by Bobretzky (1874). During embryonic development, lipids are utilized. The percentage of lipid content drops from 39 to 19%



11.2

11.3



11.4

**Fig. 11.1.** Ovary of *Armadillo officinalis* (×10)
**Fig. 11.3.** Ovary of *Schizidium tiberianum* (×9)
**Fig. 11.4.** Ovary of *Armadillo officinalis* (SEM, ×100)

(in *Ligia oceanica*, see Saudray 1954). There is a progressive increase in ash content from 4.4 to 31.6% and in non-protein N from 1.5 to 2.7% (Pandian 1972). There is also an increase in weight after hatching (Saudray and Lemercier 1960), as well as a drop in protein (41.8 to 36.8%), fat (48.8 to 27.4%) and carbohydrates (3.5 to 1.5%). Consequently, there is a drop in energy value from 5956 to 4175 Cal/g dry wt. (Pandian 1972).

The size of the eggs in the marsupium varies between species: *Trichoniscus pusillus* has an egg 0.3 mm in diameter, while *Porcellio scaber* has an egg of 0.7 mm diameter (Herold 1960). Our own observations indicate that the oocyte diameter (or size) varies even within the species among differently sized females.

## 11.4 Mating

The mere presence of males speeds up reproduction irrespective of mating (Souty-Grosset et al. 1991).

Mating takes place at any intermoult phase in *Armadillo officinalis* (Mead 1976). In the other species studied (*Trichoniscus pusillus*, *Androniscus dentiger*, *Porcellio laevis*, *Metoponorthus sexfasciatus* and *Armadillidium vulgare*), copulation takes place during the intermoult phase that precedes the parturial moult (Mead 1976). The male (of *Venezillo evergladensis*) orients towards the receptive female using olfactory cues. It taps the female's head with its antennae (Johnson 1985).

During copulation, the insemination of the left genital pore is carried out by the right endopodite (Fig. 11.5). The second copulation involves the left endopodite and ensures the insemination of the second genital pore (Mead 1978).

There are isopod species whose male frequency is so low that reproduction is mostly through parthenogenesis (Johnson 1986). This was described in *Trichoniscus pusillus* by Vandel (1960), where the male frequency was below 0.5% of the population, in the oniscid *Trichoniscus pusillus* by Frankel et al. (1981) and in the philoscid *Ocelloscia floridiana* by Johnson (1986). The varying sex ratio in isopods had already been noted in 1938 by Vandel (see Vandel 1964). His terms for an all-male population (arrhenogenic) and an all-female population (thelygenic) are still used today. Sometimes females switch from a unisex brood to a bisex one or vice versa.

## 11.5 Breeding

Breeding seasons and numbers of eggs, embryos and mancae are given for a number of British isopod species by Heeley (1941), for a large number

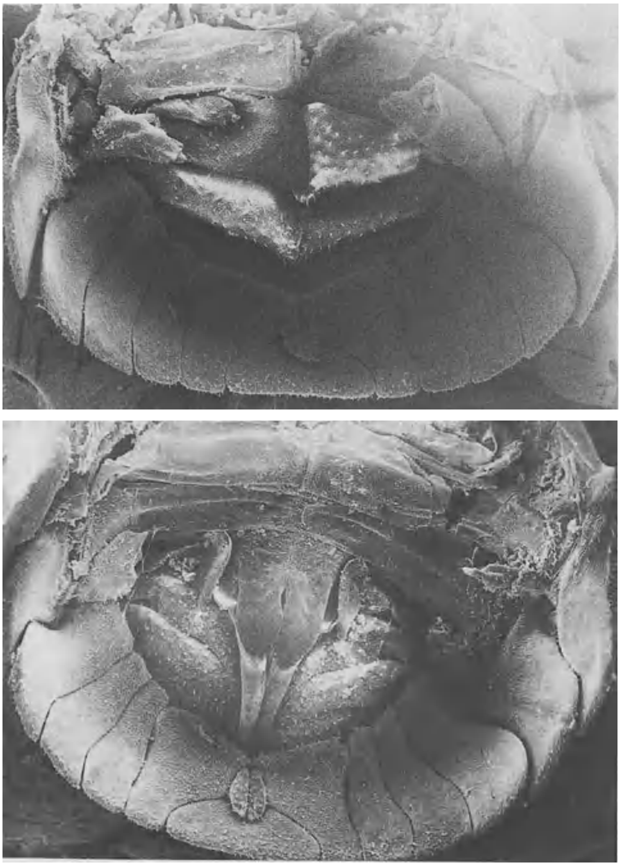


**Fig. 11.5.** Genital apparatus of male (bottom) and female *Armadillo albomarginatus* (×35)

of Danish species by Meinertz (1950) and for a number of German species by Beyer (1957/58). Carefoot (1973b) summarizes some of the reproductive data for 21 species (in his Table 1). A more detailed attempt to summarize the data was undertaken in Warburg et al. (1984, Table VIII) and in Warburg (1987b, Table 7).

Gestation is affected by temperature. At 15°C the gestation period of *Porcellio dilatatus* lasts 60 days, whereas at 25°C it last only 25 days (Mocquard et al. 1976b). There is a large variation in breeding patterns among the isopods. They differ in their breeding seasons. Thus, within the same habitat there are species breeding in spring and others that are autumn breeders (Warburg 1991). There is also a difference in the duration of the breeding season. In most isopod species studied so far in the xeric habitats of the Mediterranean region, the annual breeding season is discrete and lasts between 4 and 8 weeks (Warburg 1991). In others from tropical or temperate regions, the breeding season may last 3–6 months (Kato 1976). The number of broods, the number of eggs produced in each brood as well as the mortality of ova or mancae all vary. The number of eggs is possibly correlated with the square of the female's length (in *Armadillidium vulgare*, see Nakatsuchi 1983; Miller and Cameron 1983).

### 11.5.1 Factors Affecting Breeding

Wieser (1963a) found that 16 h of light and 8 h of darkness induced breeding of *Porcellio scaber* in the laboratory. This species normally breeds between March and August. Long days appear to cause a decreased rate in synthesis and release of VIH (vitellogenesis inhibiting hormone; Juchault et al. 1989). On the other hand, the breeding period requires between 20 and 25 photoperiods of 12–14 h light (Juchault et al. 1982). The subject has been recently reviewed by Mocquard et al. (1989).

Under continuous darkness breeding decreases in *Oniscus asellus*, *Porcellio scaber* and *Armadillidium vulgare* (Beyer 1965). In their studies, Mocquard et al. (1980) found that during the autumn the drop in daylight hours caused *Armadillidium vulgare* to cease reproducing. In contrast, increased daylight hours led to a longer reproduction period (Juchault et al. 1981). This was seen also in *Eluma purpurascens* (Juchault et al. 1980a).

Apparently related to this phenomenon, it was found that *Armadillidium vulgare* from low latitudes reacted more quickly to factors stimulating reproduction, as if they were affected by long daylight (Juchault et al. 1980b). In the tropical forest some isopods seem to have a longer reproductive period and greater numbers of broods per year (Dangerfield and Telford 1990; Ma et al. 1991b). On the other hand, in a recent study *Agabiformius* sp., a fossorial desert isopod, was found to breed continuously in the lab (study in progress). It is possible that the continuously breeding isopods perceive an external environmental cue that initiates reproduction (Dangerfield and Telford 1990). However, in the lab apparently not all species react in the same way as most of them maintain their discrete seasonal reproductive period. Females from high latitudes bred later than females from low latitudes. The subject has been discussed by Souty-Grosset et al. (1988). *Metoponorthus pruinosus* females from tropical regions apparently lack this sensitivity to day length as a trigger for reproduction (Juchault et al. 1985). Sorensen and Burkett (1977) found that the first to breed were the larger females of that species.

The initiation of reproduction depends on light intensities (Jassem et al. 1982). *Armadillidium vulgare* was capable of integrating light intensities, and thus even in darkness (except for short light flashes) reproduction could be initiated (Jassem et al. 1981). When the eyes are covered or destroyed, the delay in breeding is similar to the situation in which females were kept under total darkness (Mocquard et al. 1984).

On the other hand, in *Oniscus asellus*, daylight apparently did not alter the development time (McQueen and Steel 1980). Day length longer than 12 h caused earlier reproduction in the spring.

Temperature appears to affect reproduction as well. Increased temperature shortened the development time for mancas of *Oniscus asellus* (McQueen and Steel 1980) and accelerated the reproduction in *Armadillidium vulgare* (Mocquard et al. 1980). Environmental factors such as spring and the monsoon rains (in India) affected the breeding of *Porcellio laevis* (Nair 1984).

Jassem et al. (1982a) found that the ovarian maturation of *Armadillidium vulgare* was accelerated by the presence of a male. Moreover, the duration of the breeding period depends on a substance contained in the males' sperm. This direction of research needs to be explored further. On the other hand, the presence of other females is important, as isolated females do not develop a marsupium or produce young at the same rate as females kept together (Mead and Gabouriaut 1988a, b). They suggest that perhaps the female's faeces contain a factor that stimulates marsupial development.

There is some evidence to suggest that food can affect the breeding patterns in isopods. Thus, if fed on dicotyledonous plants, more females were found to be gravid and capable of releasing their young than when fed on monocotyledones (Rushton and Hassall 1983b). There is a trade-off between growth and reproduction (in *Ligia oceanica*, see Willows 1987b). In *Philoscia muscorum* delayed breeding allowed additional growth (Grundy and Sutton 1989).

### 11.5.2 Breeding Patterns in Isopods

The isopods vary in their breeding patterns, both interspecifically as well as intraspecifically (see discussion in Warburg 1991). They differ in the number of broods they produce during 1 year (as well as throughout their lifetime; see Tables 11.1, 11.2). They also differ among different localities of the same species in the season during which they breed (Table 11.3). Moreover, there are even marked differences in breeding patterns of the same species in different microhabitats within the same region (Hornung 1988). Finally, there is a marked variation in the number of eggs produced and, consequently, in the number of offspring emerging as mancas from the marsupium. Some of these aspects are discussed in Warburg (1991).

Heeley (1941) described the breeding patterns in British isopods. Meinertz (1950) attempted to summarize the breeding seasons and number of eggs, embryos and mancas for a large number of Danish species. Similarly, Beyer (1957/58) gave a resumė of reproduction data for several German species, as did Verhoeff (1917a, 1920) before him.

**Table 11.1.** Number of broods per year

| Species | Family | No. of broods | Source |
|---|---|---|---|
| *Tylos punctatus* | Tylidae | 1 | Hamner et al. (1969) |
| *Philoscia muscorum* | Oniscidae | 1 | Sunderland et al. (1976) |
| *Hemilepistus reaumuri* | Porcellionidae | 1 | Shachak (1980) |
| *Eluma purpurascens* | Armadillidiidae | 1 | Juchault et al. (1980a) |
| *Schizidium tiberianum* | Armadillidiidae | 1 | Warburg et al. (1984) |
| *Armadillidium opacum* | Armadillidiidae | 1 | Verhoeff (1917a) |
| *Armadillo officinalis* | Armadillidae | 1 | Shereef (1970) |
| *Venezillo arizonicus* | Armadillidae | 1 | Warburg (1965c) |
| *Ligia Oceanica* | Ligiidae | 1–2 | Nicholls (1931a) |
| *L. dilatata* | Ligiidae | 1–2 | Koop and Field (1980) |
| *Trichoniscus pusillus* | Trichoniscidae | 1–2 | Standen (1973) |
| *Trachelipus rathkei* | Porcellionidae | 1–2 | Verhoeff (1917a) |
| *Porcellio olivieri* | Porcellionidae | 1–2 | Kheirallah and Awadallah (1981) |
| *Porcellio spinicornis* | Porcellionidae | 1–2 | McQueen and Carnio (1974)<br>McQueen (1976a) |
| *Armadillidium vulgare* | Armadillidiidae | 1–2 | Lawlor (1976b) |
| *Cubaris robusta* | Armadillidae | 1–2 | Menon et al. (1970) |
| *Trichoniscus pusillus* | Trichoniscidae | 2 | Heeley (1941) |
| *Oniscus asellus* | Oniscidae | 2 | Heeley (1941) |
| *Cylisticus convexus* | Cylisticidae | 2 | Verhoeff (1917a) |
| *Tracheoniscus balticus* | Porcellionidae | 2 | Verhoeff (1917a) |
| *Porcellio scaber* | Porcellionidae | 2 | Heeley (1941) |
| *P. laevis* | Porcellionidae | 2 | Shereef (1970)<br>El-Kifl et al. (1970) |
| *P. obsoletus* | Porcellionidae | 2 | Warburg (1987b) |
| *P. dilatatus* | Porcellionidae | 2 | Collinge (1941) |
| *Trichoniscus pusillus* | Trichoniscidae | 2–3 | Tomescu (1973) |
| *Cylisticus convexus* | Cylisticidae | 2–3 | Hatchett (1947) |
| *Armadillidium vulgare* | Armadillidiidae | 2–3 | Warburg (1965c) |
| *Hyloniscus riparius* | Trichoniscidae | 3 | Beyer (1957/58) |
| *Porcellio scaber* | Porcellionidae | 3 | Verhoeff (1917a) |
| *Metoponorthus pruinosus* | Porcellionidae | 3–6 | Menon et al. (1969)<br>El-Kifl et al. (1970) |
| *Leptotrichus naupliensis* | Porcellionidae | 4–6 | Shereef (1970) |
| *Porcellio laevis* | Porcellionidae | 4–6 | Mahmoud (1954)<br>Shereef (1970) |

**Table 11.2.** Reproduction strategies in isopods

| Species | Family | Source |
|---|---|---|
| **Semelparous species:** | | |
| *Tylos punctatus* | Tylidae | Hamner et al. (1969) |
| *Philoscia muscorum* | Oniscidae | Sunderland et al. (1976) |
| *Hemilepistus reaumuri* | Porcellionidae | Warburg (1987b) |
| *Eluma purpurascens* | Armadillidiidae | Juchault et al. (1980a) |
| *Schizidium tiberianum* | Armadillidiidae | Warburg (1987b) |
| *Venezillo arizonicus* | Armadillidae | Warburg (1965c) |
| **Iteroparous species:** | | |
| *Ligidium hypnorum* | Ligiidae | Tomescu (1973) |
| *Trichoniscus pusillus* | Trichoniscidae | Heeley (1941) |
| *Hyloniscus riparius* | Trichoniscidae | Beyer (1957/58) |
| *Oniscus asellus* | Oniscidae | Heeley (1941) |
| *Cylisticus convexus* | Cylisticidae | Verhoeff (1917a) |
| *Protracheoniscus politus* | Porcellionidae | Radu and Tomescu (1976) |
| *Trachelipus riparius* | Porcellionidae | Hatchett (1947) |
| *Metoponorthus pruinosus* | Porcellionidae | Menon et al. (1969) |
| *Leptotrichus naupliensis* | Porcellionidae | Shereef (1970) |
| *Porcellio scaber* | Porcellionidae | Verhoeff (1917a) |
| *P. olivieri* | Porcellionidae | Warburg (1992) |
| *P. laevis* | Porcellionidae | Mahmoud (1954) |
| *P. spinicornis* | Porcellionidae | McQueen (1976a) |
| *P. obsoletus Ilculneus* | Porcellionidae | Warburg (1987b) |
| *Armadillidium vulgare* | Armadillidiidae | Warburg (1965c) |
| *Armadillo officinalis* | Armadillidae | Warburg (1987b) |
| *A. albomarginatus* | Armadillidae | Warburg (1992) |
| *Cubaris robusta* | Armadillidae | Menon et al. (1970) |

At first glance, it seems that whereas some isopods breed only once a year, others breed up to six times yearly (Table 11.1). However, a closer look at the data presented in Table 11.1 shows that some species are listed as having different numbers of broods based on data provided by different authors (mostly from different localities) and, thus, the discrepancy. The following is a brief description of the breeding patterns in representative isopods species of different families.

**Table 11.3.** Breeding season of some common isopod species according to various sources

| Species | Family | Months | Source |
|---|---|---|---|
| *Ligia oceanica* | Ligiidae | I–X | Vandel (1960) |
| | | V–VIII | Meinertz (1950) |
| | | V–VIII | Jöns (1965) |
| *Trichoniscus pusillus* | Trichoniscidae | II–IV | Heeley (1941) |
| | | V–IX | Meinertz (1950) |
| | | IV–VII | Sutton (1968) |
| | | V–IX | Tomescu (1973) |
| *Philoscia muscorum* | Oniscidae | V–VIII | Heeley (1941) |
| | | VI–VIII | Meinertz (1950) |
| | | VI–VIII | Sutton (1968) |
| | | IV–IX | Vandel (1962) |
| *Oniscus asellus* | Oniscidae | IV–VIII | Heeley (1941) |
| | | V–IX | Beyer (1957/58) |
| | | II–IX | Phillipson and Watson (1965) |
| *Metoponorthus pruinosus* | Porcellionidae | III–IX | Vandel (1962) |
| | | VI–X | Meinertz (1950, 1951) |
| | | IV | El-Kifl et al. (1970) |
| *Porcellio scaber* | Porcellionidae | II–III | Verhoeff (1917a) |
| | | III–VII | Heeley (1941) |
| | | III–X | Meinertz (1950, 1951) |
| | | V–IX | Beyer (1965) |
| | | III–VIII | Wieser (1963a) |
| *Porcellio laevis* | Porcellionidae | III–IV | Mahmoud (1954) |
| | | III | El-Kifl et al. (1970) |
| | | II–X | Nair (1976a, b) |
| *Hemilepistus reaumuri* | Porcellionidae | IV–V | Shachak (1980) |
| | | III–V | Warburg (1987b, 1991) |
| *Armadillidium vulgare* | Armadillidiidae | IV–IX | Vandel (1960) |
| | | V–VIII | Heeley (1941) |
| *Schizidium tiberianum* | Armadillidiidae | IV–V | Warburg and Cohen (1991) |
| *Armadillo officinalis* | Armadillidae | VI–VIII | Vandel (1962) |
| | | IV–V | Shereef (1970) |
| | | IX–X | Warburg et al. (1984) |
| *A. albomarginatus* | Armadillidae | X | Warburg (1992) |

### 11.5.3 Breeding Seasons, Eggs and Manca Numbers of Different Isopod Families

*The Tylidae.* According to the data given by Hamner et al. (1969), the females of *Tylos* breed when they are 2–3 years old, in May, and die. The brood size is 12–14 eggs or embryos (Hayes 1977), and the average number of juveniles is 13.6 (range 4–20; Hamner et al. 1969).

*The Ligiidae. Ligia oceanica* breeds once in summer (Jöns 1965), or twice according to Besse et al. (1975) and Willows (1984). The average number of eggs is 73 (Saudray and Lemercier 1960), or 53 (ranging between 39 and 63) according to Pandian (1972). Juveniles average 80, ranging between 44 and 130 according to Sutton et al. (1984). Nicholls (1931a) found that they breed twice yearly, with an average of 80 young per brood. *Ligia pallasii* breeds between May and July, producing 48 eggs (Carefoot 1973b). *Ligidium japonicum* breeds between May and July (Kato 1976), whereas *Ligidium hypnoroum* has two broods between May and August. During the first months, the 2–3-year-old females breed, while the younger 1–2-year-old females breed later in the season (Tomescu 1973).

*The Trichoniscidae. Trichoniscus pyqmaeus* has an average number of juveniles of 5.2, ranging between 2 and 9 (Sutton et al. 1984), whereas *T. pusillus* breeds 2–3 times between May and September producing between 4 and 7 eggs (Heeley 1941) or 7–18 eggs (Standen 1973). The average number of juveniles is 5.5 or 7.3, respectively, ranging between 4 and 11 (Sutton et al. 1984).

*The Squamiferidae.* These blind, cavernicolous and myrmecophilous isopods (*Platyarthrus hoffmannseggi*) have two broods per year (Collinge 1941) and produce 4.5 juveniles on average, ranging between 2 and 8 juveniles (Sutton et al. 1984). However, the *Exalloniscus maschwitzi* female produces 1–2 large embryos in her brood pouch (Ferrara et al. 1987).

*The Oniscidae. Philoscia muscorum* has one brood (Heeley 1941; Sunderland et al. 1976), or 3–4 broods according to Collinge (1941) with 14.8 juveniles on average (15–30 range), or 13 eggs according to Heeley (1941). *Oniscus asellus* produces between 27 and 33 eggs (averaging 30 eggs according to Heeley 1941).

*The Cylisticidae. Cylisticus convexus* with 2 broods yearly (Verhoeff 1917a), or 2–3 broods (Hatchett 1947), produces 24 eggs on average (Hatchett 1947).

*The Porcellionidae.* Several genera were studied of this large family. *Tracheoniscus balticum* has 2 broods in May–June and July–August (Verhoeff 1917a), *Trachelipus rathkei* breeds earlier, in March–April and June–July (see Verhoeff 1917a; Krumpal 1976), and *Protracheoniscus amoenas* breeds in its 2nd year of life (Gere 1959). McQueen (1976a, b) found that 83% of the population bred once, and 42% bred twice during the same year (in Canada). The number of eggs per female ranged between 14 and 47 and depended on the weight of the female (Hatchett 1947). The number of juveniles ranged between 20 and 25 (Gere 1959). *Trachelipus nodulosus* breeds during July/August, producing 23 eggs on average (Hornung 1989). The common garden woodlouse, *Metoponorthus pruinosus*, breeds 4–6 times yearly (Shereef 1970) between May and September (in Japan, Shimoizumi 1952). The number of eggs range between 25 and 30 (Collinge 1941). *Leptotrichus panzerii* breeds between April and October (Kheirallah 1980b), and *L. naupliensis* produces between 18 and 22 eggs or 14–18 larvae (Shereef 1970).

Finally, *Porcellio scaber* breeds twice (Collinge 1941; Heeley 1941) or three times yearly (Shereef 1970). The average number of eggs is 24, ranging between 12 and 36 eggs (Heeley 1941). The number of juveniles hatching is 24 according to Hatchett (1947), ranging between 25 and 40 (Collinge 1941) or 13–28 juveniles (Biwer 1961).

*The Armadillidiidae. Eluma purpurascens* breeds once between June and July (Juchault et al. 1980a). The much studied, cosmopolitan *Armadillidium vulgare* breeds once (Heeley 1941; Al-Dabbagh and Block 1981), twice (Collinge 1941) or up to three times yearly (Hatchett 1947) when it is 2 years old (Al-Dabbagh and Block 1981). It produces up to 113 eggs (Heeley 1941), of which 32–46 (Miller and Cameron 1983) or 30–60 mancas hatch (Collinge 1941). The female of *Schizidium tiberianum* produces once only when 2 years old and dies soon after (Warburg and Cohen 1991).

*The Armadillidae. Armadillo dorsalis*, which was studied by Watanabe (1980) in Japan, produces 9.8 juveniles. The large Mediterranean pillbug, *A. officinalis*, breeds once, producing 50 eggs or 45 larvae on average (Shereef 1970) or about 93 mancas (Warburg and Cohen 1992). This is an iteroparous species that can live for several years and is capable of producing young several times throughout its long lifetime (Warburg and Cohen 1992).

It is obvious from all these data that it is difficult to generalize about breeding patterns in isopods. There is a tremendous variability due to geographic locality, season and size of female, each of which could account, in part, for this variability. Moreover, so far almost all data result from studies on northern hemisphere species, with the exception of a few on tropical ones (Juchault et al. 1985). It is essential to have more accurate data on species of a more local distribution. In such studies the weight of each female must be taken into account in the final analysis and related to the batch/brood size.

### 11.5.4 Mortality of Eggs and Embryos in the Marsupium

The brood pouch mortality can be accurately established only in females kept separately until the mancas hatch. Then, their number can be compared with the number of eggs or embryos in the marsupium of previously dissected females. The average of a large sample of such counts can give an idea of the percentage lost in the marsupium. Some of the data obtained so far for various species are given in Table 11.4. The mortality percentage varies between 0.6% and 23%. In some studies differences are noted in the mortality rate between first and second broods (*Philoscia*) or when kept at different temperatures (*Trachelipus*). On the whole, more accurate data are needed before any generalization can be drawn on this important subject.

**Table 11.4.** Mortality of eggs or embryos in the brood pouch

| Species | Mortality (%) | Source |
|---|---|---|
| *Sphaeroma rugicauda* | 17 | Heath and Khazaeli (1985) |
| *Tylos punctatus* | 1 | Hamner et al. (1969) |
| *Ligia oceanica* | 0.66–2.83 | Willows (1987a, b) |
| *Ligidium hypnorum* | 6–10.6 | Krumpal (1976) |
| *Hyloniscus riparius* | 2.6–3.7 | Krumpal (1976) |
| *Philoscia muscorum* | 0.8 | Sutton (1986) |
| | 3.6 (1st brood) | Sunderland et al. (1976) |
| | 4.5 (2nd brood) | Sunderland et al. (1976) |
| *Trachelipus rathkei* | 20 (at 15.6 °C) | Snider and Shaddy (1980) |
| | 11 (at 26.7 °C) | Snider and Shaddy (1980) |
| | 5.7–6.7 | Krumpal (1976) |
| *Hemilepistus reaumuri* | 23 | Warburg (1987b) |
| *Porcellio laevis* | 3.9 | Nair (1976b, 1978) |
| *P. obsoletus* | 21 | Warburg (1987b) |
| *Armadillidium vulgare* | 8 | Paris and Pitelka (1962) |
| | 2.39–2.41 (of females 30–100 mg) | Lawlor (1976a, b) |
| | 3.27 (of females > 150 mg) | Lawlor (1976a, b) |

## 11.6 Reproductive Strategies

Most isopods are short-lived (even among arthropods). They are not likely to survive beyond 5 years with one known exception: *Armadillo officinalis* can survive up to 9 years (Warburg and Cohen 1992). In that sense they compare well with many insect groups who reproduce several times annually before their death. Regardless of the time scale involved, when an organism reproduces "more than once in a lifetime" (Cole 1954, p.105), it is an 'iteroparous form'. The only other mode of reproduction is the 'semelparous' form that reproduces 'only once in a lifetime' (Cole 1954, p.105). Many insects will therefore have to be considered iteroparous rather than semelparous in spite of their short life. This is based on the generation time rather than the annual cycle (Fritz et al. 1982). In that sense, isopods that have more than one brood within the same year are likewise iteroparous, even though they might not survive to the next year.

As can be seen from Table 11.2, many isopod species are known to be iteroparous, whereas fewer species (less than half) are presumed to be semelparous. It is very difficult to prove either strategy as it involves the accurate observation of an isolated female isopod over a long period of time (sometimes years!), trying to keep her alive from birth until after her second brood in order to prove iteroparity, or alternatively proving semelparity convincingly by showing that the female does not survive after parturition or is unlikely to breed a second time. There are very few such data in the literature; in fact in my laboratory over a long period of time some of the data presented here were accumulated.

A typical example for a semelparous isopod is *Hemilepistus reaumuri*, which is unable to reproduce more than once during the 18 months of its life (Warburg 1987b). In that isopod much of the energetic efforts are spent on parental care (Linsenmair 1984). As was pointed out by Giesel (1976), "organisms that devote a large proportion of available resources to reproduction at an early age are less likely to survive to later age of reproduction" (p. 61 there). Another example of a semelparous isopod could in fact illustrate this point. The female of *Schizidium tiberianum* breeds when 1 or 2 years old and dies while bearing her young. Moreover, the female provides the first meal to her numerous offspring who feed on her carcass! In other words her entire resources have been utilized for reproducing a new generation.

In the iteroparous isopod species (Table 11.2), we see that the numbers of the *Porcellionidae* family are well represented. The number of offspring varies with the mother's size, as well as with the season and presumably other unknown factors. Thus, large *Armadillidum vulgare* produce two broods per season as compared with a single brood of the smaller females (Lawlor 1976b). It was recently shown that small-sized *A. vulgare* females under conditions of stress due to excessive dehydration stop growing;

instead they reproduce, thereby reducing their chance of a second reproduction (Brody et al. 1983). When the food supply was short, the offspring were larger (in nature and in the laboratory, see Brody and Lawlor 1984). Will they become semelparous in that way? In other words, do stressful conditions promote semelparity in poikilothermous organisms? This line of research is most promising and of great interest. It would be worthwhile to examine at the same time the energetic expenditure on reproduction involved in any iteroparous species under a variety of stressful environmental conditions.

# 12 Population Structure and Fluctuation

## 12.1 Population Structure and Density

Our present knowledge on the population dynamics of isopods is based on studies of a limited number of isopod species (15), which represent only a few families (see Table X in Warburg et al. 1984). A typical characteristic of population structure is the large number of young within a population. At times they comprise the bulk of the isopod population in any single location (Sutton 1968; Sunderland et al. 1976). However, there is a large variation in the number of juveniles produced per year (Al-Dabbagh and Block 1981). The population structure changes from a bimodal pattern when the mancas leave the marsupium to a unimodal one when they grow and mature. The lowest densities are observed just before recruitment of the young (Kheirallah and Omran 1986). This change may last for a few months or up to a year and was observed in several species: *Cylisticus convexus* (Hatchett 1947), *Armadillidium vulgare* (Paris and Pitelka 1962; Al-Dabbagh and Block 1981), *Ligidium japonicum* (Saito 1965), *Trichoniscus rathkei* (Breymeyer and Brozozowska 1967), *T. pusillus* (Sutton 1968; Phillipson 1983) and *Hemilepistus reaumuri* (Shachak et al. 1979).

Recent evidence has shown that individuals born during a single breeding season to different broods (belonging to different females) may differentiate into two forms. One matures during its first year, and the other matures when 2 years old (Grundy and Sutton 1989). Furthermore, even within a single brood there are faster growing individuals that will mature sooner than their slower growing siblings (Warburg and Cohen 1991). This is cohort splitting and indicates that growth within the cohort is not homogeneous.

The difference in maturation of the population is due to differences in growth. Growth is affected also by ambient conditions (temperature, rainfall; see Pavese 1987). Climatic factors and food are both possible causes for cohort splitting ( = differential growth) in *Philoscia muscorum* (Sunderland et al. 1976). In *Ligia oceanica* the population can be divided into fast growing early breeding animals and slow growing/retarded breeding animals (Willows 1987a, b, c).

Whereas *Philoscia muscorum* breeds in its first year, *Armadillidium vulgare* breeds in its second year (Davis and Sutton 1977b). Recently we have observed that *Hemilepistus reaumuri* breeds in its first year (Warburg 1991), as it grows and matures during the same year (Shachak et al. 1979). *Schizidium tiberianum* breeds in its first or second year (Warburg and Cohen 1991). On the other hand, the long-lived isopod *Armadillo officinalis* breeds for the first time in its third year of life (Warburg and Cohen 1991). This subject was previously discussed in Chapter 11.

A typical change in the population structure of an isopod is described for *Armadillo officinalis* during 1 year of study in a pine forest in the Lower Galil Mts. of Israel (Cohen 1988). This isopod was found during the whole year, and the male-female ratio is about 1:1 (Fig. 12.1). The juveniles appear first in October. The sampling technique for the juveniles was based on soil extraction with Berlese funnels (Fig. 12.2). Because some of the isopods move downwards into the soil, it is difficult to estimate their density. In another conglobating form, *Schizidium tiberianum*, the males are much rarer in the population (Fig. 12.3).

The number of isopods can range from 50 per m$^2$ to over 500 or even 1000 (*Armadillidium vulgare*, see Warburg et al. 1984). Even larger numbers of isopods can be found in the literature (over 2000 for *Trichoniscus pusillus* in Sutton 1968, and over 20000 for *Tylos punctatus*, see Hayes 1977). The fact that such high densities occur in isopods would tend to indicate that common density regulating factors such as food abundance or shortage are of only limited significance. In *Hemilepistus reaumuri*, the food supply does not seem to be limited and thus has little effect on the abundance of this isopod (Shachak et al. 1976).

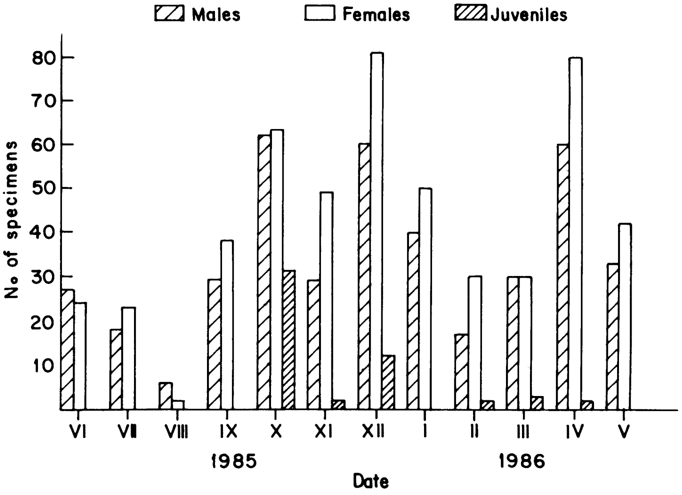


**Fig. 12.1.** Phenology and population structure of *Armadillo officinalis* in a pine forest. Note the appearance of juveniles in autumn. Census was taken twice monthly in 20 × 50 m plots in different parts of the forest (data in Cohen 1988)

**Fig. 12.2.** Modified Berlese funnels used for soil extraction. The funnels were placed in a cool room (17 °C)

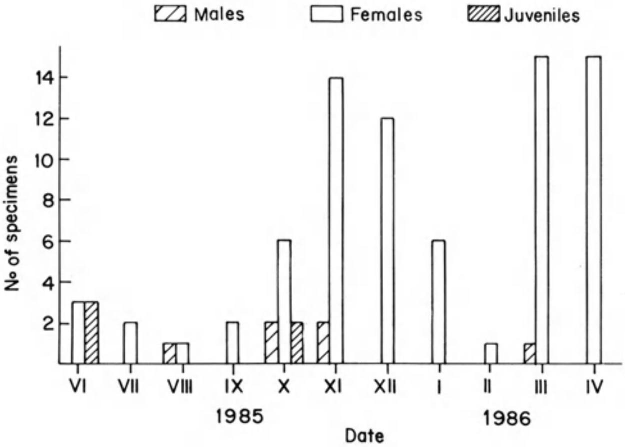


**Fig. 12.3.** Phenology and population structure of *Schizidium tiberianum* in a pine forest. Procedure as in Fig. 12.1. Note the juveniles appearing in spring (data from Cohen 1988)

When food is not in excess, the density and growth are affected, resulting in higher mortality and low survivorship (in *Armadillidium vulgare*, see Ganter 1984). Climate has a significant effect on density. This is discussed at length in Warburg et al. (1984). Thus, a warm summer will cause early breeding and rapid growth ending in high mortality (in the marine isopod, *Sphaeroma rugicauda*; see Heath and Khazaeli 1985).

## 12.2 Mortality and Longevity of Isopods

There is not much data on longevity in isopods. In only 15 species is there some information (Fig. 12.4). This indicates a life span ranging from 1 to 9 years (see also Collinge 1946; Stachurski 1968). Mortality is caused mostly by climatic factors (Kheirallah 1979a; Warburg et al. 1984). Thus, in a flood following a single storm 52% of *Periscyphis granai* drowned. Cannibalism at different developmental stages is also a cause of mortality (Heeley 1941; Brereton 1957; Menon et al. 1969; Linsenmair 1972), as well as predation (reviewed by Sutton 1970b; Sunderland and Sutton 1980; and discussed here later). It was recently shown that crowding can affect the mortality rates (Dangerfield 1986).

Food shortage and parasites are probably less effective as mortality agents, although cases of both have been reported. Maggots of tachinid flies or *Acanthocephala* and *Nematoda* helminthes (Oetinger and Nickol 1981) are sometimes found in localized populations of isopods at a rate of up to 5% in the population (see Menon et al. 1970; Sultanov et al. 1980; Sassaman and Garthwaite 1984). Iridioviruses, rickettsias and yeast-like pathogens are also abundant in isopods (Federici 1984). Predation on isopods, although more common, is not likely to be a major regulating factor for any isopod population.

The majority of the predators of isopods belong to arthopods such as arachnids (theirdiid spiders, Barmeyer 1975), or opilionids and chilopods (*Lithobius froficatus*, see Sunderland and Sutton 1980). Among the former we know that the major prey of the scorpion *Scorpio maurus palmatus* is the desert isopod *Hemilepistus reaumuri* (see also Kheirallah 1979a). Other predators of the latter include a solpugid and a scolopendrid (Warburg et al. 1984). Frogs are also predators of isopods (Zimka 1974).

A large percentage of the isopods dies within their first month of life outside the brood pouch. Thus, only 10% of *Porcellio scaber* lives longer (Brereton 1957), and 60% of *P. spinicornis* survives 50 days (McQueen and Carnio 1974), whereas 20% of *Trichoniscus pusillus* survive 2 months (Sutton 1968, 1970a). *Periscyphis* survives its first year, *Armadillidium vulgare* and *Ligia dilatatus* their 2nd year (Koop and Field 1980); some specimens survive a third year, and *Armadillo officinalis* survives 9 years and possibly longer (Warburg and Cohen 1991).

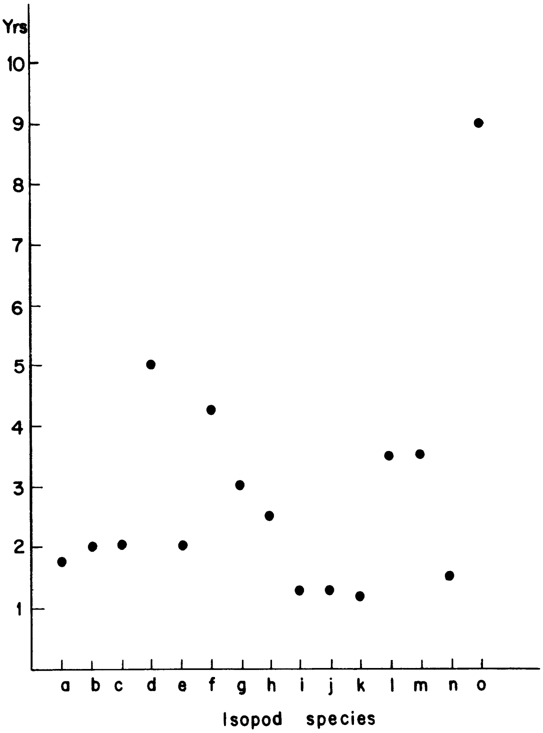


**Fig. 12.4.** Longevity of isopod species: *a*, *Ligia pallasii* (Carefoot 1973b); *b*, *L. dilatata* (Koop anf Field 1980); *c*, *Trichoniscus pusillus* (Sutton 1968); *d*, *Platyarthrus hiffmannseggii* (Collinge 1945); *e*, *Philoscia muscorum* (Sutton 1968, 1970a); *f*, *Oniscus asellus* (Collinge 1945); *g*, *Cylisticus convexus* (Hatchet 1947); *h*, *Protacheoniscus politus* (Radu and Tomescu 1972); *i*, *Porcellio laevis* (Nair 1976); *j*, *P. spinicornis* (McQueen and Carnio 1974); *k*, *Hemilepistus reaumuri* (Shachak 1980); *l*, *Armadillidium vulgare* (Paris and Pitelka 1962); *m*, *A. vulgare* (Al-Dabbagh and Block 1981); *n*, *Schizidium tiberianum* (Cohen 1988); *o*, *Armadillo officinalis* (Cohen 1988)

Most mortality is due to climatic factors: high temperatures, drought or flood (see Warburg et al. 1984, for discussion). In *Hemilepistus* 88% of the population is lost before settling down in their burrows (Shachak and Brand 1988). Catastrophic losses due to beach erosions were seen (in *Tylos punctatus*, see Hayes 1977). On the other hand, there is some evidence to suggest that some are affected by competition for 'high quality' food among the survivors (Rushton and Hassall 1987). Apparently, larger broods have lower survivorship under such conditions (Dangerfield 1989). Limited food availability affected the mortality of *Armadillidium nasutum* (Ganter 1984).

## 12.3 Density and Competition in Isopods

There is increasing evidence for inter- and intraspecific competition in terrestrial isopods. It seemed to have affected the female's size at first reproduction (Ganter 1984). Moreover, the percentage of gravid females was reduced in dense populations (Dangerfield 1989). Likewise, density had a negative effect on the growth rate of *Armadillidium vulgare* (Hassall and Dangerfield 1990). Individual pillbugs were smaller in the more dense populations (Dangerfield 1989). Furthermore, in a mixed population of *A. vulgare* and *Porcellio scaber* the growth rate of *A. vulgare* was affected (Dangerfield 1986; Hassall and Dangerfield 1989). Thus, in dense populations there is possibly competition for food items of 'better quality', which reduces growth (Rushton and Hassall 1987). Furthermore, such competition exists between two cohorts (1st year and 2nd year) in *A. vulgare* (Hassall and Dangerfield 1990). The density of *A. vulgare* on grazed sites was about 1.5 times larger than on ungrazed ones (Al-Dabbagh and Block 1981). Similarly, in a mixed population of different isopod species, *Porcellio scaber* is more abundant on heavily grazed plots, whereas *Philoscia muscorum* is more abundant on the slightly grazed ones (Hassall and Dangerfield 1989). The prevention of sheep from grazing in the grassland caused a reversal of this pattern. In recent laboratory studies on the density effects on cohorts ( = age classes) of *Armadillo officinalis*, I was unable to detect any effects of density on the abundance of the pillbugs even after 3 years (in preparation).

## 12.4 Population Fluctuations

The fluctuation in numbers within an isopod population can be largely explained by environmental-climatic factors. This was shown in *Armadillo officinalis*, *Metoponorthus* and *Philoscia*, where the number of isopods increased in response to the previous (last year's) rainy season (Warburg et al. 1984). This study was carried out in an oak woodland within the xeric Mediterranean region with an average of 650 mm rainfall (Warburg et al. 1984). The population size seemed to be affected by the amount of rainfall during the previous rainy season a year ago. In the tropics rainfall affects the population numbers at a much shorter time lag of 2–3 weeks (Ma et al. 1991b). Recently, this relationship was seen also in *Armadillidium vulgare* by Miller and Cameron (1987). In a grassland the abundance of *Trachelipus nodulosus* was correlated with the amount of precipitation (Hornung 1989). In the desert isopod *Hemilepistus* the abundance is correlated with the accumulated amount of rainfall (Shachak and Yair 1984). The fluctuation in population numbers can be small, probably dependent on comparatively constant ambient conditions. This was shown in *Philoscia muscorum* (Sunderland et al. 1976), *Porcellio* *scaber* (Davis and Sutton 1977b) and in *Periscyphis granai* (Kheirallah 1979b). In tropical regions, air temperature was shown to be the main factor affecting the seasonal variations in population density (Ma et al. 1991a).

## 12.5 Population Explosion and Migration

In recent years I have followed very closely an annual phenomenon of an outbreak of large numbers of isopods belonging to a small porcellionid (Fig. 10.8). This takes place during the late summer and autumn on the eastern slopes of the Upper Galil Mts. of Israel. The phenomenon was first described by Warburg et al. (1984). During the period of outbreak an unimaginably large number of isopods emerged from the ground, marching in one direction during day and night irrespective of obstacles (such as houses) on the way. They would climb such high obstacles up to several metres. Eventually they perished in masses. The phenomenon has not been studied ecologically or physiologically but indicates to me that it is a population explosion resulting in a directional movement. During the period the male:female ratio was 1:4. A similar ratio was observed by Shimoizumi (1952) in *Metoponorthus pruinosus* (1:3 male to female). The fact that in this case it seems to be a movement for the sake of moving indicates that it is a migration type of phenomenon (Southwood 1962). A similar phenomenon was previously observed on a single occasion in the Negev Desert, when masses of *Hemilepistus reaumuri* moved in a single direction for over 1 km, but nothing is known of the causes (Warburg et al. 1984). In the early literature, phenomena of this nature have been mentioned in *Porcellio scaber* wandering up houses and in the surroundings of Berlin (Fritsche 1934). Lokke (1966) believes that weather conditions are responsible for such phenomena. The solution will have to await a detailed study.

# 13 Conclusions

Perhaps the most outstanding feature of isopod life is their success in surviving on land. The structural features enabling this life pattern are largely the marsupium, pseudotracheae and cuticle. The marsupium is unique in that it enables an additional sheltered period for the embryos, thus, the emerging mancas will be comparatively mature enough to cope with terrestrial life. The survival rate of these young is probably only about 0.1% (or even less) of their original cohort. Does this survival rate change during a population explosion? Alternatively, is the reproductive pattern disrupted under special (currently unknown) circumstances? We have seen the diversity in reproductive patterns and strategies of the oniscid isopods. What could be the cause for having both semelparous and iteroparous strategies in the same region, habitat or even under the same stone? How can one explain the evolutionary need for the long life expectancy of *Armadillo officinalis*, whereas the short-lived species *Hemilepistus reaumuri* is apparently just as 'successful'. All these subjects need further investigation.

The physiology of terrestrial isopods is on the whole less well-known than that of comparable other arthropod groups such as insects or other crustaceans, the main reason for this being the lack of any economic or medical importance of this group. Consequently, there is much less interest in them by the funding agencies, which makes it more difficult to spend either time or material conducting appropriate research on this group. This is regrettable as many basic features concerning the endocrine control of the colour change or the physiology of the water balance started in such a group as the oniscid isopods. Thus, from an evolutionary point of view their study is indeed rewarding. They can be considered as intermediate steps (although no doubt successful in their own right) to the ultimate goal of the dominant insectan life pattern, to mention only the unique desert isopods, such as *Hemilepistus reaumuri*, diurnal, abundant in the deserts although semelparous and most of all with a social life pattern. This isopod can be compared with any coleopteran or hymenopteran insect in many aspects.

Although much is known in this group, even more needs to be studied in order to gain a better understanding. Some of these areas of research have been pointed out in the text. Other important aspects are discussed below according to their respective subjects

## Cuticle

The study of the isopod integument is still at the descriptive level, but now using modern instrumentation like the TEM and SEM. Diverse forms of cuticular structures have been described, but no known function can be attributed to them. Some structures may be involved in lipid secretion, the water-conducting system, pheromone production or other functions. Future research should combine the study of both structure and function of the integumental organelles.

## Endocrine System

Very little is known about the dynamic changes in endocrine glands or neurosecretory cells. The main routes of endocrinological control of moulting and reproduction demand better understanding. Nothing is known about the endocrine control of excretion, ion and water balance or the behavioural responses. There is a need for experimental physiological research in this field. The approach should combine the extirpation of glands, blocking secretory routes or injecting hormones.

## Respiration

A detailed study of respiration in isopods is greatly needed. The techniques used should be standardized. The procedure should be strict and the experimental period short enough so that other physiological functions will not interfere. The isopod species should be selected carefully, the sex, size and age of the experimental animals should be known, and their physiological condition needs to be monitored. It would be useful to use animals belonging to the same cohort and of known age. Another alternative could be to study size groups (not necessarily of the same age) collected freshly from the same site. Thus, special attention should be taken of moulting or reproductive conditions. It is essential to control ambient conditions throughout the experimental period.

Only after establishing a pattern for respiration of the individual isopod can one start a study at the population level involving metabolism.

## Excretion and Water Loss

Our knowledge of the ultrastructure of the antennal and maxillary glands is rather basic. There is hardly any information on the ultrastructure, cytochemistry or ultracytochemistry of these glands. Likewise, no information is available at the physiological level.

As so little is known about excretion in isopods, in so few species and using old techniques, any new information on this subject will be most useful. Do all terrestrial isopod species have a similar excretory pattern?

Alternatively, does the proportion of ammonia in the nitrogen balance vary among the different species? Is there a relationship between the nitrogenous excretory routes and the degree of terrestrialism? Furthermore, does the excretion change in time during the ontogenesis of the isopod? Is there a rhythmic pattern in excretion, diurnal or annual? What is the relationship between the diet and nitrogenous excretion?

Only after having obtained some information on these subjects is the background set for experimental studies. How does excretion change under different water stress conditions? Is there a response to any of the antidiuretic hormones?

## Behaviour

The behavioural responses of individual isopods ought to be studied as far as possible under semi-natural conditions. New approaches to the subjects involved should combine an integration of behavioural and physiological states. Does the response to humidity or soil moisture change with the water balance of the isopod under natural conditions? Is there a seasonal change? Similarly, what is the role played by chemoreception in the formation of aggregates, in mating or in territorial behaviour?

The phenomenon of the mass migratory movements of isopods ought to be studied by combining physiological, ecological and behavioural approaches. What are the behavioural mechanisms taking part in the orientation of isopod masses under such conditions? Finally, the ambient conditions under such circumstances ought to be defined

Another problem of great significance is: what makes a good colonizing species? We know of a few isopods that are cosmopolitan in their distribution, although they originated in the Mediterranean basin. Such species are *Armadillidium vulgare* and *Porcellionides* ( = *Metoponorthus*) *pruinosus*. The colonizing of a new habitat in another geographical region of different latitude, climate and ambient conditions most likely involves a series of physiological and behavioural adaptations. Feeding habits, reproductive patterns and perhaps behavioural responses all need to be changed.

Not less interesting is the question of restricted distribution ( = endemism). What causes a species to be restricted in its distribution? Is it a specialization in food items, a restricted behavioural pattern or, alternatively, a rather restricted ambient range of moisture/temperature conditions of significance for survival, growth or reproduction?

## Food, Feeding and Resource Utilization

There are very few behavioural studies in which the responses of the isopod towards food items have been analyzed. What kinds of behavioural responses are involved? Is it chemoreaction at first, changing into a gustatory response later? Is photoreception involved in this behaviour? This field is well studied in insects; thus, techniques are available and can be adapted to isopods as well.

What is the meaning of food preference? Does it imply that a food item was selected because it is more tasteful, of better quality, of greater nourishing value or perhaps more abundant? An abundant food item can be obtained at a lower energetic cost. A choice food item may require more searching and can be energetically more costly, as well as more dangerous to the isopod due to enemies or adverse climatic conditions. This subject has received major attention by mammalogists working on foraging strategies in small and large mammals, and their techniques could perhaps be adapted to isopod research as well.

Nothing is known about the significance of various food items to growth or to reproduction. These are long-term studies that need to be planned properly on isopods with known life-history patterns. This study may shed some light on the problem of the role food plays in regulating isopod numbers. Do isopods indeed compete for special food items? This subject ought to be approached by setting up laboratory experiments, preferably with members of a single cohort ( = age class) or of similar size (although possibly of different age).

## Reproductive Strategies

Our understanding of the reproductive strategies of isopods is still very minimal. Only a few species have been studied, and these mostly in the laboratory. There is very little ecological field work combined with laboratory study on this subject. Furthermore, so far, the endocrine control of reproduction is hardly understood. What is the physiological mechanism that causes the disruption of the normal breeding pattern in isopods under unfavourable conditions? Research methods used by insect physiologists could be useful here, too.

The question of what causes continuous breeding in isopods needs to be studied, especially in view of the periodic outbreaks of isopods which are combined with migration.

## Population Studies

There is a special need to combine field studies with laboratory ones under semi-natural conditions. This could be done by using enclosures and following the growth of single cohorts (year classes) over a period of time. Our understanding of 'cohort splitting' is still elementary. What is the cause of this differential growth in isopods? Is it genetically controlled and a result of multi-parenthood? Perhaps it is environmentally controlled, and different members of the cohort grow at a greater speed under certain conditions (moisture, food), whereas others grow better under other conditions. This way the continuous survival of the species can be assured, because the two different parts of the cohort will breed during different seasons. As a result, environmental catastrophies can be avoided.

# References

Ábrahám A, Wolsky A (1930a) Über ein neues Sinnesorgan der Landisopoden. Zool Anz 87: 88–93

Ábrahám A, Wolsky A (1930b) Die Geruchsorgane der Landisopoden. Z Morphol Ökol Tiere 17: 441–463

Akahira Y (1956) The function of thoracic processes found in females of the common wood-louse, *Porcellio scaber*. J Fac Sci Hokkaido Univ Ser VI Zool 12: 493–498

Al-Dabbagh KY, Block W (1981) Population ecology of a terrestrial isopod in two breckland grass heaths. J Anim Ecol 50: 61–67

Al-Dabbagh KY, Marina BA (1985) The effect of starvation and breeding conditions on the respiration rate of *Metoponorthus pruinosus* (Brandt). Ekol Pol 33: 705–714

Al-Dabbagh KY, Marina BA (1986) Relationship between oxygen uptake and temperature in the terrestrial isopod *Porcellionides pruinosus*. J Arid Environ 11: 227–233

Alexander CG (1969) Structure and properties of mechanoreceptors in the pereiopods of *Ligia oceanica* Linn. (Crustacea, Isopoda). Comp Biochem Physiol 29: 1197–1205

Alexander CG (1970) Studies on the nervous system of an isopod crustacean, *Ligia oceanica*. Comp Biochem Physiol 33: 323–332

Alexander CG (1971) Observations on receptor mechanisms in *Ligia oceanica* (Linn.). Comp Biochem Physiol 40A: 339–347

Alexander CG (1977) Antennal sense organs in the isopod *Ligia oceanica* (Linn.). Mar Behav Physiol 5: 61–77

Alexander DE, Chen T (1989) The respiratory roles of swimming and non-swimming pleopods in isopod crustaceans. Comp Biochem Physiol 94A: 689–692

Alikhan MA (1968) The internal anatomy of the woodlouse *Metoponorthus pruinosus* (Brandt) (Porcellionidae, Peracarida). Can J Zool 46: 321–327

Alikhan MA (1969a) The physiology of the woodlouse, *Porcellio laevis* Latreille (Porcellionidae, Peracarida). I. Studies on the gut epithelium cytology and its relation to maltase secretion. Can J Zool 47: 65–75

Alikhan MA (1969b) The physiology of the woodlouse, *Porcellio laevis* (Porcellionidae: Peracarida) III. A study of the relationship of the a-glucosidase production and the cytology of the glandula intestini. Entomol Exp Appl 12: 275–287

Alikhan MA (1971) The fine structure of the midgut epithelium in the woodlouse, *Porcellio laevis* Latreille (Isopoda, Porcellionidae). Crustaceana Suppl 3: 101–109

Alikhan MA (1972a) Haemolymph and hepatopancreas copper in *Porcellio laevis* Latreille (Porcellionidae, Peracarida). Comp Biochem Physiol 42A: 823–832

Alikhan MA (1972b) Changes in the hepatopancreas metabolic reserves of *Porcellio laevis* latreille during starvation and moult-cycle. Am Midl Nat 87 : 503–514

Alikhan MA (1973) Ionic content of the haemolymph in *Porcellio laevis* Latreille (Porcellionidae, Isopoda). Comp Biochem Physiol 44A : 47–54

Alikhan MA (1983a) Oxygen consumption and haemolymph pressure measurements in *Armadillidium vulgare* (Latreille) (Armadillidiidae : Isopoda) during ecdysis. J Crustacean Biol 3 : 25–33

Alikhan MA (1983b) Physiological adaptations in Crustacea to the environment: oxygen consumption as a function of body weight and environmental temperature in the terrestrial isopod *Porcellio laevis* Latreille (Isopoda, Oniscoidea). Crustaceana 36 : 277–286

Alikhan MA (1989) Magnesium and manganese regulation during moult-cycle in *Porcellio spinicornis* Say (Porcellionidae, Isopoda). Bull Environ Contam Toxicol 42 : 699–706

Alikhan MA (1990) Effects of temperature and dietary magnesium and nickel levels on magnesium and nickel concentrations during the moult-cycle in *Oniscus asellus* (Porcellionidae, Isopoda, Crustacea). Arch Int Physiol Biochim 98 : 11–18

Alikhan MA (1991) Effects of temperature and copper and nickel accumulations on the metabolic rate and membrane electrical potential of the hepatopancreatic cells of *Oniscus asellus* Linnaeus (Porcellionidae, Isopoda, Crustacea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 149–155

Alikhan MA, Pani AK (1988) The effect of magnesium and manganese uptake and accumulation on oxygen consumption and ammonia excretion in *Porcellio spinicornis* Say (Porcellionidae, Isopoda). Arch Int Physiol Biochim 96 : 147–154

Alikhan MA, Pani AK (1989) Magnesium and manganese uptake and accumulation in the body tissue and their effect on the oxygen and nitrogen metabolism in *Porcellio spinicornis* Say 1818 (Porcellionidae, Isopoda). Monit Zool Ital (NS) Monogr 4 : 211–225

Alikhan MA, Saleem M (1977) The role of phosphomonoesterases in the development and the moult-cycle in *Porcellio laevis* Latreille (Porcellionidae, Isopoda). Zool Pol 26 : 177–185

Alikhan MA, Storch V (1990) Copper and nickel uptake and accumulation, and their effects on redox and electrical potentials of hepatopancreatic cells of *Oniscus asellus* Linnaeus (Porcellionidae, Isopoda). Can J Zool 68 : 651–655

Allee WC (1926) Studies in animal aggregations: causes and effects of bunching in land isopods. J Exp Zool 45 : 255–277

Armitage KB (1960) Chromatophore behavior in the isopod *Ligia occidentalis* Dana, 1853. Crustaceana 1 : 193–207

Aubin PA (1914) Some notes on the terrestrial Isopoda. J Econ Biol 9 : 15–20

Auzou ML (1953) Recherches biologiques et physiologiques sur deux isopodes onisciens : *Porcellio scaber* Lat. et *Oniscus asellus* L. Ann Sci Nat 11 Ser: 71–98

Babula A (1979) Structure of the respiratory organs of the fresh-water isopod *Asellus aquaticus* L. (Crustacea). Bull Soc Amis Sci Lett Poznan Sci Biol 19 : 75–82

Babula A (1981) Scanning electron microscope investigations of the external surface of respiratory organs of *Porcellio scaber* Latr. (Isopoda; Crustacea).

Bull Soc Amis Sci Lett Poznan Ser D Sci Biol 21 : 47–50

Babula A, Bielawski J (1976) Ultrastructure of respiratory epithelium in the terrestrial isopod *Porcellio scaber* Latr. (Crustacea). Ann Med Sect Pol Acad Sci 21 : 7–8

Babula A, Bielawski J (1981) Ultramorphological study of gill epithelium in *Mesidotea entomon* (L.) (Isopoda, Crustacea). Bull Soc Amis Sci Lett Poznan Ser D Sci Biol 21 : 51–58

Bagatto G, Alikhan MA (1986) Effects of growth-stage and nutritional status on the oxygen consumption and ammonia production in *Porcellio spinicornis* Say (Isopoda, Porcellionidae). Crustaceana 51 : 1–8

Barlow CA, Kuenen DJ (1957) A new thermopreferendum apparatus used for terrestrial isopods I. K Ned Akad Wet-Amsterdam Ser C 60 : 240–254

Barmeyer RA (1975) Predation on the isopod crustacean *Porcellio scaber* by the theridiid spider *Steatoda grossa*. Bull South Calif Acad Sci 74 : 30–36

Barnes TC (1932) Salt requirements and space orientation of the littoral isopod *Ligia* in Bermuda. Biol Bull 63 : 496–504

Barres F, Chaigneau J (1981) Étude en microscopie électronique à balayage de l'organe de Bellonci du crustacé isopode *Sphaeroma serratum*, et comparaison avec les observations en microscopie à transmission. Ann Sci Nat Zool Paris 13th 3 : 191–201

Bateman JB (1933) Osmotic and ionic regulation in the shore crab, *Carcinus maenas*, with notes on the blood concentrations of *Gammarus locusta* and *Ligia oceanica*. J Exp Biol 10 : 355–371

Bauers C (1953) Über die Orientierung wirbelloser Tiere zum Licht. Zool Jahrb Physiol 64 : 348–388

Bayly IAE, Ellis P (1969) *Haloniscus searlei* Chilton: an aquatic "terrestrial" isopod with remarkable powers of osmotic regulation. Comp Biochem Physiol 31 : 523–528

Beck L, Brestowsky E (1980) Auswahl und Verwertung verschiedener Fallaubarten durch *Oniscus asellus* (Isopoda). Pedobiologia 20 : 428–441

Becker FD, Mann ME (1938) The reproductive system of the male isopod, *Porcellio scaber* Latreille. Trans Am Microsc Soc 57 : 395–399

Becker-Carus C (1966) Zur geschlechtlichen Differenzierung der Keimdrüsen in der Gattung *Armadillidium* (Crust. Isop.). Zool Anz 176 : 235–253

Bellonci G (1886) Intorno al ganglio ottico degli artropodi superiori. Int Monatsschr Anat Histol Physiol 3 : 195–204

Bepler H (1909) Über die Atmung der Oniscoideen. Ph D Thesis, Universität Greifswald, 49 pp.

Besse G, Picaud JL, Mocquard JP (1975) Étude d'une population de *Ligia oceanica* L. (Crustacé, Isopode) de la Cote Charentaise. II. Le cycle de reproduction et les variations saisonnières de la biomasse. Bull Ecol 6 : 67–78

Bettica A, Shay MT, Vernon G, Witkus R (1984) An ultrastructural study of cell differentiation and associated acid phosphatase activity in the hepatopancreas of *Porcellio scaber*. Symp Zool Soc Lond 53 : 199–215

Bettica A, Witkus R, Vernon GM (1987) Ultrastructure of the foregut-hindgut junction in *Porcellio scaber* Latreille. J Crustacean Biol 7 : 619–623

Beyer R (1957/58) Ökologische und brutbiologische Untersuchungen an Landisopoden der Umgebung von Leipzig. Wiss Z Karl-Marx-Univ Leipz Math Naturwiss Reihe 7 : 291–308

Beyer R (1964) Faunistisch-ökologische Untersuchungen an Landisopoden in Mitteldeutschland. Zool Jahrb Syst 91:341–402

Beyer R (1965) Über den Einfluss des Lichtes auf die Entwicklung der Landasseln (Crustacea: Isopoda). Pedobiologia 5:122–130

Bielawski J, Babula A (1980) Respiratory epithelium of *Porcellio scaber* Latr. (Isopoda, Crustacea). Bull Soc Amis Sci Lett Poznan Sci Biol 20:85–94

Biliński S (1979) Ultrastructural study of yolk formation in *Porcellio scaber* Latr. (Isopoda). Cytobios 26:123–130

Biwer A (1961) Quantitative Untersuchungen über die Bedeutung der Asseln und der Bakterien für die Fallaubzersetzung unter Berücksichtigung der Wirkung künstlicher Düngemittelzusätze, Teil I. Z Angew Entomol 48:307–328

Bizé V, Célérier ML (1986) Étude d'une écosystème forestier mixte. XI. Contribution à la connaissance du bilan énegétique de *Philoscia muscorum* (Scopoli 1763) (cructacé, isopode). Rev Ecol Biol Sol 23:259–269

Blinn DW, Blinn SL, Bayly IAE (1989) Feeding ecology of *Haloniscus searlei* Chilton an oniscoid isopod living in athalassic saline waters. Aust J Mar Freshwater Res 40:295–301

Bobretzky N (1874) Zur Embryologie des *Oniscus murarius.* Z Wiss Zool 24:179–203

Bocquet-Vedrine J (1979) Role des espaces intercellulaires epitheliaux dans le transport de l'eau lors de l'exuviation chez un crustace: *Crinoniscus equitans* Perez (isopode cryptonisciens). C R Acad Sci Paris 288:1479–1481

Bodenheimer FS (1935) Animal life in Palestine. Mayer, Jerusalem, 506 pp

Böhm GA, Eibisch H (1976) Untersuchungen zum Mineralstoffwechsel der Crustaceen *Orconectes limosus* (Decapoda) und *Armadillidium nasutum* (Isopoda) in der Vorhäutungsphase. Zool Jahrb Physiol 80:175–183

Böhm GA, Gersch M (1976) Experimentelle Untersuchungen zur stadienspezifischen hormonalen Regulation der Häutung von *Armadillidium nasutum* (Crustacea, Isopoda). Zool Jahrb Physiol 80:371–382

Bouchon D, Chaigneau J (1991) Comparison of cuticular adhesive structures linking anatomical parts in Crustacea, and thier adaptative significance (Decapoda and Isopoda). Crustaceana 60:7–17

Brecko D, Licar P, Rode J, Struš J (1991) Microscopic anatomy of the foregut-hindgut junction in terrestrial isopods (Isopoda, Crustacea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 201–202

Brereton J Le G (1957) The distribution of woodland isopods. Oikos 8:85–106

Breymeyer A, Brzozowska D (1967) Density, activity and consumption of Isopoda on a Stellario-Deschampsietum meadow. In: Phillipson J (ed) Methods of study of soil ecology. UNESCO, New York, pp 225–230

Brody MS, Lawlor LR (1984) Adaptive variation in offspring size in the terrestrial isopod, *Armadillidium vulgare.* Oecologia (Berl) 61:55–59

Brody MS, Edgar MH, Lawlor LR (1983) A cost of reproduction in a terrestrial isopod. Evolution 37:653–655

Brooks JL (1942) Notes on the ecology and the occurrence in America of the myrmecophilous sowbug, *Platyarthrus hoffmanseggi* (Brandt). Ecology 23:427–437

Brown MF, Steinberger Y (1983) The importance of geological formations and slope aspect to desert isopod survival. J Arid Environ 6:373–384

Bubel A (1976) Histological and electron microscopical observations on the effects of different salinities and heavy metal ions, on the gills of *Jaera* *nordmanni* (Rathke) (Crustacea, Isopoda). Cell Tissue Res 167 : 65–95

Bubel A, Jones MB (1974) Fine structure of the gills of *Jaera nordmanni* (Rathke) [Crustacea, Isopoda]. J Mar Biol Assoc UK 54 : 737–743

Bukhari NA, Alikhan MA (1984) The energy budget of *Porcellio spinicornis* Say (Porcellionidae, Isopoda) under laboratory conditions. Arch Int Physiol Biochim 92 : 73–79

Bursell E (1955) The transpiration of terrestrial isopods. J Exp Biol 32 : 238–255

Carefoot TH (1973a) Feeding, food preference, and the uptake of food energy by the supralittoral isopod *Ligia pallasii*. Mar Biol 18 : 228–236

Carefoot TH (1973b) Studies on the growth, reproduction and life cycle of the supralittoral isopod *Ligia pallasii*. Mar Biol 18 : 302–311

Carefoot TH (1979) Microhabitat preferences of young *Ligia pallasii* Brandt (Isopoda). Crustaceana 36 : 209–214

Carefoot TH (1984a) Studies on nutrition of the supralittoral isopod *Ligia pallasii* using chemically defined artificial diets: assesment of vitamin, carbohydrate, fatty acid, cholesterol and mineral requirements. Comp Biochem Physiol 79A : 655–665

Carefoot TH (1984b) Nutrition and growth of *Ligia pallasii*. Symp Zool Soc Lond 53 : 455–467

Carefoot TH (1989) Diet and its effect on oxygen consumption in the semiterrestrial isopod *Ligia*. Monit Zool Ital (NS) Monogr 4 : 193–210

Carefoot TH, Mann M, Kalv̌a S (1991) The effect of desiccation on oxygen uptake in terrestrial isopods. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 157–164

Carlisle DB (1956) Studies on the endocrinology of isopod crustaceans. Moulting in *Ligia oceanica* (L.) J Mar Biol Assoc UK 35 : 515–520

Carlisle DB, Knowles F (1959) Endocrine control in crustaceans. Univ. Press, Cambridge, 120 pp

Castrucci AM de, Mendes EG (1975) Ultrastructure of the pigmentary system and chromatophorotropic activity in land isopods. Biol Bull (Woods Hole) 149 : 467–479

Cervek S, Blejec A, Potochnik F (1983) Dekomposzicija ekskrementov mokrice *Porcellio scaber* latreille (Isopoda) v naravnih pogojih. Biol Vestn 31 : 107–128

Chaigneau J (1971) L'organe de Bellonci du crustacé isopode *Sphaeroma serratum* (Fabricius). Ultrastructure significant. Z. Zellforsch 112 : 166–187

Chaigneau J (1978) L'organe de Bellonci des Crustacés. Historique et état actuel de nos connaissances. Arch Zool Exp Gén 119 : 185–199

Chaigneau J (1985) Neurohemal organs in Crustacea. In: Gupta AP (ed) Neurohemal organs of arthropods. Thomas, Springfield, pp 53–89

Chaigneau J, Chataigner JP (1977) The connections of the sensory organ of Bellonci with the brain in Isopoda (Crustacea). Cell Tissue Res 182 : 61–72

Charmantier G (1980) Contrôle endocrine et neuroendocrine de la mue de puberté chez les mâles de *Sphaeroma serratum* (Fabricius, 1787) (Crustacea, Isopoda, Flabellifera). Gen Comp Endocrinol 41 : 349–364

Charmantier G (1982) Les glandes cephaliques de *Paragnathia formica* (Hesse, 1864) (Isopoda, Gnathiidae): localisation et ultrastructure. Crustaceana 42 : 179–193

Charmantier G, Trilles JP (1976) Ecdysterone, premue et exuviation chez *Sphaeroma serratum* (Fabricius, 1787) (Crustacea, Isopoda, Flabellifera). Gen Comp Endocrinol 28 : 249–254

Charmantier G, Trilles JP (1977a) Contrôle endocrine des phénomènes de la mue par les organes Y chez *Sphaeroma serratum* (Fabricius 1787) (Crustacea, Isopoda, Flabellifera). C R Acad Sci Paris Ser D 285 : 905–908

Charmantier G, Trilles JP (1977b) Influence des glandes antennaires sur la regulation ionique, la teneur en eau et eventuellement la mue de *Sphaeroma serratum* (Crustacea, Isopoda, Flabellifera). Gen Comp Endocrinol 31 : 295–301

Charmantier G, Trilles JP (1979) La dégénérescence de l'organe Y chez *Sphaeroma serratum* (Fabricius, 1787) (Isopoda, Flabellifera): étude ultrastructurale. Crustaceana 36 : 29–38

Charmantier G, Ollé M, Trilles JP (1977) Évolution du taux d'ecdystérone, dégénérescence des organes Y et sénescence chez les mâles pubères de *Sphaeroma serratum* (Fabricius, 1787) (Crustacea, Isopoda, Flabellifera). C R Acad Sci Paris 285 : 1487–1489

Chataigner JP, Martin G, Juchault P (1978) Etude histologique, cytologique, et expérimentale des centres neurosécréteurs céphaliques du flabellifère *Sphaeroma serratum* (crustacé, isopode). Gen Comp Endocrinol 35 : 52–69

Chelazzi G, Ferrara F (1978) Researches on the coast of Somalia, the shore and the dune of Sar Uanle. 19. Zonation and activity of terrestrial isopods (Oniscoidea). Monit Zool Ital NS Suppl XI 8 : 189–219

Chiang RG, Steel CGH (1984) Neuroendocrinology of growth and moulting in terrestrial isopods. Symp Zool Soc Lond 53 : 109–125

Chiang RG, Steel CGH (1985a) Structural organization of neurosecretory cells terminating in the sinus gland of the terrestrial isopod, *Oniscus asellus*, revealed by paraldehyde fuchsin and cobalt backfilling. Can J Zool 63 : 543–549

Chiang RG, Steel CGH (1985b) Ultrastructure and distribution of identified neurosecretory terminals in the sinus gland of the terrestrial isopod *Oniscus asellus*. Tissue Cell 17 : 405–415

Chiang RG, Steel CGH (1985c) Coupling of electrical activity from contralateral sinus glands. Brain Res 331 : 142–144

Chiang RG, Steel CGH (1986) Electrical activity of the sinus gland of the terrestrial isopod, *Oniscus asellus*: characteristics of identified potentials recorded extracellularly from the neurosecretory terminals. Brain Res 377 : 83–95

Chiang RG, Steel CGH (1987) Changes during the moult cycle in the bursting firing pattern of the electrical activity recorded extracellularly from the sinus gland of the terrestrial isopod, *Oniscus asellus*. Brain Res 402 : 49–57

Chiang RG, Steel CGH (1989) Neurobiology of the brain-sinus gland neurosecretory system of the terrestrial isopod *Oniscus asellus* L.1758. Monit Zool Ital (NS) Monogr 4 : 333–349

Clifford B, Witkus ER (1971) The fine structure of the hepatopancreas of the woodlouse, *Oniscus asellus*. J Morphol 135 : 335–350

Cloudsley-Thompson JL (1952) Studies in diurnal rhythms II. Changes in the physiological responses of the woodlouse *Oniscus asellus* to environmental stimuli. J Exp Biol 29 : 295–303

Cloudsley-Thompson JL (1956a) 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

Cloudsley-Thompson JL (1956b) Studies in diurnal rhythms VII. Humidity responses and noturnal activity in woodlice (Isopoda). J Exp Biol 33 : 576–582

Cloudsley-Thompson JL (1969) Acclimation, water and temperature relations of the woodlice *Metoponorthus pruinosus* and *Periscyphis jannonei* in the Sudan. J Zool Lond 158 : 267–276

Cloudsley-Thompson JL (1974) Climatic factors affecting the nocturnal emergence of woodlice and other arthropods. Entomol Mon Mag 109 : 123–124

Cloudsley-Thompson JL (1975) Adaptations of Arthropoda to arid environments. Ann Rev Entomol 20 : 261–283

Cloudsley-Thompson JL (1977) The water and temperature relations of woodlice. Meadowfield Press, Durham, 84 pp

Cloudsley-Thompson JL, Constantinou C (1987) Humidity reactions and aggregation in woodlice (Isopoda, Oniscoidea). Crustaceana 53 : 43–48

Coenen-Stass D (1981) Some aspects of the water balance of two desert woodlice, *Hemilepistus aphganicus* and *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). Comp Biochem Physiol 70A : 405–419

Coenen-Stass D (1984a) Die kutikuläre Wasserdampfabsorption bei Landasseln (Crustacea, Isopoda, Oniscoidea). Ein Vergleich zwischen der Wüstenassel *Hemilepistus reaumuri* und den einheimischen Asselarten *Porcellio scaber* und *Armadillidium vulgare*. Verh Dtsch Zool Ges 77 : 156

Coenen-Stass D (1984b) Observations on the distribution of the desert woodlouse *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea) in North Africa. Symp Zool Soc Lond 53 : 369–380

Coenen-Stass D (1985) Effects of desiccation and hydration on the osmolality and ionic concentration in the blood of the desert woodlouse *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). Comp Biochem Physiol 81B : 717–721

Cohen N (1988) Soil invertebrate communities in the Segev wood. Population structure and reproductive strategies of two pillbugs: *Armadillo officinalis* and *Schizidium tiberianum* in the Segev wood. M Sc Thesis, Technion, Haifa, 119 pp (in Hebrew)

Cole LJ (1907) An experimental study of the image-forming powers of various types of eyes. Proc Am Acad Arts Sci 42 : 335–417

Cole LC (1946) A study of the cryptozoa of an Illinois woodland. Ecol Monogr 16 : 49–86

Cole LC (1954) The population consequences of life history phenomena. Q Rev Biol 29 : 103–137

Collinge WE (1915) Some observations on the life-history and habits of the terrestrial Isopoda (woodlice). Scott Nat, pp 299–307

Collinge WE (1941) Notes on the terrestrial Isopoda (Woodlice). VIII. On the reproduction of woodlice. Northwest Nat 1941 : 251–253

Collinge WE (1946) The duration of life in terrestrial Isopoda. Ann Mag Nat Hist 13 : 719–720

Colosi I de S (1933) L'assunzione dell'acqua per via cutanea. Publ Staz Zool Napoli 131 : 12–38

Compere P (1991) Fine structure and elaboration of the epicuticle and the pore canal system in tergite cuticle of the land isopod *Oniscus asellus* during a moulting cycle. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 169–175

Constantinou C, Cloudsley-Thompson JL (1987) Water relations of some woodlice (Oniscoidea) from arid and mesic environments. Qatar Univ Sci Bull 7 : 203–216

Coruzzi L, Witkus R, Vernon GM (1982) Function-related structural characters and their modifications in the hindgut epithelium of two terrestrial isopods, *Armadillidium vulgare* and *Oniscus asellus*. Exp Cell Biol 50: 229–240

Coughtrey PJ, Martin MH, Chard J, Shales SW (1980) Micro-organisms and metal retention in the woodlouse *Oniscus asellus*. Soil Biol Biochem 12: 23–27

Couteaux MM, Celerier ML, Bottner P (1991) *Oniscus asellus* (Isopoda) as a participant in food webs with increasing complexity in the decomposition of sweet chestnut leaf litter produced in ambient air and in $CO_2$ enriched atmosphere. In: Juchault P, Mocguard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 49–55

Cruz AA de la (1963) Observations on the feeding activity of the isopod, *Idothea baltica* (Pallas). Publ Seto Mar Biol Lab 11: 165–170

Dallinger R (1977) The flow of copper through a terrestrial food chain III. Selection of an optimum copper diet by isopods. Oecologia (Ber) 30: 273–276

Dallinger R, Prosi F (1988) Heavy metals in the terrestrial isopod *Porcellio scaber* Latreille. II. Subcellular fractionation of metal-accumulating Iysosomes from hepatopancreas. Cell Biol Toxicol 4: 97–109

Dallinger R, Wieser W (1977) The flow of copper through a terrestrial food chain. I. Copper and nutrition in isopods. Oecologia (Berl) 30: 253–264

Dangerfield JM (1989) Competition and the effects of density on terrestrial isopods. Monit Zool Ital (NS) Monogr 4: 411–423

Dangerfield JM, Telford SR (1990) Breeding phenology, variation in reproductive effort and offspring size in a tropical population of the woodlouse *Porcellionides pruinosus*. Oecologia 82: 251–258

Dangerfield JM, Telford SR (1991) Distribution patterns of *Aphiloscia maculicornis* Budde Lund (Crustacea, Oniscidea) in a moist tropical forest above Victoria Falls, Zimbabwe. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 57–63

Davis RC (1989) Rates of water loss and survival of some Kenyan woodlice in relation to the habitat in which they live. Monit Zool Ital (NS) Monogr 4: 227–247

Davis RC, Sutton SL (1977a) Spatial distribution and niche separation of woodlice and millipedes in a dune grassland ecosystem. In: Soil organisms as components of ecosystems. Ecol Bull (Stockh) 25: 45–55

Davis RC, Sutton SL (1977b) A comparative study of changes in biomass of isopods inhabiting dune grassland. Sci Proc R Dublin Soc 6A: 223–233

Davis RC, Hassall M, Sutton SL (1977) The vertical distribution of isopods and diplopods in a dune grassland. Pedobiologia 17: 320–329

Debry JM, Lebrun P (1979) Effets d'un enrichissement en $CuSO_4$ sur le bilan alimentaire de *Oniscus asellus* (Isopoda). Rev Écol Biol Sol 16: 113–124

Debry JM, Muyango S (1979) Effets du cuivre sur le bilan alimentaire de *Oniscus asellus* (Isopoda) avec réference particulière au cuivre contenu dans le lisier de porcs. Pedobiologia 19: 129–137

Delaleu JC, Giry G (1967) Les organes neuro-hémaux céphaliques et leurs corrélations avec l'organe Y, le systeme stomatogastrique et le tronc cardiaque chez l'oniscoide *Helleria brevicornis* (Ebner). C R Acad Sci Paris 264: 641–642

Demassieux C (1979) Le système neurosécréteur du crustacé isopode *Asellus aquaticus* (Linné). Crustaceana 37: 71–79

Demassieux C, Balesdent ML (1977) Les cellules à caractère neurosécréteur des ganglions cérébraux et de la chaine nerveuse chez le crustacé isopode *Asellus aquaticus* Linné. Variations cycliques des cellules de type ß en fonction de la reproduction. C R Acad Sci Paris 284:207–210

Demassieux C, Balesdent ML (1978) Variations cycliques des cellules neurosécrétrices protocérébrales de type ß en fonction de la physiologie sexulle chez le crustacé isopode *Asellus aquaticus* L. femelle. Arch Biol 89:89–105

Den Boer PJ (1961) The ecological significance of activity patterns in the woodlouse *Porcellio scaber* Latr. (Isopoda). Arch Néer Zool 14:283–409

Dorgelo J (1981) Blood osmoregulation and temperature in crustaceans. Hydrobiologia 81:113–130

Dresel EIB, Moyle V (1950) Nitrogenous excretion of amphipods and isopods. J Exp Biol 27:210–225

Dubinsky Z, Steinberger Y, Shachak M (1979) The survival of the desert isopod *Hemilepistus reaumurii* (Audouin) in relation to temperature (Isopoda, Oniscoidea). Crustaceana 36:147–154

Dudgeon D, Ma HHT, Lam PKS (1990) Differential palatability of leaf litter of four sympatric isopods in a Hong Kong forest. Oecologia 84:398–403

Ebbe B (1981) Beitrag zur Morphologie, Ultrastruktur und Funktion des Respirationsapparates von *Tylos granulatus* Krauss (Isopoda, Oniscoidea). Zool Jahrb Anat 105:551–570

Ebisuno T, Takimoto M, Takeda N (1982) Preliminary characterization of the aggregation pheromone in the sow bug, *Porcellionides pruinosus* (Brandt) (Isopoda:Oniscoidea). Appl Entomol Zool 17:584–586

Edney EB (1951a) The evaporation of water from woodlice and the millipede *Glomeris*. J Exp Biol 28:91–115

Edney EB (1951b) The body temperature of woodlice. J Exp Biol 28:271–280

Edney EB (1953) The temperature of woodlice in the sun. J Exp Biol 30:331–349

Edney EB (1954) Woodlice and the land habitat. Biol Rev (Camb) 29:185–219

Edney EB (1957) The water relations of terrestrial arthropods. Cambridge Univ. Press, 109pp

Edney EB (1964a) Acclimation to temperature in terrestrial isopods. I. Lethal temperatures. Physiol Zool 37:364–377

Edney EB (1964b) Acclimation to temperature in terrestrial isopods. II. Heart rate and standard metabolic rate. Physiol Zool 37:378–394

Edney EB (1967) Water balance in desert arthropods. Science 156:1059–1066

Edney EB (1968) Transition from water to land in isopod crustaceans. Am Zool 8:309–326

Edney EB (1977) Water balance in land arthropods. Springer, Berlin, Heidelberg New York, 282 pp

Edney EB, Spencer JO (1955) Cutaneous respiration in woodlice. J Exp Biol 32:256–269

Edney EB, Allen W, McFarlane J (1974) Predation by terrestrial isopods. Ecology 55:428–433

Elkaim B, Hoestlandt H, Lejuez R, Plateaux L (1980) Sur le thermopreferendum de *Sphaeroma serratum* (F.) (isopode flabellifere). Arch Zool Exp Gen 121:87–96

El-Kifl AH, Wafa AK, Shafiee MF, Shereef GM (1970) Studies on land Isopoda in Giza region. Bull Soc Entomol Egypte 54:283–317

Ellenby C (1951) Body size in relation to oxygen consumption and pleopod beat in *Ligia oceanica* L. J Exp Biol 28 : 492–507

Enami M (1941a) Melanophore responses in an isopod crustacean, *Ligia exotica* I. General responses. Jpn J Zool 9 : 497–514

Enami M (1941b) Melanophore responses in an isopod crustacean, *Ligia exotica.* II. Humoral control of melanophores. JpnJ Zool 9 : 515–531

Enright JT (1972) A virtuoso isopod, circa-lunar rhythms and their tidal fine structure. J Comp Physiol 77 : 141–162

Enright JT (1976) Plasticity in an isopod's clockworks: shaking shapes form and affects phase and frequency. J Comp Physiol 107 : 13–37

Farr JA (1978) Orientation and social behavior in the supralittoral isopod *Ligia exotica* (Crustacea: Oniscoidea). Bull Mar Sci 28 : 659–666

Federici BA (1984) Diseases of terrestrial isopods. Symp Zool Soc Lond 53 : 233–245

Ferrara F, Maschwitz U, Steghaus Kovač S, Taiti S (1987) The genus *Exalloniscus* Stebbing, 1911 (Crustacea, Oniscidea) and its relationship with social insects. Publ Istit Entomol Univ Pavia 36 : 43–46

Ferrara F, Paoli P, Taiti S (1991) Morphology of the pleopodal lungs in the Eubelidae (Crustacea, Oniscidea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 9–16

Fincham AA (1973) Rhythmic swimming behaviour of the New Zealand sand beach isopod *Pseudaega punctata* Thomson. J Exp Mar Biol Ecol 11 : 229–237

Fincham AA (1974) Rhythmic swimming of the isopod *Exosphaeroma obtusum* (Dana). N Z J Mar Freshwater Res 8 : 655–662

Fingerman M (1987) The endocrine mechanisms of crustaceans. J Crustacean Biol 7 : 1–24

Fingerman M, Oguro C (1963) Hormonal control of the reflecting retinal pigment in the isopod *Ligia olfersi* Brandt. Tulane Stud Zool 11 : 75–78

Fischbach E (1954) Licht-, Schwere- und Geruchssin bei Isopoden. Zool Jahrb Allg Zool Physiol Tiere 65 : 141–170

Flasarova M (1967) Die Morphologie des Magens einiger Arten der Familien Trichoniscidae Sars und Buddelundiellidae Verhoeff (Isopoda, Oniscoidea). Acta Soc Zool Bohemoslav 31 : 197–212

Fogarty CT, Witkus R (1989) A comparative cytophotometric study of the epithelial cell nuclei of the hindgut and hepatopancreas of *Porcellio scaber* Latreille, 1804 (Crustacea Isopoda). Monit Zool Ital (NS) Monogr 4 : 175–190

Frankel B, Sutton SL, Fussey GD (1981) The sex ratios of *Trichoniscus pusillus* Brandt (Crustacea: Oniscoidea). J Nat Hist 15 : 301–307

Frenzel J (1884) Über die Mitteldarmdrüse der Crustaceen. Mitt Zool Staz Neapel 5 : 50–101

Friedländer CP (1964) Thigmokinesis in woodlice. Anim Behav 12 : 164–174

Friedländer CP (1965) Aggregation in *Oniscus asellus* Linn. Anim Behav 13 : 342–346

Friedrich H (1883) Die Geschlechtsverhältnisse der Onisciden. Z Naturwiss 56 : 447–474

Fritsche H (1934) Über Wanderungen von *Porcellio scaber* (Sars). Zool Anz 107 : 62–64

Fritz RS, Stamp NE, Halverson TG (1982) Iteroparity and semelparity in insects. Am Nat 120 : 264–268

Fuse H, Yamamoto Y (1985) Neuroendocrine system on the color change in the isopod crustacean, *Ligia exotica*. Zool Sci 2 : 969

Gabe M (1952a) Sur l'existence d'un cycle sécrétoire dans la glande du sinus (organe pseudofrontal) chez *Oniscus asellus* L. CR Acad Sci Paris 235 : 900–902

Gabe M (1952b) Particularités hitologiques de la glande du sinus et de l'organe X (organe de Bellonci) chez *Sphaeroma serratum* Fabr. CR Acad Sci Paris 235 : 973–975

Gabe M (1966) Neurosecretion. Pergamon Press, Oxford, 872 pp

Ganter PF (1984) The effects of crowding on terrestrial isopods. Ecology 65 : 438–445

George RW, Sheard K (1954) Ecdysis in the isopod *Porcellio scaber* (Latreille). Aust J Zool 2 : 75–85

Gere G (1956) The examination of the feeding biology and the humificative function of Diplopoda and Isopoda. Acta Biol 6 : 257–271.

Gere G (1959) Beobachtungen über die Entwicklung des *Protracheoniscus amoenus* C.L. Koch im Freiland. Opusc Zool (Budap) 3 : 29–36

Gere G (1962) Nahrungsverbrauch der Diplopoden und Isopoden in Freilandsuntersuchungen. Acta Zool Acad Sci Hung 7 : 385–416

Gersch M, Eibisch H (1976) Der Blutzuckergehalt von *Armadillidium nasutum* (Crustacea, Isopoda). Zool Jahrb Physiol 80 : 267–273

Ghabbour SI, Rizk MA (1979) Patterns of growth and body water content in xeric and mesic isopods. Pedobiologia 19 : 18–25

Giesel JT (1976) Reproductive strategies as adaptations to life in temporally heterogeneous environments. Annu Rev Ecol Syst 7 : 57–79

Girard P, Maissiat R (1983) Variations du taux des ecdystéroides hémolymphatiques chez le mâle de *Ligia oceanica* (L.) (Cructacea, Isopoda, Oniscoidea) en fonction du cycle de mue et des modifications structurales de l'organe Y. Can J Zool 61 : 534–538

Gohar M, Souty C (1984) Action temporelle d'ecdystéroides sur la synthese protéique ovarienne in vitro chez le crustacé isopode terrestre *Porcellio dilatatus* (Brandt). Reprod Nutr Dév 24 : 137–145

Gohar M, Souty C, Picaud JL (1983) Diurnal rhythms in the synthesis and release of haemolymph proteins in the crustacean Isopoda, *Porcellio dilatatus* (Brandt), with special reference to vitellogenin. Reprod Nutr Dév 23 : 93–100

Gohar M, Souty-Grosset C, Martin G, Juchault P (1984) Mise en evidence d'une inhibition de la synthèse de la vitellogénine par un facteur neurohumoral (V.I.H.) chez le crustacé isopode terrestre *Porcellio dilatatus* Brandt. CR Acad Sci Paris Ser III 299 : 785–787

Gohar M, Souty-Grosset C, Juchault P (1985) Rhythme nycthéméral de la synthèse protéique ovarienne chez le crustacé oniscoide *Porcellio dilatatus* Brandt et rôle du protocérébron. Can J Zool 63 : 799–803

Gondko R, Helszer Z, Serafin E (1984) Protein and cation content of the hemolymph of some Oniscoidea. Comp Biochem Physiol 78A : 367–369

Gorvett H (1946) The tegumental glands in the land Isopoda. A. The rosette glands. J Microsc Sci 87 : 209–235

Gorvett H (1956) Tegumental glands and terrestrial life in woodlice. Proc Zool Soc Lond 126 : 291–314

Goudeau M (1976) Secretion of embryonic envelopes and embryonic molting cycles in *Hemioniscus balani* Buchholz, Isopoda, Epicaridea. J Morphol 148 : 427–452

Gräber H (1933) Über die Gehirne der Amphipoden und Isopoden. Z Morphol Ökol Tiere 26:334–371

Greenaway P (1985) Calcium balance and moulting in the Crustacea. Biol Rev (Camb) 60:425–454

Griffith BS, Wood S (1985) Microorganisms associated with the hindgut of *Oniscus asellus* (Crustacea, Isopoda). Pedobiologia 28:377–381

Gromysz-Kalkowska K, Szubartowska E (1984) Oxygen consumption in two terrestrial species of Crustaceans (Isopoda). Bull Pol Acad Sci Biol Sci 32:47–56

Grundy AJ, Sutton SL (1989) Year class splitting in the woodlouse *Philoscia muscorum* explained through studies of growth and survivorship. Holarct Ecol 12:112–119

Grüner HE (1966) Die Tierwelt Deutschlands. 53. Krebstiere oder Crustacea. V. Isopoda. 2 Lieferung. Fischer, Jena

Gunn DL (1937) The humidity reactions of the woodlouse, *Porcellio scaber* (Latreille). J Exp Biol 14:178–186

Gunnarsson T (1987) Selective feeding on a maple leaf by *Oniscus asellus* (Isopoda). Pedobiologia 30:161–165

Gunnarsson T, Tunlid A (1986) Recycling of fecal pellets in isopods: microorganisms and nitrogen compounds as potential food for *Oniscus asellus* L. Soil Biol Biochem 18:595–600

Gupta M (1962) Contact chemoreception in *Oniscus asellus* L. and *Porcellio scaber* Latr. (Crustacea, Isopoda). J Zool Soc India 14:145–149

Hadley NF, Hendricks GM (1985) Cuticular microstructures and their relationship to structural color and transpiration in the terrestrial isopod *Porcellionides pruinosus*. Can J Zool 63:649–656

Hadley NF, Hendricks GM (1987) X-ray microanalysis of the cuticle surface of the terrestrial isopod *Porcellionides pruinosus*. Can J Zool 65:1218–1223

Hadley NF, Quinlan MC (1984) Cuticular transpiration in the isopod *Porcellio laevis*: chemical and morphological factors involved in its control. Symp Zool Soc Lond 53:97–107

Hadley NF, Warburg MR (1986) Water loss in three species of xeric adapted isopods: correlation with cuticular lipids. Comp Biochem Physiol 85A:669–672

Hames CAC, Hopkin SP (1989) The structure and function of the digestive system of terrestrial isopods. J Zool Lond 217:599–627

Hamner WM, Smyth M, Mulford ED (1968) Orientation of the sand-beach isopod, *Tylos punctatus*. Anim Behav 16:405–409

Hamner WM, Smyth M, Mulford ED (1969) The behavior and life history of a sand-beach isopod, *Tylos punctatus*. Ecology 50:442–453

Hanström B (1924) Untersuchungen über das Gehirn, insbesondere die Sehganglien der Crustaceen. Ark Zool 16:1–119

Hariyama T, Tsukahara Y (1985) Polarization sensitivity in the retinular cells of *Ligia exotica*. Zool Sci 2:868

Hariyama T, Meyer-Rochow VB, Eguchi E (1986) Diurnal changes in structure and function of the compound eye of *Ligia exotica* (Crustacea, Isopoda). J Exp Biol 123:1–26

Hartenstein R (1964a) Histochemical and spectrophotometrical studies on several dehydrogenases of carbohydrate metabolism in *Oniscus asellus*. J Insect Physiol 10:623–631

Hartenstein R (1964b) Feeding, digestion, glycogen and the environmental conditions of the digestive system in *Oniscus asellus*. J Insect Physiol 10 : 611–621

Hartenstein R (1968) Nitrogen metabolism in the terrestrial isopod, *Oniscus asellus*. Am Zool 8 : 507–519

Hartenstein R (1970) Nitrogen metabolism in non-insect arthropods. In: Campbell JW (ed) Comparative biochemistry of nitrogen metabolism. 1. The invertebrates. Academic Press, London, pp 299–385

Hasegawa Y, Katakura Y (1981) Androgenic gland hormone and development of oviducts in the isopod crustacean, *Armadillidium vulgare*, Dev Growth Differ 23 : 59–62

Hasegawa Y, Katakura Y (1983) Masculinization of WW females in the isopod crustacean, *Armadillidium vulgare*. Annot Zool Jpn 56 : 163–166

Hasegawa Y, Katakura Y (1985) Masculinization of female by the newly-formed androgenic glands in the ZW and WW females of the isopod crustacean, *Armadillidium vulgare*. Zool Sci 2 : 419–422

Hasegawa Y, Haino-Fukushima K, Katakura Y (1987) Isolation and properties of androgenic gland hormone from the terrestrial isopod, *Armadillidium vulgare*. Gen Comp Endocrinol 67 : 101–110

Hassall M (1977) The functional morphology of the mouthparts and foregut in the terrestrial isopod *Philoscia muscorum* (Scopoli, 1763). Crustaceana 33 : 225–236

Hassall M (1983) Population metabolism of the terrestrial isopod *Philoscia muscorum* in a dune grassland ecosystem. Oikos 41 : 17–26

Hassall M, Dangerfield JM (1989) Inter-specific competition and the relative abundance of grassland isopods. Monit Zool Ital (NS) Monog 4 : 379–397

Hassall M, Dangerfield JM (1990) Density dependent processes in the population dynamics of *Armadillidium vulgare* (Isopoda: Oniscidea). J Anim Ecol 59 : 941–958

Hassall M, Jennings JB (1975) Adaptive features of gut structure and digestive physiology in the terrestrial isopod *Philoscia muscorum* (Scopoli) 1763. Biol Bull (Woods Hole) 149 : 348–364

Hassall M, Rushton SP (1982) The role of coprophagy in the feeding strategies of terrestrial isopods. Oecologia (Berl) 53 : 374–381

Hassall M, Rushton SP (1984) Feeding behaviour of terrestrial isopods in relation to plant defences and microbial activity. Symp Zool Soc Lond 53 : 487–505

Hassall M, Rushton SP (1985) The adaptive significance of coprophagous behaviour in the terrestrial isopod *Porcellio scaber*. Pedobiologia 28 : 169–175

Hassall M, Sutton SL (1977) The role of isopods as decomposers in a dune grassland ecosystem, Sci Proc R Dublin Soc 6 : 235–245

Hassall M, Sutton SP (1984) Feeding behaviour of terrestrial isopods in relation to plant defences microbial activity. Symp Zool Soc Lond 53 : 485–505

Hassall M, Sutton SL (1985) Immobilization of mineral nutrients by *Philoscia muscorum* (Isopoda, Oniscoidea) in a dune grassland ecosystem. In: Striganova BR (ed) Soil fauna and soil fertility. Proc 9th Int Coltoq Soil Zool, Moscow, pp 29–37

Hassall M, Turner JG, Rands MRW (1987) Effects of terrestrial isopods on the decomposition of woodland leaf litter. Oecologia 72 : 597–604

Hastings MH (1981) The entraining effect of turbulence on the circa-tidal activity rhythm and its semi-lunar modulation in *Eurydice pulchra*. J Mar Biol Assoc UK 61 : 151–160

Hastings MH, Naylor E (1980) Ontogeny of an endogenous rhythm in *Eurydice pulchra*. J Exp Mar Biol Ecol 46 : 137–145

Hatanaka T (1989) Responses of dorsal tricorn-type sensilla on *Ligia exotica*. Comp Biochem Physiol 92A : 513–519

Hatchett SP (1947) Biology of the Isopoda of Michigan. Ecol Monogr 17 : 47–7

Haug T, Altner H (1984a) A cryofixation study of a subcuticular receptor organ in the antennular tip of the terrestrial isopod, *Porcellio scaber*. Latr. (Crustacea). J Ultrastruct Res 87 : 62–74

Haug T, Altner H (1984b) A cryofixation study of presumptive hygroreceptors on the antennule of a terrestrial isopod. Tissue Cell 16 : 377–391

Hayes WB (1974) Sand-beach energetics: importance of the isopod *Tylos punctatus*. Ecology 55 : 838–847

Hayes WB (1977) Factors affecting the distribution of *Tylos punctatus* (Isopoda, Oniscoidea) on beaches in southern California and northern Mexico. Pac Sci 31 : 165–186

Heath DJ, Khazaeli AA (1985) Population dynamics of the estuarine isopod *Sphaeroma rugicauda*. Estuarine Coastal Shelf Sci 20 : 105–116

Heeley W (1941) Observations on the life-histories of some terrestrial isopods. Proc Zool Soc Lond 111 : 79–149

Heeley W (1941/42) The habits and life-histories of woodlice. Essex Nat Trust Bull 27 : 105–114

Heimann P (1984) Fine structure and molting of aesthetasc sense organs on the antennules of the isopod, *Asellus aquaticus*. (Crustacea). Cell Tissue Res 235 : 117–128

Henke K (1930) Die Lichtorientierung und die Bedingungen der Lichtstimmungbei der Rollassel *Armaillidium cinereum* Zenker. Z Vgl Physiol 13 : 534–625

Herold W (1913) Beiträge zur Anatomie und Physiologie einiger Landisopoden. Zool Jahrb Anat Ontog Tiere 35 : 456–526

Herold W (1925) Untersuchungen zur Ökologie und Morphologie einiger Landasseln. Z Morphol Ökol Tiere 4 : 337–415

Herold W (1960) Die Vermehrungsgrösse einiger deutscher Land-Isopoden. Mitt Zool Mus Berl 36 : 101–104

Hewitt CG (1907) *Ligia*. Proc Trans Liverpool Biol Soc 21 : 65–100

Hoarau F, Hirn M (1978) Évolution du taux des ecdystéroides au cours du cycle de mue chez *Helleria brevicornis* Ebner (Isopode terrestre). CR Acad Sci Paris Ser D 286 : 1443–1446

Hoese B (1981) Morphologie und Funktion des Wasserleitungssystems der terrestrischen Isopoden (Crustacea, Isopoda, Oniscoidea). Zoomorphology 98 : 135–167

Hoese B (1982a) Der Ligia-Typ des Wasserleitungssystems bei terrestrischen Isopoden und seine Entwicklung in der Familie Ligiidae (Crustacea, Isopoda, Oniscoidea). Zool Jahrb Anat 108 : 225–261

Hoese B (1982b) Morphologie und Evolution der Lungen bei den terrestrischen Isopoden (Crustacea, Isopoda, Oniscoidea). Zool Jahrb Anat 107 : 396–422

Hoese B (1983) Struktur und Entwicklung der Lungen der Tylidae (Crustacea, Isopoda, Oniscoidea). Zool Jahrb Anat 109 : 487–501

Hoese B (1984) The marsupium in terrestrial isopods. Symp Zool Soc Lond 53 : 65–76

Hoese B (1989) Morphological and comparative studies on the second antennae of terrestrial isopods. Monit Zool Ital (NS) Monogr 4 : 127–152

Hoese B, Janssen HH (1989) Morphological and physiological studies on the marsupium in terrestrial isopods. Monit Zool Ital (NS) Monogr 4 : 153–173

Hoese B, Schneider P (1990) Antennal movements of the second antennae in some land isopods (Oniscidea) during mobility of search. Zool Anz 225 : 1–19 (In German)

Hoese B, Schneider P (1991) Antennal movements of the second antennae and orientation in some terrestrial isopods (Oniscidea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 139–140

Hoffmann G (1983a) The random elements in the systematic search behavior of the desert isopod *Hemilepistus reaumuri*. Behav Ecol Sociobiol 13 : 81–92

Hoffmann G (1983b) The search behavior of the desert isopod *Hemilepistus reaumuri* as compared with a systematic search. Behav Ecol Sociobiol 13 : 93–106

Hoffmann G (1984a) Orientation behaviour of the desert woodlouse *Hemilepistus reaumuri*: adaptations to ecological and physiological problems. Symp Zool Soc Lond 53 : 405–422

Hoffmann G (1984b) Homing by systematic search. In: Varjú D, Schnitzler H-U (eds) Localization and orientation in biology and engineering. Springer, Berlin Heidelberg New York, pp 192–199

Hoffmann G (1985a) The influence of landmarks on the systematic search behaviour of the desert isopod *Hemilepistus reaumuri*. I. Role of the landmark made by the animal. Behav Ecol Sociobiol 17 : 325–334

Hoffmann G (1985b) The influence of landmarks on the systematic search behaviour of the desert isopod *Hemilepistus reaumuri*. II. Problems with similar landmarks and their solution. Behav Ecol Sociobiol 17 : 335–348

Holanov SH, Hendrickson JR (1980) The relationship of sand moisture to burrowing depth of the sand-beach isopod *Tylos punctatus* Holmes and Gay. J Exp Mar Biol Ecol 46 : 81–88

Holdich DM (1984) The cuticular surface of woodlice: a search for receptors. Symp Zool Soc Lond 53 : 9–48

Holdich DM, Lincoln RJ (1974) An investigation of the surface of the cuticle and associated sensory structures of the terrestrial isopod, *Porcellio scaber*. J Zool (Lond) 172 : 469–482

Holdich DM, Mayes KR (1975) A fine-structural re-examination of the so-called "midgut" of the isopod *Porcellio*. Crustaceana 29 : 186–192

Holdich DM, Mayes KR (1976) Blood volume and total water content of the woodlouse, *Oniscus asellus*, in conditions of hydration and desiccation. J Insect Physiol 22 : 547–553

Holdich DM, Lincoln RJ, Ellis JP (1984) The biology of terrestrial isopods: terminology and classification. Symp Zool Soc Lond 53 : 1–6

Holliday CW (1988) Branchial $Na^+/K^+$ ATPase and osmoregulation in the isopod *Idotea wosnesenskii*. J Exp Biol 136 : 259–272

Holmquist JG (1985) The grooming behavior of the terrestrial amphipod *Talitroides alluaudi*. J Crustacean Biol 5 : 334–340

Hopkin SP (1990) Species-specific differences in the net assimilation of zinc, cadmium, lead, copper and iron by the terrestrial isopods *Oniscus asellus* and *Porcellio scaber*. J Appl Ecol 27 : 460–474

Hopkin SP, Martin MH (1982) The distribution of zinc, cadmium, lead and copper within the woodlouse *Oniscus asellus* (Crustacea, Isopoda). Oecologia (Berl) 54 : 227–232

Hopkin SP, Martin MH (1984) Heavy metals in woodlice. Symp Zool Soc Lond 53 : 143–166

Hopkin SP, Hardisty GN, Martin MH (1986) The woodlouse *Porcellio scaber* as a 'biological indicator' of zinc, cadmium, lead and copper pollution. Environ Pollut Ser B 11 : 271–229

Hopkin SP, Hames CAC, Bragg S (1989) Terrestrial isopods as biological indicators of zinc pollution in the Reading area, south east England. Monit Zool Ital (NS) Mongr 4 : 477–488

Hørlyck V (1973) Seasonal and diel variation in the rhythmicity of *Idotea baltica* (Pallas) and *Idotea granulosa* Rathke. Ophelia 12 : 117–127

Hornung E (1981) Data on the oxygen consumption of Isopoda and Diplopoda species. Acta Biol Szeged 27 : 209–213

Hornung E (1984) Characteristics of the population of an Isopoda species (*Trachelipus nodulosus* C.L. Koch) at sandy soil grassland. Acta Biol Szeged 30 : 153–158

Hornung E (1988) Preliminary data to the clutch-size of *Trachelipus nodulosus* C.L. Koch in different habitats. Acta Biol Szeged 34 : 169–171

Hornung E (1989) Population dynamics and spatial distribution of *Trachelipus nodulosus* (C.L. Koch 1838) (Crustacea, Isopoda) in a sandy grassland. Monit Zool Ital (NS) Monogr 4 : 399–409

Hornung E (1991) Isopod distribution in a heterogeneous grassland habitat. In: Juchault P, Mocqurad JP (eds) Biology of terrestrial isopods, Univ. Press Poitiers, pp 73–79

Horowitz M (1970) The water balance of the terrestrial isopod *Porcellio scaber*. Entomol Exp Appl 13 : 173–178

Howard HW (1980) The distribution at breeding time of the sexes of the woodlouse *Armadillidium vulgare* (Latreille, 1802) (Isopoda). Crustaceana 39 : 52–58

Hryniewiecka-Szyfter Z (1972) Ultrastructure of hepatopancreas of *Porcellio scaber* Latr. in relation to the function of iron and copper accumulation. Bull Soc Amis Sci Lett Poznan Sci Biol 13 : 135–142

Hryniewiecka-Szyfter Z, Storch V (1986) The influence of starvation and different diets on the hindgut of Isopoda (*Mesidotea entomon*, *Oniscus asellus*, *Porcellio scaber*). Protoplasma 134 : 53–59

Hryniewiecka-Szyfter Z, Tyczewska J (1975) Ultrastructure of rectum epithelium in Isopoda (Crustacea). Ann Med Sect Pol Acad Sci 20 : 83–84

Hubbel SP, Sikora A, Paris OH (1965) Radiotracer, gravimetric and calorimetric studies of ingestion and assimilation rates of an isopod. Health Phys 11 : 1485–1501

Hughes RN (1989) Essential involvement of species legs in turn alternation of the woodlouse *Porcellio scaber*. Comp Biochem Physiol 93A : 493–497

Husain MZ, Alikhan MA (1979a) Physiological adaptations in Crustacea to the environment: oxygen consumption as a function of body weight and environmental temperature in the terrestrial isopod, *Porcellio laevis* Latreille (Isopoda, Oniscoidea). Crustaceana 36 : 277–286

Husain MZ, Alikhan MA (1979b) A comparative study of the respiratory metabolism in *Porcellio laevis* (Lat.) and *Armadillidium vulgare* (Lat.): response to temperature, photoperiod and oxygen concentration. Arch Int Physiol Biochim 87 : 697–710

Iga T, Kitamura S (1975) The circus movement of a sand-beach isopod, *Tylos* *granulatus*. Miers. Mem Fac Lit Sci Shimane Univ Nat Sci 9: 89–101

Imafuku M (1976) On the nocturnal behavior of *Tylos granulatus* Miers (Crustacea: Isopoda). Publ Seto Mar Biol Lab 23: 299–340

Jans DE, Ross KFA (1963) A histological study of the peripheral receptors in the thorax of land isopods, with special reference to the location of possible hygroreceptors. Q J Microsc Sci 104: 337–350

Jassem W, Mocquard JP, Juchault P (1981) Seuil de l'intensité lumineuse du signal photopériodique induisant l'entrée en reproduction chez *Armadillidium vulgare*, Latr. (Crustacé, Isopode terrestre). Bull Soc Zool Fr 106: 451–455

Jassem W, Juchault P, Mocquard JP (1982a) Déterminisme de la reproduction saisonnière des femelles d'*Armadillidium vulgare* Latr. (Crustace, Isopode, Oniscoide). V. Rôle du mâle dans le cycle de reproduction des femelles. Ann Sci Nat Zool Paris 13th Ser 4: 195–201

Jassem W, Mocquard JP, Juchault P (1982b) Déterminisme de la reproduction saisonnière des femelles d'*Armadillidium vulgare* Latr. (Crustacé, Isopode, Oniscoide). IV. Contribution à la connaissance de la perception du signal photopériodique induisant l'entrée en reproduction: mode de discrimination entre le jour et la nuit; longueurs d'onde actives. Ann Sci Nat Zool Paris 13th Ser 4: 85–90

Johnson C (1982) Multiple insemination and sperm storage in the isopod, *Venezillo evergladensis* Schultz, 1963. Crustaceana 42: 225–232

Johnnson C (1985) Mating behavior of the terrestrial isopod, *Venezillo evergladensis* (Oniscoidea, Armadillidae). Am Midl Nat 114: 216–224

Johnson C (1986) Parthenogenetic reproduction in the philosciid isopod, *Oscelloscia floridana* (Van Name, 1940). Crustaceana 51: 123–132

Johnson WS (1976) Population energetics of the intertidal isopod *Cirolana harfordi*. Mar Biol 36: 351–357

Jones DA, Naylor E (1970) The swimming rhythm of the sand beach isopod *Eurydice pulchra*. J Exp Mar Biol Ecol 4: 188–199

Jöns D (1965) Zur Biologie und Ökologie von *Ligia oceanica* (L.) in der westlichen Ostsee. Kiel Meeresforsch 21: 203–207

Joose ENG, Van Vliet LHH (1984) Iron, manganese and zinc inputs in soil and litter near blast-furnace plant and the effects on respiration of woodlice. Pedobiologia 26: 249–255

Juchault P, Kouigan S (1975) Contribution a l'étude des systèmes de neurosécrétion céphalique chez l'oniscoide *Ligia oceanica* L. (crustace isopode): les centres neurosécréteurs protocérébraux et le plexus nerveux latéral. Bull Soc Zool Fr 100: 457–467

Juchault P, Legrand JJ (1974) Nature et action interspécifique du facteur épigénétique feminisant responsable d'une perturbation totale ou partielle de l'equilibre endocrinien contrôlant le phenotype sexuel du crustacé *Armadillidium vulgare* (Isopode Oniscoide). Ann Endocrinol 35: 387–392

Juchault P, Legrand JJ (1978) Etude du fonctionnement de la glande androgène dans le cas d'implantations croisées entre deux espèces de crustacés isopodes terrestres, *Procellio dilatatus* Brandt et *Armadillidium vulgare* Latreille: notion de spécificité de l'hormone androgene et des neurohormones impliquées dans le contrôle de la fonction androgène. Gen Comp Endocrinol 36: 175–186

Juchault P, Legrand JJ (1985) Contribution à l'étude du mécanisme de l'etat réfractaire à l'hormone androgène chez les *Armadillidium vulgare* Latr. (Crustacé, Isopode, Oniscoide) hébergeant une bacterie féminisante. Gen Comp Endocrinol 60 : 463–467

Juchault P, Legrand JJ (1989) Sex determination and monogeny in terrestrial isopods *Armadillidium vulgare* (Latreille, 1804) and *Armadillidium nasatum* Budde-Lund, 1885. Monit Zool Ital (NS) Monogr 4 : 359–375

Juchault P, Legrand JJ, Martin G (1974) Action interspécifique du facteur épigenétique féminisant responsable de la thélygénie et de l'intersexualité du crustacé *Armadillidium vulgare* (isopode, oniscoide). Ann Embryol Morphog 7 : 265–276

Juchault P, Maissiat J, Legrand JJ (1978) Caractérisation chimique d'une substance ayant les effets biologiques de l'hormone androgène chez le crustacé isopode terrestre *Armadillidium vulgare* Latreille. C R Acad Sci Paris Ser D 286 : 73–76

Juchault P, Mocquard JP, Bougrier N, Besse G (1980a) Croissance et cycle reproducteur du crustacé isopode oniscoide *Eluma purpurascens* Budde-Lund. Etude dans la nature et au laboratoire, sous différentes conditions se température et de photopériode, d'une population due centre-ouest de la France. Vie Milieu 30 : 149–156

Juchault P, Pavese A, Mocquard JP (1980b) Déterminisme de la reproduction saisonnière des femelles d'*Armadillidium vulgare* Latr. (Crustacé, Isopode, Oniscoide). II. Étude en conditions expérimentales de femelles d'origines géographiques différentes. Ann Sci Nat Zool Paris 14th Ser 2 : 99–108

Juchault P, Mocquard JP, Legrand JJ (1981) Déterminisme de la reproduction saisonniére des femelles d'*Armadillidium vulgare* Latr. (Crustacé, Isopode, Oniscoide). III. Suppression ou prolongation de la période de repos sexuel saisonnier obtenue par application de programmes photopériodiques. Ann Sci Nat Zool Paris 13th Ser 3 : 141–145

Juchault P, Jassem W, Mocquard JP (1982) Déterminisme de la reproduction saisonnière des femelles d'*Armadillidium vulgare* Latr. (Crustacé, Isopode, Oniscoide). VI. Mise en évidence d'une photopériode critique permettant l'entrée en reproduction; modalités du maintein en reproduction. Ann Sci Nat Zool Paris 13th Ser 4 : 203–210

Juchault P, Mocquard JP, Kouigan S (1985) Étude expérimentale de l'influence des facteurs externes (température et photopériode) sur le cycle de reproduction du crustacé oniscoide *Porcellionides pruinosus* (Brandt) provenant de populations Africaine (Togo) et Européenne (France). Crustaceana 48 : 307–315

Juchault P, Martin G, Mocquard JP, Souty-Grosset C, Picaud JL, Raimond R (1989) La reproduction saisonniére chez les isopodes terrestres: contrôle photopériodique et neurohurmonal. Invert Reprod Dev 16 : 63–73

Katakura Y (1960) Transformation of ovary into testis following implantation of androgenous glands in *Armadillidium vulgare*, an isopod crustacean. Annot Zool Jpn 33 : 241–244

Katakura Y (1961a) Hormonal control of development of sexual characters in the isopod crustacean, *Armadillidium vulgare*. Annot Zool Jpn 34 : 60–71

Katakura Y (1961b) Progeny from the mating of the normal female and the masculinized female of *Armadillidium vulgare*, an isopod crustacean. Annot Zool Jpn 34 : 197–199

Katakura Y (1984) Sex differentiation and androgenic gland hormone in the terrestrial isopod *Armadillidium vulgare*. Symp Zool Soc Lond 53 : 127–142

Katakura Y, Hasegawa Y (1983) Masculinization of females of the isopod crustacean, *Armadillidium vulgare*, following injections of an active extract of the androgenic gland. Gen Comp Endocrinol 48 : 57–62

Katakura Y, Fujimaki Y, Unno K (1975) Partial purification and chracterization of androgenic gland hormone from the isopod crustacean, *Armadillidium vulgare*. Annot Zool Jpn 48 : 203–209

Kato H (1976) Life histories and vertical distributions in the soil of *Ligidium japonicum* and *Ligidium sp.* (Isopoda). Preliminary report. Rev Ecol Biol Sol 13 : 103–116

Kensley B (1972) Behavioural adaptions of the isopod *Tylos granulatus* Krauss. Zool Afr 7 : 1–4

Kensley B (1974) Aspects of the biology and ecology of the genus *Tylos latreille*. Ann S Afr Mus 65 : 401–471

Kheirallah AM (1979a) The ecology of the isopod *Periscyphis granai* (Arcangeli) in the western highlands of Saudi Arabia. J Arid Environ 2 : 51–59

Kheirallah AM (1979b) The population dynamics of *Periscyphis granai* (Isopoda: Oniscoidea) in the western highlands of Saudi Arabia. J Arid Environ 2 : 329–337

Kheirallah AM (1980a) Aspects of the distribution and community structure of isopods in the Mediterranean coastal desert of Egypt. J Arid Environ 3 : 69–74

Kheirallah AM (1980b) The life history and ecology of *Leptotrichus panzerii* (Crustacea: Isopoda) in Egypt. Rev Ecol Biol Sol 17 : 393–403

Kheirallah AM, Awadallah A (1981) The life history of the isopod *Porcellio olivieri* in the Mediterranean coastal desert of Egypt. Pedobiologia 22 : 246–253

Kheirallah AM, El-Sharkawy K (1981) Growth and natality of *Porcellio olivieri* (Crustacea: Isopoda) on different foods. Pedobiologia 22 : 262–267

Kheirallah AM, Omran HMM (1986) Population density, biomass and life history of the terrestrial isopod *Leptotricus naupliensis* (Verhoeff) in a grassland of Abeis region, Egypt. Rev Ecol Biol Sol 23 : 319–332

King SD (1926) Óogeneśis in *Oniscus asellus*. Proc R Soc Lond B Biol Sci 100 : 1–10

Kivivuori L, Lagerspetz KYH (1990) Temperature selection behaviour of the isopod *Saduria entomon* (L.). J Therm Biol 15 : 83–86

Klapow LA (1972a) Fortnightly molting and reproductive cycles in the sand-beach isopod, *Excirolana chiltoni*. Biol Bull (Woods Hole) 143 : 568–591

Klapow LA (1972b) Natural and artificial rephasing of a tidal rhythm. J Comp Physiol 79 : 233–258

Kleinholz LH (1937) Studies in the pigmentary system of Crustacea. I Color changes and diurnal rhythm in *Ligia baudiniana*. Biol Bull (Woods Hole) 7 : 24–36

Knowles FGW, Carlisle DB (1956) Endocrine control in the Crustacea. Biol Rev 31 : 396–473

Koop K, Field JG (1980) The influence of food availability on population dynamics of a supralittoral isopod, *Ligia dilatata* Brandt. J Exp Mar Biol Ecol 48 : 61–72

Koop K, Field JG (1981) Energy transformation by the supralittoral isopod *Ligia dilatata* Brandt. J Exp Mar Biol Ecol 53 : 221–233

Koscielny L (1983) Colonization mechanisms and succession of isopods (Crustacea, Isopoda, Oniscoidea) on differently treated refuse tip covers. In: Lebrun P, Andre HM, DeMedts A, Gregoire-Wibo C, Wauthy G (eds) New trends in soil biology. Dieu-Brichart, Leuwen La Neure, Belgium, pp 535–540

Kozlovskaja LS, Striganova BR (1977) Food, digestion and assimilation in desert woodlice and their relations to the soil microflora. In: Soil organisms as components of ecosystems. Ecol Bull (Stokh) 25:240–245

Krumpál M (1976) Knowledge from biology of isopode reproduction in Jurský šúr. Acta Fac Rerum Nat Univ Comenianae Zool Bratislava 20:63–67

Kuenen DJ (1959) Excretion and waterbalance in some land-isopods. Entomol Exp Appl 2:287–294

Kuenen DJ, Nooteboom HP (1963) Olfactory orientation in some land-isopods (Oniscoidea, Crustacea). Entomol Exp Appl 6:133–142

Kukor JJ, Martin MM (1986) The effect of acquired microbial enzymes on assimilation efficiency in the common woodlouse, *Tracheoniscus rathkei*. Oecologia (Berl) 69:360–366

Kümmel G (1981) Fine structural indications of an osmoregulatory function of the "gills" in terrestrial isopods (Crustacea, Oniscoidea). Cell Tissue Res 214:663–666

Kümmel G (1984) Fine-structural investigations of the pleopodal endopods of terrestrial isopods with some remarks on their function. Symp Zool Soc Lond 53:77–95

Lagarrigue JG (1968) Recherches biochimiques sur le squelette tégumentaire des isopodes terrestres. Vie Milieu 19:173–188

Lagarrigue JG (1969) Composition ionique de l'hemolymphe des Oniscoides. Bull Soc Zool Fr 94:137–146

Lane RL (1980) Histochemistry of the reproductive systems of *Armadillidium vulgare* (Latreille) and *Porcellionides pruinosus* (Brandt) (Isopoda). Crustaceana 38:73–81

Lane RL (1988) The digestive system of *Porcellio scaber* Latreille, 1804 (Isopoda, Oniscoidae): histology and histochemistry. Crustaceana 55:113–128

Lattin G, Gross FJ (1953) Die Resinflussbarkeit sekundärer Geschlechtsmerkmale von *Oniscus asellus* durch die Gonaden. Experientia 9:338–339

Lawlor LR (1976a) Parental investment and offspring fitness in the terrestrial isopod *Armadillidium vulgare* (Latr.) (Crustacea: Oniscoidea). Evolution 30:775–785

Lawlor LR (1976b) Molting, growth and reproductive strategies in the terrestrial isopod, *Armadillidium vulgare*. Ecology 57:1179–1194

Leboeuf RD, Howe NR (1981) Melanophores and their role in color change and the ecology of the marine isopod, *Sphaeroma quadridentatum* Say. Crustaceana 40:225–234

Legrand JJ (1967) Contribution à l'étude du contrôle génétique et humoral de l'inversion du sexe chez les crustacés isopodes notion de balance génique sexuelle. Ann Biol 6:241–258

Legrand JJ, Legrand-Hamelin E (1975) Déterminisme de l'intersexualité et de la monogénie chez les crustacés isopodes. Pub Staz Zool Napoli 39:443–461

Legrand JJ, Martin G, Juchault P, Besse G (1982) Contrôle neuroendocrine de la reproduction chez les Crustacés. J Physiol (Paris) 78:543–552

Legrand JJ, Legrand-Hamelin E, Juchault P (1987) Sex determination in Crustacea. Biol Rev 62:439–470

Leichman G (1891) Beiträge zur Naturgeschichte der Isopoden. I. Zur Anatomie der Genitalorgane. Bibl Zool (Cassel) 10:1–44

Lewis F (1991) The relationship between broodpouch cotyledons, aridity and advancement. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 81–87

Lindqvist OV (1968) Water regulation in terrestrial isopods, with comments on their behavior in a stimulus gradient. Ann Zool Fenn 5 : 279–311

Lindqvist OV (1970) The blood osmotic pressure of the terrestrial isopods *Porcellio scaber* Latr. and *Oniscus asellus* L., with reference to the effect of temperature and body size. Comp Biochem Physiol 37 : 503–510

Lindqvist OV (1971) Evaporation in terrestrial isopods is determined by oral and anal discharge. Experientia 27 : 1496–1498

Lindqvist OV (1972a) Humidity reactions of the young of the terrestrial isopods *Porcellio scaber* Latr. and *Tracheoniscus rathkei* (Brandt). Ann Zool Fenn 9 : 10–14

Lindqvist OV (1972b) Components of water loss in terrestrial isopods. Physiol Zool 45 : 316–324

Lindqvist OV, Fitzgerald G (1976) Osmotic interrelationship between blood and gut fluid in the isopod *Porcellio scaber* Latr. (Cructacea). Comp Biochem Physiol 53A : 57–59

Lindqvist OV, Salminen I, Winston PW (1972) Water content and water activity in the cuticle of terrestrial isopods. J Exp Biol 56 : 49–55

Linsenmair KE (1972) Die Bedeutung familienspezifischer “Abzeichen” für den Familienzusammenhalt bei der sozialen Wüstenassel *Hemilepistus reaumuri* Audouin u. Savigny (Crustacea, Isopoda, Oniscoidea). Z Tierpsychol 31 : 131–162

Linsenmair KE (1984) Comparative studies on the social behaviour of the desert isopod *Hemilepistus reaumuri* and of a *Porcellio species*. Symp Zool Soc Lond 53 : 423–453

Linsenmair KE (1985) Individual and family recognition in subsocial arthorpods, in particular in the desert isopod *Hemilepistus reaumuri*. In: Hölldobler G, Lindauer G (eds) Experimental behavioral ecology. Fischer, Stuttgart, pp 411–436

Linsenmair KE (1987) Kin recognition in subsocial arthropods in particular in the desert isopod *Hemilepistus reaumuri*. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. Wiley, New York pp 121–208

Linsenmair KE (1989) Sex-specific reproductive patterns in some terrestrial isopods. In: Rasa AE, Vogel C, Voland E (eds) The sociobiology of sexual and reproductive strategies. Chapman and Hall, London, pp 19–47

Linsenmair KE, Linsenmair C (1971) Paarbildung und Paarzusammenhalt bei der monogamen Wüstenassel *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). Z Tierpsychol 29 : 134–155

Lokke DH (1966) Mass movements of terrestrial isopods related to atmospheric circulation patterns. Trans Kans Acad Sci 69 : 117–122

Ludwig G (1978) Zur kinästhetischen Verrechnung von Hindernissen bei der Assel *Porcellio scaber*. Zool Jahrb Physiol 82 : 185–199

Lueken W (1963) Zur Spermienspeicherung bei Armadillidien (Isopoda Terestria). Crustaceana 5 : 27–34

Lueken W (1968) Mehrmaliges Kopulieren von *Armadillidium*-Weibchen (Isopoda) während einer Parturialhäutung. Crustaceana 14 : 113–118

Ma HHT, Dudgeon D, Lam PKS (1991a) Seasonal changes in populations of three sympatric isopods in a Hong Kong forest. J Zool Lond 224 : 347–365

Ma HHT, Lam PKS, Dudgeon D (1991b) Inter- and intraspecific variation in the life histories of three sympatric isopods in a Hong Kong forest. J Zool Lond 224: 677–687

Maccagno TP (1939) L'apparato tracheale del genere *Tracheoniscus* Verh. Boll Mus Zool Anat Comp Univ Torino 47: 104: 1–14

Madhavan K, Shribbs JM (1981) Role of photoperiod and low temperature in the control of ovigerous molt in the terrestrial isopod, *Armadillidium vulgare* (Latreille 1804). Crustaceana 41: 263–270

Mahmoud MF (1954) Some notes on the biology of the terrestrial isopod *Porcellio laevis* Latr. Bull Soc Zool Egypt 12: 33–41

Mahmoud MF (1956) The respiratory organs of the terrestrial isopod *Porcellio laevis* Latr. Proc Egypt Acad Sci 12: 73–77

Maissiat J (1972) Contribution à l'étude du rôle endocrine de la glande antennaire l'oniscoide *Porcellio dilatatus* Brandt. Effect de son ablation sur l'équilibre hydro-minéral. CR Seances Soc Biol 166: 916–919

Maissiat J (1989) L'organe antennaire des isopodes: est-il l'homologue de l'organe mandibulaire des decapodes? Invert Reprod Dev 16: 95–102

Maissiat J, Graf F (1973) Action de l'ecdystérone sur l'apolysis et l'ecdysis de divers crustacés isopodes. J Insect Physiol 19: 1265–1276

Maissiat R, Maissiat J (1976) Structure et ultrastructure de la glande de mue et synthèse des ecdysones en fonction des étapes du cycle de la mue chez *Ligia oceanica* (crustacé isopode oniscoide). Bull Soc Zool Fr 101: 545–558

Maissiat R, Maissiat J (1978) Étude ultrastructurale de la cytolyse naturelle de l'organe Y après acquisition de la puberté mâle chez *Sphaeroma serratum* Fabr. (crustacé, isopode, flabellifère). CR Seances Soc Biol 172: 308–315

Maissiat R, Denanot MF, Besse C, Maissiat J (1979a) Observations cytochimiques et ultrastructurales sur les inclusions à structure périodique de l'organe Y de *Ligia oceanica* (L.) (crustace isopode). CR Acad Sci Paris Ser D 288: 527–530

Maissiat R, Martin G, Maissiat J, Juchault P (1979b) Ultrastructural development of the neurohemal organ joined to the ecdysial gland after imaginal moulting in the male isopod *Sphaeroma serratum* Fab. (Crustacea, Flabellifera). Cell Tissue Res 203: 403–414

Maissiat R, Maissiat J, Girard P (1980) Structure et ultrastructure de la glande antennaire de *Ligia oceanica*. Biol Cell 38: 14A

Malo N (1970) Premières observations ultrastructurales de la glande androgène d'*Oniscus asellus*, crustacé, isopode, et ses modifications en fonction de la temperature d'elevage. CR Acad Sci Paris Ser D 270: 2843–2845

Malo N, Juchault P (1970) Contribution à l'étude des variations ultrastructurales de la glande androgène des Oniscoides superieurs (crustaces isopodes) à la suite de la dècèrèbration. CR Acad Sci Paris 271: 230–232

Marcaillou C, Truchet M, Martoja R (1986) Rôle des cellules S de l'épithélium caecal des crustacés isopodes dans la capture et la dégradation de protéines hémolymphatiques, et dans le stockage de catabolites (acide urique, sulfure de cuivre, phosphates). Can J Zool 64: 2757–2769

Marsh BA, Branch GM (1979) Circadian and circatidal rhythms of oxygen consumption in the sandy-beach isopod *Tylos granulatus* Krauss. J Exp Mar Biol Ecol 37: 77–89

Martin G (1972a) Analyse ultrastructurale des cellules neurosécrétrices du protocérébron de *Porcellio dilatatus* (Brandt) (crustacé isopode oniscoide). CR

Acad Sci Paris, Ser D 274 : 243–246

Martin G (1972b) Cycle fonctionnel des cellules neurosécrétrices ß du protocérébron de *Porcellio dilatatus* Brandt (crustacé isopode oniscoide) et ses modifications provoquées respectivement par ablation des glandes de mue et par ovariectomie. CR Acad Sci Paris, Ser D 274 : 1331–1334

Martin G (1972c) Contribution à l'étude ultrastructurale de la glande du sinus de l'oniscoide *Porcellio dilatatus* Brandt. CR Acad Sci Paris, Ser D 275 : 839–842

Martin G (1976) Mise en evidence et étude ultrastructurale des ocelles médians chez les crustacés isopodes. Ann Sci Nat Zool 18 : 405–436

Martin G (1978) Action de la sérotonine sur la glycémie et sur la libération des neurosécrétions contenues dans la glande du sinus de *Porcellio dilatatus* Brandt (crustacé, isopode, oniscoide). CR Seances Soc Biol 172 : 304–308

Martin G (1982) Etude ultrastructurale de la régénération de la glande du sinus chez l'oniscoide *Porcellio dilatatus* Brandt: données complémentaires sur l'origine des terminaisons de cet organe neurohémal. J Physiol (Paris) 78 : 558–565

Martin G, Maissiat J (1973) Action de l'ecdystérone sur les péricaryones ß du protocérébron et sur la glande du sinus de *Porcellio dilatatus* Brandt (crustacé, isopode, oniscoide). CR Acad Sci Paris, Ser D 277 : 1663–1666

Martin G, Besse G, Mocquard JP (1980) Controle neurohumoral du cycle de mue chez les males de l'oniscoide *Porcellio dilatatus* Brandt. Bull Soc Zool Fr 105 : 73–81

Martin G, Maissiat R, Girard P (1983) Ultrastructure of the sinus gland and lateral cephalic nerve plexus in the isopod *Ligia oceanica* (Crustacea, Oniscoidea). Gen Comp Endocrinol 52 : 38–50

Martin G, Jaros PP, Besse G, Keller R (1984a) The hyperglycemic neuropeptide of the terrestrial isopod, *Porcellio dilatatus*. II. Immunocytochemical demonstration in neurosecretory structures of the nervous system. Gen Comp Endocrinol 55 : 217–226

Martin G, Keller R, Kegel G, Besse G, Jaros PP (1984b) The hyperglycemic neuropeptide of the terrestrial isopod, *Porcellio dilatatus*. I. Isolation and characterization. Gen Comp Endocrinol 55 : 208–216

Martin G, Juchault P, Sorokine O, Van Dorsselaer A (1990) Purification and characterization of androgenic hormone from the terrestrial isopod *Armadillidium vulgare* Latr. (Crustacea, Oniscidea). Gen Comp Endocrinol 80 : 349–354

Mathes I, Strouhal H (1954) Zur Ökologie und Biologie der Ameisenassel *Platyarthrus hoffmannseggii* Brdt. Z Morphol Ökol Tiere 43 : 82–93

Mathur RS (1961) The male genitalia of *Oniscus asellus* (Linnaeus). JR Microsc Soc 80 : 9–17

Matsumoto K (1959) Neurosecretory cells of an isopod, *Armadillidium vulgare* (Latreillle). Biol J Okayama Univ 5 : 43–50

Mayes KR, Holdich DM (1976) The water content of muscle and cuticle of the woodlouse *Oniscus asellus* in conditions of hydration and desiccation. Comp Biochem Physiol 53A : 253–258

McMurrich JP (1898) The epithelium of the so-called midgut of the terrestrial isopods. J Morphol 14 : 83–108

McQueen DJ (1976a) *Porcellio spinicornis* Say (Isopoda) demography. II. A comparison between field and laboratory data. Can J Zool 54 : 825–842

McQueen DJ (1976b) The influence of climatic factors on the demography of the terrestrial isopod *Tracheoniscus rathkei* Brandt. Can J Zool 54 : 2185–2199

McQueen DJ, Carnio JS (1974) A laboratory study of the effects of some climatic factors on the demography of the terrestrial isopod *Porcellio spinicornis* Say. Can J Zool 52: 599–611

McQueen DJ, Steel CGH (1980) The role of photoperiod and temperature in the initiation of reproduction in the terrestrial isopod *Oniscus asellus* Linnaeus. Can J Zool 58: 235–240

McWhinnie MA, Sweeney HM (1955) The demonstration of two chromatophorotropically active substances in the land isopod, *Trachelipus rathkei*. Biol Bull (Woods Hole) 108: 160–174

Mead F (1963) Sur l'existence d'une cavité incubatrice complexe chez l'isopode terrestre *Helleria brevicornis* Ebner. CR Acad Sci Paris 257: 775–777

Mead F (1965) Sur l'existence d'un sac incubateur interne chez l'isopode terrestre *Tylos latreillei* Audouin. CR Acad Sci Paris 260: 2336–2337

Mead F (1968) Observations sur l'écologie de *Tylos latreillei* Audouin (isopode Tylidae) et sur son comportement en milieu naturel. Vie Milieu Ser C Biol terr 19: 345–362

Mead F (1976) La place de'laccouplement dans le cycle de reproduction des isopodes terrestres (Oniscoidea). Crustaceana 31: 27–41

Mead F (1978) Analyse comparative de la séquence sexuelle chez les isopodes Oniscoidea de la série ligienne en relation avec le developpement de la volvation chez les Armadillidiidae et les Armadillidae. Z Tierpsychol 46: 30–42

Mead F, Gabouriaut D (1988a) Belated and decreased reproduction in isolated females of *Helleria brevicornis* Ebner (Crustacea, Oniscoidea). Recuperation after the addition of faeces to the female environment. Int J Invert Reprod Dev 14: 95–104

Mead F, Gabouriaut D (1988b) Influence du groupement dur la formation du marsupium et la production des jeunes chez *Helleria brevicornis* (Ebner) (Isopoda, Oniscoidea, Tylidae). Crustaceana 54: 244–255

Mead F, Gabouriaut D, Corbière-Tichané G (1976) Structure de l'organe sensoriel apical de l'antenne chez l'isopode terrestre *Metoponorthus sexfasciatus* Budde-Lund (Crustacea, Isopoda). Zoomorphologie 83: 253–269

Mead M, Mead F (1972/73) Étude de l'orientation chez l'isopode terrestre *Tylos latreillei*. ssp Sardous. Vie Milieu 23: 81–93

Mead-Briggs AR (1956) The effect of temperature upon the permeability to water of arthropod cuticles. J Exp Biol 33: 737–749

Mehely LV (1931) Beiträge zur Anatomie der Trichonisciden (German summary). Stud Zool Regiae Sci Univ Hung Budapestinensis Fundatae a Petro Pazmany II: 83–119

Meinertz T (1944) Beiträge zur Ökologie der Landisopoden mit besonderer Berücksichtigung ihrer Atmungsorgane. Zool Jb Syst 76: 501–518

Meinertz T (1950) Über die Geschlechtsverhältnisse und die Brutzeit der dänischen Landisopoden. Arch Zool Soc Bot Fenn "Vanamo" 4: 143–150

Meinertz T (1951) Die Vermehrungsintensität bei Landisopoden. Zool Jahrb Allg Zool Physiol 63: 1–24

Menon PKB, Tandon KK, Jolly R (1969) Bionomics of a terrestrial isopod *Porcellionides pruinosus* (Brandt). Zool Pol 19: 369–391

Menon PKB, Tandon KK, Rait HK (1970) Further studies on the bionomics of terrestrial isopods *Porcellionides pruinosus* (Brandt) and *Cubaris robusta* (Collinge). Zool Pol 20: 345–372

Merriam HG (1971) Sensitivity of terrestrial isopod populations ( *Armadillidium*) to food quality differences. Can J Zool 49 : 667–674

Messner B (1963) Neue histologische Befunde zur Neurosekretion bei terresrischen Isopoden (*Porcellio scaber* Latr. und *Oniscus asellus* (L.)). Naturwissenschaften 50 : 338–339

Messner B (1965) Ein morphologisch-histologischer Beitrag zur Häutung von *Porcellio scaber* Latr. und *Oniscus asellus* L. (Isopoda terrestria). Crustaceana 9 : 285–301

Messner B (1966) Histologische Untersuchungen zum Hormonsystem terrestrischer Isopoden (*Porcellio scaber* Latr. und *Oniscus asellus* L.) in Beziehung zur Häutung. Crustaceana 10 : 225–240

Meyer E, Phillipson J (1983) Respiratory metabolism of the isopod *Trichoniscus pusillus provisorius*. Oikos 40 : 69–74

Miller MA (1938) Comparative ecological studies on the terrestrial isopod Crustacea of the San Francisco Bay region. Univ Calif Publ Zool 43 : 113–142

Miller RH, Cameron GN (1983) Intraspecific variation of life history parameters in the terrestrial isopod, *Armadillidium vulgare*. Oecologia (Berl) 57 : 216–226

Miller RH, Cameron GN (1987) Effects of temperature and rainfall on populations of *Armadillidium vulgare* (Crutacea : Isopoda) in Texas. Am Midl Nat 117 : 192–198

Miyawaki M (1958) On the neurosecretory system of the isopod, *Idotea japoncia*. Annot Zool Jpn 31 : 216–221

Mocquard JP, Besse G, Juchault P, Legrand JJ, Maissiat J, Noulin G (1971) Contribution à l'analyse du controle neurohumoral de la croissance, de la mue et de la physiologie sexuelle male et femelle chez l'oniscoide *Ligia oceanica* L. (crustacé, isopode). Ann Embryol Morphog 4 : 45–63

Mocquard JP, Besse G, Juchault P, Legrand JJ, Maissiat J, Martin G, Picaud JL (1976a) Durées des cycles de mue chez les femelles de l'oniscoide *Porcellio dilatatus* Brandt, suivant leur état sexuel et les conditions d'élevage : température, photopériode et groupement. Bull Ecol 7 : 297–314

Mocquard JP, Besse G, Juchault P, Legrand JJ, Maissiat J, Martin G, Picaud JL (1976b) Durees de la periode de reproduction chez les femelles de l'oniscoide *Porcellio dilatatus* Brandt cuivant les conditions d'élevage: température, photopériode et groupement. Vie Milieu 26 : 51–76

Mocquard JP, Besse G, Juchault P, Legrand JJ, Maissiat J, Martin G, Picaud JL (1978) Action de la temperature et de la photopériode sur l'induction des mues parturielles des femelles de *Porcellio dilatatus* Brandt (crustace, isopode, oniscoide). Arch Zool Exp Gen 119 : 409–432

Mocquard JP, Pavese A, Juchault P (1980) Determinisme de la reproduction saisonniere des femelles d'*Armadillidium vulgare* Latr. (crustace, isopode, oniscoide). I. Action de la temperature et de la photperiode. Ann Sci Nat Zool Paris Ser 14 (2) : 91–97

Mocquard JP, Jassem W, Juchault P, Martin G (1984) Déterminisme de la reproduction saisonnière des femelles d'*Armadillidium vulgare* Latr. (crustacé, isopode, oniscoide). VII. Mise en évidence du rôle des yeux composés dans la perception du stimulus photopériodique induisant l'entrée en reproduction. Ann Sci Nat Zool Paris Ser 13 (6) : 71–76

Mocquard JP, Juchault P, Souty-Grosset C (1989) The role of environmental factors (temperature and photoperiod) in the reproduction of the terrestrial isopod *Armadillidium vulgare* (Latreille, 1804). Monit Zool Ital (NS) Monogr 4:455–475

Mödlinger G (1931) Beiträge zur Morphologie der Respirationsorgane der Landisopoden. Stud Zool (Budap) 2:52–79

Morgan AJ, Gregory ZDE, Winters C (1990) Responses of hepatopancreatic 'B' cells of a terrestrial isopod, *Oniscus asellus*, to metals accumulated from a contaminated habitat: a morphometric analysis. Bull Environ Contam Toxicol 44:363–368

Müller A (1925) Über Lichtreaktionen von Landasseln. Z Vl Physiol 3:113–144

Munuswamy N, Subramoniam T (1980) An electophoretic investigation on yolk utilisation in an isopod *Ligia exotica* Roux (Crustacea: Isopoda). Zool Jahrb Physiol 84:417–422

Murlin JR (1902) Absorption and secretion in the digestive system of the land isopods. Proc Acad Nat Sci Phila 54:284–359

Nagano T (1949) Physiological studies on the pigmentary system of Crustacea. III. The color change of an isopod *Ligia exotica* (Roux). Sci Rep Tohoku Univ Fourth Ser (Biol) 18:167–175

Nair GA (1976a) Food and reproduction of the soil isopod, *Porcellio laevis*. Int J Ecol Environ Sci 2:7–13

Nair GA (1976b) Life cycle of *Porcellio laevis* (Latreille) (Isopoda, Porcellionidae). Proc Indian Acad Sci 84B:165–172

Nair GA (1978) Some aspects of the population characteristics of the soil isopod, *Porcellio laevis* (Latreille), in Delhi region. Zool Anz 201:86–96

Nair GA (1984) Breeding and population biology of the terrestrial isopod, *Porcellio laevis* (Latreille), in the Delhi region. Symp Zool Soc Lond 53:315–337

Nair GA, Nair NB, Nair TV (1989) Nutritional biology of *Porcellionides pruinosus* (Brandt, 1833) (Porcellionidae, Oniscoidea) with special reference to conversion efficiency. Monit Zool Ital (NS) Monogr 4:271–283

Nakatsuchi Y (1983) Change in the frequency of oogonial mitosis in *Armdillidium vulgare* (terrestrial isopod) during the reproductive season. J Fac Sci Univ Tokyo Sect IV Zool 15:321–324

Nash J (1979) The effect of daily fluctuating temperatures on the oxygen consumption of *Oniscus asellus* L. Comp Biochem Physiol 62A:983–987

Needham AE (1942) The structure and development of the segmental èxcretory organs of *Asellus aquaticus* (Linne). Q J Microsc Sci 83:205–243

Negishi S, Hasegawa Y (1991) Pigment granule formation in the isopod, *Armadillidium vulgare*. Invert Reprod Dev 19:167–173

Němec B (1895) Studie o Isopodech I. Sitzungsber böhm Ges Wiss Math-Naturwiss 45:1–46

Němec B (1896a) Studie o Isopodech II. Sitzungsber böhm Ges Wiss Math-Naturwiss 25:1–55

Němec B (1896b) Über Excretionsorgane und Geschlechtsverhältnisse einiger Isopoden. Zool Anz 19:297–301

Neuhauser E, Hartenstein R (1976) Degradation of phenol, cinnamic and quinic acid in the terrestrial crustacean, *Oniscus asellus*. Soil Biol Biochem 8:95–98

Neuhauser EF, Hartenstein R (1978) Phenolic content and palatability of leaves and wood to soil isopods and diplopods. Pedobiologia 18:99–109

Neuhauser E, Youmell C, Hartenstein R (1974) Degradation of benzoic acid in the terrestrial crustacean, *Oniscus asellus*. Soil Biol Biochem 6:101–107

Newell RC, Wieser W, Pye VI (1974) Factors affecting oxygen consumption in the woodlouse *Porcellio scaber* Latr. Oecologia (Berl) 16 : 31–51

Newell RC, Roy A, Armitage KB (1976) An analysis of factors affecting the oxygen consumption of the isopod *Ligia oceanica*. Physiol Zool 49 : 109–137

Newstead JD, Dornfeld EJ (1965) Epithelial structure in the anterior segment of the vas deferens of an isopod, *Porcellio scaber* (Latreille). Z Zellforsch 68 : 795–817

Nicholls AG (1931a) Studies on *Ligia oceanica*. I. A. Habitat and effect of change of environment on respiration. B. Observations on moulting and breeding. J Mar Biol Assoc UK 17 : 655–673

Nicholls AG (1931b) Studies on *Ligia oceanica*. II. The processes of feeding, digestion and absorption, with a description of the structure of the foregut. J Mar Biol Assoc UK 17 : 675–705

Niida A, Sadakane K, Yamaguchi T (1990) Stretch receptor organs in the thorax of a terrestrial isopod (*Armdillidium vulgare*). J Exp Biol 149 : 515–519

Nilsson DE, Nilsson HL (1981) A crustacean compound eye adapted for low light intensities (Isopoda). J Comp Physiol A 143 : 503–510

Noulin G, Maissiat J (1974) Etude du rôle de l'organe Y et de l'effet de l'ectystérone dans la régénération d'un appendice chez l'oniscoide *Porcellio dilatatus*. J Insect Physiol 20: 1963–1974

Numanoi H (1937) Migration of calcium through blood in *Ligia exotica* during its moulting. Jpn J Zool 7 : 241–249

Numanoi H (1939) Hepatopancreas in relation to the moulting of *Ligia exotica*. Jpn J Zool 8 : 365–369

Nusbaum-Hilarowicz J (1921) Zur Histologie und Physiologie der Verdauungsorgane der Landasseln, zugleich ein Beitrag zur Kenntnis der Resorptionsvorgänge im Tierreich. Bull Int Acad Pol Sci Lett Ser B 1920 : 67–117

Oetinger DF, Nickol BB (1981) Effects of acanthocephalans on pigmentation of freshwater isopods. J Parasitol 67 : 672–684

Oguro C (1959) On the physiology of melanophores in the marine isopod, *Idotea japonica. I.* Endocrinol Jpn 6 : 246–252

Oguro C, Sakai E (1971) Copper content in some isopods. Proc Jpn Soc Syst Zool 7 : 49–53

Okay S (1943) Changement de coloration chez *Sphaeroma serratum* Fabr. Rev Fac Sci Univ Istanbul Ser B 9 : 204–227

Ondo Y (1958) Daily rhythmic activity of *Tylos granulatus*. IV. Characteristic movement of the shore sowbug accompanied with the periodic movement of waves (in comparison with *Talorchestia brito*). Jpn J Ecol 8 : 84–90

Ondo Y (1959) Daily rhythmic activity of *Tylos granulatus* Miers. V. Studies on the mechanisms of periodic behavior accompanied with periodic movement of waves. Jpn J Ecol 9 : 159–167

O'Rourke FJ (1950) The isopod *Platyarthrus hoffmannseggi*. Brandt, and its relation to ants. Entomol Rec 72 : 27–30

Palackal T, Faso L, Zung JL, Vernon G, Witkus R (1984) The ultrastructure of the hindgut epithelium of terrestrial isopods and its role in osmoregulation. Symp Zool Soc Lond 53 : 185–198

Pandian TJ (1972) Egg incubation and yolk utilization in the isopod *Ligia oceanica*. Proc Indian Natl Sci Acad 38 : 430–441

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

Paris OH (1965) Vagility of P32-labelled isopods in grassland. Ecology 46: 635–648

Paris OH, Pitelka FA (1962) Population characteristics of the terrestrial isopod *Armadillidium vulgare* in California grassland. Ecology 43: 229–248

Paris OH, Sikora A (1965) Radiotracer demonstration of isopod herbivory. Ecology 46: 729–734

Paris OH, Sikora A (1967) Radiotracer analysis of the trophic dynamics of natural isopod populations. In: Petrusewicz K (ed) Secondary productivity of terrestrial ecosystems (principles and methods), vol II. Institute of Ecology Polish Academy of Sciences, Warsaw, pp 741–771

Parry G (1953) Osmotic and ionic regulation in the isopod crustacean *Ligia oceanica.* J Exp Biol 30: 567–574

Patanè L (1940) Sulla struttura e la funzioni del marsupio di *Porcellio laevis* Latreille. Arch Zool Ital 28: 271–295

Patanè L, Giuffrida AM (1962) Organo di Zenker ed escrezione dell'acido urico in isopodi marini e terrestri. Boll Acad Gioenia Sci Nat Catania Ser IV 6: 373: 391

Patrick DM (1926) An experimental study of the cells of the hepato-pancreas of *Ligia.* Brit J Exp Biol 4: 27–37

Pavese A (1987) Etude d'une population naturelle du crustace isopode oniscoide *Armadillidium vulgare* sous le climat de Marrakech. Dynamique de la population et cycle reproducteur. Vie Milieu 37: 139–147

Perttunen V (1961) Reactions de *Ligia italica* F. a la lumiere et a l'humidite de l'air. Vie Milieu 12: 219–259

Perttunen V (1963) Effect of desiccation on the light reactions of some terrestrial arthropods. Ergeb Biol 26: 90–97

Phillipson J (1983) Life cycle, numbers, biomass and respiratory metabolism of *Trichoniscus pusillus* (Crustacea, Isopoda) in a beech woodland—Wytham Woods, Oxford. Oecologia (Berl) 57: 339–343

Phillipson J, Watson J (1965) Respiratory metabolism of the terrestrial isopod *Oniscus asellus* L. Oikos 16: 78–87

Picaud JL (1980) Vitellogenin synthesis by the fat body of *Porcellio dilatatus* Brandt (Crustacea, Isopoda). Int J Invert Rep 2: 341–349

Picaud JL, Souty C (1980a) Démonstration immunohistochimique de la présence de vitelogénine dans le tissu adipeux et l'hepatopancreas du crustacé isopode oniscoide *Porcellio delatatus* (Brandt.) CR Acad Sci Paris Ser D 290: 123–125

Picaud JL, Souty C (1980b) Démonstration par immunaoutoradiographie de la synthèse de la vitellogénine par le tissu adipeux de *Porcellio dilatatus* Brandt (crustacé, isopode). CR Acad Sci Paris Ser D 290: 1019–1021

Picaud JL, Souty C (1981) Approche quantitative de l'influence de l'ovariectomie sur la synthese de la vitellogénine chez *Porcellio dilatatus* Brandt (crustace, isopode). CR Acad Sci Paris 293: 479–482

Picaud JL, Souty-Grosset C, Martin G (1989) Vitellogenesis in terrestrial isopods: female specific proteins and their control. Monit Zool Ital (NS) Monogr 4: 305–331

Piearce TG (1989) Acceptability of pteridophyte litters to *Lumbricus terretris* and *Oniscus asellus*, and implications for the nature of ancient soils. Pedobiologia 33: 91–100

Pobozsny M (1978) Nahrungsansprüche einiger diplopoden- und Isopoden-Arten in mesophilen Laubwäldern Ungarns. Acta Zool Acad Sci Hung 24: 397–406

Powell CVL, Halcrow K (1982) The surface microstructure of marine and terrestrial Isopoda (Crustacea, Peracarida). Zoomorphology 101 : 151–164

Price JB, Holdich DM (1980a) The formation of the epicuticle and associated structures in *Oniscus asellus* (Crustacea, Isopoda). Zoomorphologie 94 : 321–332

Price JB, Holdich DM (1980b) An ultrastructural study of the integument during the moult cycle of the woodlouse, *Oniscus asellus* (Crustacea, Isopoda). Zoomorphologie 95 : 250–263

Price JB, Holdich DM (1980c) Changes in osmotic pressure and sodium concentration of the haemolymph of woodlice with progressive desiccation. Comp Biochem Physiol 66 A : 297–305

Prosi F, Dallinger R (1988) Heavy metals in the terrestrial isopod *Porcellio scaber* Latreille. I Histochemical and ultrastructural characterization of metal-containing lysosomes. Cell Biol Toxicol 4 : 81–96

Prosi F, Storch V, Janssen HH (1983) Small cells in the midgut glands of terrestrial Isopoda: sites of heavy metal accumulation. Zoomorphology 102 : 53–64

Pynnönen K (1985) The structure of long distance (antennular) chemoreceptors in *Saduria entomon* (L.), Isopoda, and their role in feeding behaviour. Ann Zool Fenn 22 : 423–432

Quinlan MC, Hadley NF (1983) Water relations of the terrestrial isopods *Porcellio laevis* and *Porcellionides pruinosus* (Crustacea, Oniscoidea). J Comp Physiol 151 : 155–161

Radu VG, Crăciun C (1969) Le cycle annuel des phases spermatogénétiques chez *Armadillidium vulgare* Latr. (isopode terrestre). Rev Roum Biol Ser Zool 14 : 375–384

Radu VG, Crăciun C (1971) Le cycle annuel des cellules glandulaires de la vésciule séminale chez *Armadillidium vulgare* Latr. (isopod terrestre) dans les conditions climatiques de Roumanie. Rev Roum Biol Ser Zool 16 : 29–37

Radu VG, Crăciun C (1976) The ultrastructure of the androgenic gland in *Porcellio scaber* Latr. (terrestrial isopods). Cell Tissue Res 175 : 245–263

Radu VG, Tomescu N (1976) Quantitativ-ökologische Untersuchungen an Landisopoden. Pedobiologia 16 : 36–43

Radu VG, Tomescu N, Racovita L, Imreh S (1971) Radioisotope researches concerning the feeding and the assimilation of $Ca^{45}$ in terrestrial isopods. Pedobiologia 11 : 296–303

Raimond R, Juchault P (1983) Masculinisation des femelles prépubères et pubères de *Sphaeroma serratum* Fabr. (crustacé, isopode, flabellifere) par implantation d'une glande androgène de mâle pubère. Gen Comp Endocrinol 50 : 146–155

Refinetti R (1984) Behavioral temperature regulation in the pill bug, *Armadillidium vulgare* (Isopoda). Crustaceana 47 : 29–43

Reichle DE (1967) Radioisotope turnover and energy flow in terrestrial isopod populations. Ecology 48 : 351–366

Reichle DE (1968) Relation of body size to food intake, oxygen consumption, and trace element metabolism in forest floor arthropods. Ecology 49 : 538–542

Reid DG, Naylor E (1985) Free-running, endogenous semilunar rhythmicity in a marine isopod crustacean. J Mar Biol Assoc UK 65 : 85–91

Reinders DE (1933) Die Funktion der Corpora alba bei *Porcellio scaber*. Z Vgl Physiol 20 : 291–298

Risler H (1976) Die Ultrastruktur eines Chordotonalorgans in der Geissel der Antenne von *Armadillidium nasutum* Budde-Lund (Isopoda, Crustacea). Zool Jahrb Anat 95 : 94–104

Risler H (1977) Die Sinnesorgane der Antennula von *Porcellio scaber* Latr. (Crustacea, Isopoda). Zool Jahrb Anat 98 : 29–52

Risler H (1978) Die Sinnesorgane der Antennula von *Ligidium hypnorum* (Cuvier) (Isopoda, Crustacea). Zool Jahrb Anat 100 : 514–541

Rushton SP, Hassall M (1983a) The effects of food quality on the life history parameters of the terrestrial isopod (*Armadillidium vulgare* (Latreille)). Oecologia (Berl) 57 : 257–261

Rushton SP, Hassall M (1983b) Food and feeding rates of the terrestrial isopod *Armadillidium vulgare* (Latreille). Oecologia (Berl) 57 : 415–419

Rushton SP, Hassall M (1987) Effects of food quality on isopod population dynamics. Funct Ecol 1 : 359–367

Saito S (1965) Structure and energetics of the population of *Ligidium japonica* (Isopoda) in a warm temperate forest ecosystem. Jpn J Ecol 15 : 47–55

Saleem M, Alikhan MA (1974) The distribution of phosphomonesterases in the digestive gut of *Porcellio laevis* Latreille (Porcellionidae, Isopoda). Comp Biochem Physiol 48A : 375–385

Salemaa H (1987) Herbivory and microhabitat preferences of *Idotea spp.* (Isopoda) in the Northern Baltic Sea. Ophelia 27 : 1–15

Salminen I, Lindqvist OV (1972) Cuticular water content and the rate of evaporation in the terrestrial isopod *Porcellio scaber* Latr. J Exp Biol 57 : 569–574

Sassaman C (1978) Mating systems in porcellionid isopods: multiple paternity and sperm mixing in *Porcellio scaber* Latr. Heredity 41 : 385–397

Sassaman C, Garthwaite R (1984) The interaction between the terrestrial isopod *Porcellio scaber* Latreille and one of its dipteran parasites, *Melanophora roralis* (L.) (Rhinophoridae). J Crustacean Biol 4 : 595–603

Satija RC, Sharma SP, Singla OP (1967) Preliminary studies on the brain of *Porcellionides pruinosus* Brandt (Isopoda, Crustacea). Res Bull (NS) Punjab Univ 18 : 231–235

Saudray Y (1954) Utilisation des rèserves lipidiques au cours de la ponte et du développement embryonnaire chez deux crustacés: *Ligia oceanica* Fab. et *Homarus vulgaris* Edw. C R Soc Biol 148 : 814–816

Saudray Y, Lemercier A (1960) Observations sur le développement des oeufs de *Ligia oceanica* Fabr. crustacé isopode oniscoide. Bull Inst Océanogr (Monaco) 1162 : 1–11

Schäfer MW (1982) Gegendrehung und Winkelsinn in der Orientierung verschiedener Arthropoden. Zool Jahrb Physiol 86 : 1–16

Schäfer MW (1986) Ergänzende Untersuchungen zum Gegendrehungsverhalten der Asseln *Oniscus asellus* L. und *Porcellio scaber* Latr. Zool Jahrb Physiol 90 : 285–296

Schildknecht H, Esswein U, Hering W, Blaschke C (1988) Diskriminierungspheromone der sozialen Wüstenassel *Hemilepistus reaumuri*. Z Naturforsch 43C : 613–620

Schliebe U (1991) Orientation to the conspecific in *Oniscus asellus* L. (Crustacea, Isopoda, Oniscoidea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 89–96

Schmalfuss H (1975) Morphologie, Funktion und Evolution der Tergithöcker bei Landisopoden (Oniscoidea, Isopoda, Crustacea). Z Morphol Tiere 80 : 287–316

Schmalfuss H (1977) Morphologie und Funktion der tergalen Längsrippen bei Landisopoden (Oniscoidea, Isopoda, Crustacea). Zoomorphologie 86 : 155–167

Schmalfuss H (1978a) Morphology and function of cuticular micro-scales and corresponding structures in terrestrial isopods (Crust., Isop., Oniscoidea). Zoomorphologie 91 : 263–274

Schmalfuss H (1978b) *Ligia simoni*: a model for the evolution of terrestrial isopods. Stuttg Beitr Naturkd Ser A (Biol) 317 : 1–5

Schmalfuss H (1983) Asseln. Stuttg Beitr Naturk Ser C 17 : 28 pp

Schmalfuss H (1984) Eco-morphological strategies in terrestrial isopods. Symp Zool Soc Lond 53 : 49–63

Schmitz EH (1989) Anatomy of the central nervous system of *Armadillidium vulgare* (Latraeille) (Isopoda). J Crustacean Biol 9 : 217–227

Schmitz EH, Schultz TW (1969) Digestive anatomy of terrestrial isopoda: *Armadillidium vulgare* and *Armadillidium nasatum*. Am Midl Nat 82 : 161–181

Schmölzer K (1965) Ordnung Isopoda (Landasseln), Lieferung 4. Akademie Verlag, Berlin, 186 pp

Schneider P (1971) Lebensweise und soziales Verhalten der Wüstenassel *Hemilepistus aphganicus* Borutzky 1958. Z Tierpsychol 29 : 121–133

Schneider P (1973) Über die Geruchsrezeptoren der afghanischen Wüstenassel. Naturwissenschatten 60 : 106–107

Schneider P (1975) Beitrag zur Biologie der afghanischen Wüstenassel *Hemilepistus aphganicus* Borutzky 1958 (Isopoda, Oniscoidea). Aktivitätsverlauf. Zool Anz 195 : 155–170

Schneider P, Jakobs B (1977) Versuche zum intra-und interspezifischen Verhalten terrestrischer Isopoden (Crustacea, Oniscoidea). Zool Anz 199 : 173–186

Schneider P, Krczal G (1984) Amount and choice of food in woodlice on cultivated plants. Z Angew Entomol 97 : 333–341

Schneider P, Tschakaroff-Schuster J (1978) Beitrag zur Orientierung und Ernährungsbiologie einheimischer Asseln (Crustacea, Isopoda). Mitt Dtsch Ges allg angew Entomol 1 : 47–57

Schöbl J (1880) Ueber die Fortpflanzung isopoder Crustaceen. Arch Mikrosk Anat Entwick Mechanik 17 : 125–140

Schönichen W (1899) Der Darmkanal der Onisciden und Aselliden. Z Wiss Zool 65 : 143–178

Seelinger G (1977) Der Antennenendzapfen der tunesischen Wüstenassel *Hemilepistus reaumuri*. ein komplexes Sinnesorgan (Crustacea, Isopoda). J Comp Physiol 113 : 95–103

Seelinger G (1983) Response characteristics and specificity of chemoreceptors in *Hemilepistus reaumuri* (Crustacea, Isopoda). J Comp Physiol 152 : 219–229

Sevilla C (1975) Étude des constituants organiques de l'hemolymophe des oniscoides (crustacés, isopodes). Bull Soc Zool Fr 100 : 443–456

Sevilla C, Lagarrigue JG (1974) Acides aminés libres de l'hémolymphe de *Ligia italica*, *Porcellio laevis*, *Armadillidium vulgare* et *Armadillo officinalis* (crustaces, isopodes). C R Acad Sci Paris Ser D 278 : 1079–1082

Sevilla C, Lagarrigue JG (1975) Etude préliminaire sur la teneur en lipides de l'hémolymphe de quatre espèces d'Oniscoides (crustaces, isopodes). C R Acad Sci Paris 280 : 1115–1117

Shachak M (1980) Energy allocation and life history strategy of the desert isopod *H. reaumuri*. Oecologia (Berl) 45 : 404–413

Shachak M, Brand S (1988) Relationship among settling, demography and habitat selection: an approach and a case study. Oecologia (Berl) 76 : 620–626

Shachak M, Newton PG (1985) The relationship between brood care and environmental unpredictability in the desert isopod *Hemilepistus reumuri*. J Arid Environ 9 : 199–209

Shachak M, Yair A (1984) Population dynamics and role of *Hemilepistus reaumuri* (Audouin & Savigny) in a desert ecosystem. Symp Zool Soc Lond 53 : 295–314

Shachak M, Chapman EA, Steinberger Y (1976) Feeding, energy flow and soil turnover in the desert isopod, *Hemilepistus reaumuri*. Oecologia (Berl) 24 : 57–69

Shachak M, Steinberger Y, Orr Y (1979) Phenology, activity and regulation of radiation load in the desert isopod, *Hemilepistus reaumuri*. Oecologia (Berl) 40 : 133–140

Sharma SP (1970) Studies on the deutocerebrum in a terrestrial isopod, *Cubaris robusta* Collinge (family: Armadillidae, Isopoda, Crustacea). Zool Anz 184 : 217–220

Sharma SP (1977) Studies on the tritocerebrum of a terrestrial isopod, *Cubaris robusta* Collinge (family: Armadillidae-Crustacea). Zool Jahrb Anat 97 : 141–146

Sharma SP (1979a) Microanatomy of the deutocerebrum in the isopod crustaceans. Zool Jahrb Anat 102 : 1–11

Sharma SP (1979b) Histological study of the pseudofrontal organ in *Cubaris robusta* Collinge (Crustacea). Zool Jahrb Anat 102 : 431–434

Sharma SP (1982) Microanatomical studies on the optic neuropiles of an isopod, *Ligia exotica* Roux (Crustacea). Folia Morphol 30 : 70–74

Shereef GM (1970) Biological observations on the woodlice (Isopoda) in Egypt. Rev Écol Biol Sol 7 : 367–379

Shimoizumi M (1952) The breeding habits of *Metoponorthus pruinosus* Brandt. J Gakugei Tokushima Univ 2 : 31–34

Shimoizumi M (1955) Studies on the sexuality of the land isopod, *Metoponorthus pruinosus*. IV. "Female-breeder". J Gakugei, Tokushima Univ 6 : 1–10

Smith WJ, Witkus ER, Grillo RS (1969) Structural adaptations for ion and water transport in the hindgut of the woodlouse *Oniscus asellus*. J Cell Biol 43 : 135a–136a

Snider R, Shaddy JH (1980) The ecobiology of *Trachelipus rathkei* (Isopoda). Pedobiologia 20 : 394–410

Soma K, Saito T (1983) Ecological studies of soil organisms with references to the decomposition of pine needles. II. Litter feeding and breakdown by the woodlouse *Porcellio scaber*. Plant Soil 75 : 139–151

Sörensen EMB, Burkett RD (1977) A population study of the isopod, *Armadillidium vulgare*. in northeastern Texas. Southwest Nat 22 : 375–387

Sorensen KA, Bell WJ (1986) Orientation responses of an isopod to temporal changes in relative humidity: simulation of a "humid patch" in a "dry habitat". J Insect Physiol 32 : 51–57

Southwood TRE (1962) Migration of terrestrial arthopods in relation to habitat. Biol Rev (Camb) 37 : 171–214

Souty C (1980) Electron microscopic study of follicle cell development during vitellogenesis in the marine crustacean Isopoda, *Idotea balthica basteri*. Rep Nutr Dév 20 : 653–663

Souty C, Picaud JL (1981) Vitellogenin synthesis in the fat body of the marine crustacean Isopoda, *Idotea balthica basteri* during vitellogenesis. Rep Nutr Dév 21 : 95–101

Souty C, Picaud JL (1984) Effet de l'injection d'une gonadotropine hormaine sur la synthèse et la libération de la vitellogénine par le tissu adipeux du crustacé isopode marin *Idotea balthica basteri* Audouin. Gen Comp Endocrinol 54 : 418–421

Souty C, Besse G, Picaud JL (1982) Stimulation par l'ecdysone du taux hémolymphatique de la vittellogénine chez le crustacé isopode terrestre *Porcellio dilatatus*. C R Acad Sci Paris 294 : 1057–1059

Souty-Grosset C, Juchault P (1987) Etude de la synthese de la vitellogenine chez les mâles intersexués d'*Armadillidium vulgare* Latreille (crustace isopode oniscoide): Comparaison avec les mâles et les femalles intactes ou ovariectomisees. Gen Comp Endocrinol 66 : 163–170

Souty-Grosset C, Chentoufi A, Mocquard JP, Juchault P (1988) Seasonal reproduction in the terrestrial isopod *Armadillidium vulgare* (Latreille): geographical variability and genetic control of the response to photoperiod and temperature. Invert Reprod Dev 14 : 131–151

Souty-Grosset C, Jassem W, Juchault P, Mocquard JP (1991) Coaction "male-female" and reproductive patterns in *Armadillidium vulgare* Latr. (Crustacea, Oniscoidea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 107–112

Spencer JO, Edney EB (1954) The absorption of water by woodlice. J Exp Biol 31 : 491–496

Stachurski A (1968) Emigration and mortality rates and the food-shelter conditions of *Ligidium hypnorum* L. (Isopoda). Ekol Pol Ser A 16 : 445–449

Standen V (1973) The life cycle and annual production of *Trichoniscus pusillus pusillus* (Crustacea : Isopoda) in a Cheshire wood. Pedobiologia 13 : 273–291

Standing JD, Beatty DD (1978) Humidity behaviour and reception in the sphaeromatid isopod *Gnorimosphaeroma oregonensis* (Dana). Can J Zool 56 : 2004–2014

Steel CGH (1982) Stages of the intermoult cycle in the terrestrial isopod *Oniscus asellus* and their relation to biphasic cuticle secretion. Can J Zool 60 : 429–437

Steinberger Y (1989) Energy and protein budget in the desert isopod *Hemilepistus reaumuri*. Acta Oecol Oecol Gen 10 : 117–134

Stevenson JR (1961) Polyphenol oxidase in the tegumental glands in relation to the molting cycle of the isopod crustacean *Armadillidium vulgare*. Biol Bull (Woods Hole) 121 : 554–560

Stevenson JR (1964) Development of the tegumental glands in the pillbug, *Armadillidium vulgare* in relation to the molting cycle. Trans Am Microsc Soc 89 : 252–260

Stöckli H (1990) Das Unterscheidungsvermögen von *Porcellio scaber* (Crustacea, Isopoda) zwichen Blättern einer Baumart, unter Berücksichtigung der makroskopisch sichtbaren Verpilzung. Pedobiologia 34 : 191–205

Stoller JH (1899) On the organs of respiration of the Oniscoidea. Bibl Zool 10 (25) : 1–29

Storch V (1982) Der Einfluss der Ernährung auf die Ultrastruktur der grossen Zellen in den Mitteldarmdrüsen terrestrischer Isopoda (*Armadillidium vulgare*, *Porcellio scaber*). Zoomorphology 100 : 131–142

Storch V (1984) The influence of nutritional stress on the ultrastructure of the hepatopancreas of terrestrial isopods. Symp Zool Soc Lond 53 : 167–184

Storch V (1987) Microscopic anatomy and ultrastructure of the stomach of *Porcellio scaber* (Crustacea, Isopoda). Zoomorphology 106 : 301–311

Storch V, Lehnert-Moritz K (1980) The effects of starvation on the hepatopancreas of the isopod *Ligia oceanica*. Zool Anz 204 : 137–146

Storch V, Štruš J (1989) Microscopic anatomy and ultrastructure of the alimentary canal in terrestrial isopods. Monit Zool Ital (NS) Monogr 4:105–126

Striganova BR, Kondeva EA (1980) Food requirements and growth of land woodlice (Oniscoidea). Zool Zhurn 59 (12):1792–1799 (in Russian)

Striganova BR, Samedov NG, Loginova NG (1981) The quantitative estimation of wood lice (*Armadillidium vulgare* Latr.) role in decomposition of plant remains and in migration of ash elements in semi-desert. Zool Zh 42:528–531 (in Russian)

Strömberg JO (1964) On the embryology of the isopod *Idotea*. Årk Zool 17:421–473

Strong KM, Daborn GR (1980) The influence of moulting on the ingestion rate of an isopod crustacean. Oikos 34:159–162

Štruš J, Burkhardt P, Storch V (1985) The ultrastructure of the midgut glands in *Ligia italica* (Isopoda) under different nutritional conditions. Helgol Meeresunters 39:367–374

Strüve-Kusenberg R (1989) Zur Nahrungsbiologie der Asseln (Isopoda) eines Kalekbuchenwaldes. Verh Ges Ökol Göttingen 17:267–272

Stutt I, Laverack MS (1979) Proprioceptors in the uropods of *Ligia oceanica* (L.) (Isopoda: Crustacea). Mar Behav Physiol 6:269–276

Sultanov MA, Kabilov TK, Siddikov BK (1980) Infestation of wood lice *Hemilepistus pectinatus* Isopoda by the larval forms of helminths. Uzb Biol Zh 3:45–47 (in Russian)

Sunderland KD, Sutton SL (1980) A serological study of arthropod predation on woodlice in a dune grassland ecosystem. J Anim Ecol 49:987–1004

Sunderland KD, Hassall M, Sutton SL (1976) The population dynamics of *Philoscia muscorum* (Crustacea, Oniscoidea) in a dune grassland ecosystem. J Anim Ecol 45:487-506

Sutton SL (1968) The population dynamics of *Trichoniscus pusillus* and *Philoscia muscorum* (Crustacea, Oniscoidea) in limestone grassland. J Anim Ecol 37:425–444

Sutton SL (1970a) Growth patterns in *Trichoniscus pusillus* and *Philoscia muscorum* (Crustacea: Oniscoidea). Pedobiologia 10:434–441

Sutton SL (1970b) Predation on woodlice: an investigation using the precipitin test. Entomol Exp Appl 13:279–285

Sutton SL, Hassall M, Willows R, Davis RC, Grundy A, Sunderland KD (1984) Life histories of terrestrial isopods: a study of intra- and interspecific variation. Symp Zool Soc Lond 53:269–294

Suzuki S (1986) Effect of Y-organ ablation on oocyte growth in the terrestrial isopod, *Armadillidium vulgare*. Biol Bull (Woods Hole) 170:350–355

Suzuki S (1987) Vitellins and vitellogenins of the terrestrial isopod, *Armadillidium vulgare*. Biol Bull (Woods Hole) 173:345–354

Suzuki S, Yamasaki K (1989) Ovarian control of oostegite formation in *Armadillidium vulgare* (Crustacea, Isopod). Zool Sci 6:1132

Suzuki S, Yamasaki K (1991) Sex-reversal of male *Armadilllidium vulgare* (Isopoda, Malacostraca, Crustacea) following andrecotomy and partial gonadectomy. Gen Comp Endocrinol 83:375–378

Suzuki S, Yamasaki K, Katakura Y (1990) Vitellogenin synthesis in andrectomized males of the terrestrial isopod, *Armadillidium vulgare* (Malacostraca Crustacea). Gen Comp Endocrinol 77:283–291

Szlavecz K, Maiorana VC (1991) Food selection by isopods paired choice tests. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 115–119

Szyfter Z (1966) The correlation of moulting and changes occurring in the hepatopancreas of *Porcellio scaber* Latr. (Crustacea, Isopoda). Bull Soc Amis Sci Lett Poz Ser D 7:95–114

Tait J (1917) Experiments and observations on Crustacea. Part II. Moulting of isopods. Proc R Soc Edinb 37:59–67

Taiti S, Ferrara F, Schmalfuss H (1991) Evolution and biogeography of the family Eubelidae (Crustacea, Oniscoidea). In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ. Press, Poitiers, pp 23–30

Takeda N (1980) The aggregation pheromone of some terrestrial isopod crustaceans. Experientia 36:1296–1297

Takeda N (1984) The aggregation phenomenon in terrestrial isopods. Symp Zool Soc Lond 53:381–404

Takeda N, Mizuno J (1989) Land adaptation and neuropeptides in terrestrial isopods. Monit Zool Ital (NS) Monogr 4:249–270

Taketomi Y, Ban T (1986) Ultrastructure of the sinus gland in a terrestrial isopod, *Armadillidium vulgare*. Cell Biol Int Rep 10:837–843

Ter-Poghossian A (1909) Beiträge zur Kenntnis der Exkretionsorgane der Isopoden. Z Naturwiss Halle 81:1–50

Todd M (1963) Osmoregulation in *Ligia oceanica* and *Idotea granulosa*. J Exp Biol 40:381–392

Tomescu N (1972) $Ca^{45}$ assimilation from food and its distribution in the body of some species of terrestrial isopods. Rev Roum Biol Ser Zool 17:419–425

Tomescu N (1973) Reproduction and postembryonic ontogenetic development in *Ligidium hypnorum* (Cuvier) and *Trichoniscus pusillus* (Brandt 1833) (Crustacea, Isopoda). Rev Roum Biol Ser Zool 18:403–413

Tomescu N, Radu VG (1971) Temperaturile letale superioare la cîteva specii de izopode terrestre. Stud Cercet Biol Ser Zool 23:263–267

Tongiorgi P (1968–69) Ricerche ecologiche sugli artropodi di una spiaggia sabbiosa del litorale tirrenico. III. Migrazioni e ritmo di attivita locomotoria nell'isopode *Tylos latreilli* (Aud. and Sav.) e nei Tenebrionidi *Phaleria provincialis* Fauv. E. *Halammobia pellucida* Herbst. Redia 51:1–19

Torrey HB, Hays GP (1914) The role of random movements in the orientation of *Porcellio scaber* to light. J Anim Behav 4:110–120

Tsukamoto J (1977) Soil macro-animals on a slope in a deciduous broad-leaved forest. I. Two species of terrestrial Isopoda: *Ligidium japonicum* and *L. paulum*. Jpn J Ecol 26:201–206

Unwin EE (1931) On the structure of the respiratory organs of the terrestrial Isopoda. Pap Proc R Soc Tasmania 1931:37–104

Vader W, De Wolf L (1988) Biotope and biology of *Armadillidium album* Dollfus, a terrestrial isopod of sandy beaches, in the SW Netherlands. Neth J Sea Res 22:175–183

Vandel A (1943) Essai sur l'origine, l'evolution et la classification des Oniscoidea (isopodes terrestres). Suppl Bull Biol Fr Belg 30:1–136

Vandel A (1960) Faune de France no 64, isopodes terrestres. Lechevalier, Paris, pp 1–416

Vandel A (1962) Faune de France, no 66, isopodes terrestres, Lechevalier, Paris, pp 417–927

Vandel A (1964) De l'emploi des appareils respiratoires pour l'etablissement d'une classification rationnelle des isopodes terrestres "Oniscoidea". Bull Soc Zool Fr 89 : 730–736

Verhoeff KW (1917a) Über die Larven, das Marsupium und die Bruten der Oniscoidea. Arch Natur 83 : 1–54

Verhoeff KW (1917b) Zur Kenntnis der Atmung und der Atmungsorgane der Isopoda-Oniscoidea. Biol Zentralbl 37 : 113–127

Verhoeff KW (1917c) Zur Kenntnis der Entwicklung der Trachealsysteme und der Untergattungen von *Porcellio* und *Tracheoniscus*. Sitzungsber Ges Naturforsch Freunde Berlin 1917(3) : 195–223

Verhoeff KW (1920) Zur Kenntnis der Larven, des Brutsackes und der Bruten der Oniscoidea. Zool Anz 51 : 169–189

Verhoeff KW (1921) Über die Atmung der Landasseln. Z Wiss Zool 118 : 365–447

Verhoeff KW (1931) Vergleichende geographisch-ökologische Untersuchungen über die Isopoda terrestria von Deutschland, den Alpenländern und anschliessenden Mediterrangebieten. Z Morphol Ökol Tiere 22 : 231–268

Verhoeff KW (1940) Über die Doppelhäutung der Land-Isopoden. Z Morphol Ökol Tiere 37 : 126–143

Verhoeff KW (1949) *Tylos*. eine terrestrisch-maritime Rückwanderer-Gattung der Isopoden. Arch Hydrobiol 42 : 329–340

Vernon GM, Herold L, Witkus ER (1974) Fine structure of the digestive tract epithelium in the terrestrial isopod, *Armadillidium vulgare*. J Morphol 144 : 337–360

Vitéz I (1970) On the cytomorphology of the neurosecretory system of terrestrial isopods. Ann Univ Sci Budap Rolando Eötvös Nominatae Sect Biol 12 : 281–283

Vitéz I (1971) Histophysiological studies on the effect of environmental conditions on terrestrial isopodes. Ann Univ Sci Budap Rolando Eötvös Nominatae Sect Biol 13 : 329–338

Wägele JW (1982) Ultrastructure of the pleopods of the estuarine isopod *Cyathura carinata* (Crustacea: Isopoda: Anthuridea). Zoomorphology 101 : 215–226

Walker R (1935) The central nervous system of *Oniscus* (Isopoda). J Comp Neurol 62 : 197–238

Waloff N (1941) The mechanisms of humidity reactions of terrestrial isopods. J Exp Biol 18 : 115–135

Warburg MR (1964) The response of isopods towards temperature, humidity and light. Anim Behav 12 : 175–186

Warburg MR (1965a) The evaporative water loss of three isopods from semi-arid habitats in South Australia. Crustaceana 9 : 302–308

Warburg MR (1965b) Water relation and internal body temperature of isopods from mesic and xeric habitats. Physiol Zool 38 : 99–109

Warburg MR (1965c) The evolutionary significance of the ecological niche. Oikos 16 : 205–213

Warburg MR (1968a) Simultaneous measurement of body temperature and water loss in isopods. Crustaceana 14 : 39–44

Warburg MR (1968b) Behavioral adaptations of terrestrial isopods. Am Zool 8 : 545–559

Warburg MR (1987a) Haemolymph osmolality, ion concentration and the distribution of water in body compartments of terrestrial isopods under different ambient conditions. Comp Biochem Physiol 86A : 433–437

Warburg MR (1987b) Isopods and their terrestrial environment. Adv Ecol Res

17 : 187–242

Warburg MR (1989) The role of water in the life of terrestrial isopods. Monit Zool Ital (NS) Monogr 4 : 285–304

Warburg MR (1991) Reproductive patterns in oniscid isopods. In: Juchault P, Mocquard JP (eds) Biology of terrestrial isopods. Univ Press, Poitiers, pp 132–137

Warburg MR (1992) Reproductive patterns in three isopod species from the Negev desert. J Arid Environ 22 : 73–85

Warburg MR, Berkovitz K (1978a) Hygroreaction of normal and desiccated *Armadillo officinalis* isopods. Entomol Exp Appl 24 : 55–64

Warburg MR, Berkovitz K (1978b) Thermal effects on photoreaction of the oak-woodland pillbug *Armadillo officinalis* (Isopoda; Oniscoidea), at different humidities, J Therm Biol 3 : 75–78

Warburg MR, Cohen N (1991) Reproductive pattern, allocation, and potential in a semelparous isopod from the Mediterranean region of Israel. J Crustacean Biol 11 : 368–374

Warburg MR, Cohen N (1992) Reproductive pattern, allocation and potential of an iteroparous isopod from a xeric habitat in the Mediterranean region. J Arid Environ 22 : 161–172

Warburg MR, Rosenberg M (1978) Neurosecretory cells in the brain of *Porcellio obsoletus* (Isopoda: Oniscoidea). Int J Insect Morphol Embryol 7 : 195–204

Warburg MR, Rosenberg M (1989) Ultracytochemical identification of $Na^+$, $K^+$-ATPase activity in the isopodan hindgut epithelium. J Crustacean Biol 9 : 525–528

Warburg MR, Rankevich D, Chasanmus K (1978) Isopod species diversity and community structure in mesic and xeric habitats of the Mediterranean region. J Arid Environ 1 : 157–163

Warburg MR, Linsenmair KE, Bercovitz K (1984) The effect of climate on the distribution and abundance of isopods. Symp Zool Soc Lond 53 : 339–367

Watanabe H (1978) A food selection experiment on palatability of woodlouse, *Armadillidium vulgare* Latreille. Edaphologia 18 : 2–8

Watanabe H (1980) A study of the three species of isopods in an evergreen broad-leaved forest in southwestern Japan. Rev Ecol Biol 17 : 229–239

Weber M (1881) Anatomisches über Trichonisciden. Zugleich ein Beitrag zur Frage nach der Bedeutung der Chromatophoren, Pigmente und verzweigten Zellen der Hautdecke. Arch Mikrosk Anat 19 : 579–648

Wenig J (1903) Über neue Sinnesorgane der Isopoden. Sitzungsber Böhm Ges Wiss Math Naturwiss 39 : 1–11

White JJ (1968) Bioenergetics of the woodlouse *Tracheoniscus rathkei* Brandt in relation to litter decomposition in a deciduous forest. Ecology 49 : 694–704

Widmann E (1936) Osmoregulation bei einheimischen Wasser- und Feuchtluft-Crustaceen. Z Wiss Zool 147 : 132–169

Wieser W (1962) Parameter des Sauerstoffverbrauches. I. Der Sauerstoffverbrauch einiger Landisopoden. Z Vgl Physiol 45 : 247–271

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

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

Wieser W (1964a) Über die Häutung von *Porcellio scaber* Latr. Verh Dtsch Zool Ges Kiel 1964 : 178–195

Wieser W (1964b) Die Steuerung von Stoffwechselvorgängen bei *Porcellio scaber* Latr. durch Temperatur und Licht. Verh Dtsch Zool Ges, Kiel pp 359–364

Wieser W (1965) Untersuchungen über die Ernährung und den Gesamtstoffwechsel von *Porcellio scaber* (Crustacea: Isopoda). Pedobiologia 5 : 304–331

Wieser W (1966) Copper and the role of isopods in degradation of organic matter. Science 153 : 67–69

Wieser W (1968) Aspects of nutrition and the metabolism of copper in isopods. Am Zool 8 : 495–506

Wieser W (1972a) Oxygen consumption and ammonia excretion in *Ligia beaudiane* M.-E. Comp Biochem Physiol 43A : 869–876

Wieser W (1972b) O/N ratios of terrestrial isopods at two temperatures. Comp Biochem Physiol 43A : 859–868

Wieser W (1978) Consumer strategies of terrestrial gastropods and isopods. Oecologia (Berl) 36 : 191–201

Wieser W (1984) Ecophysiological adaptations of terrestrial isopods: a brief review. Symp Zool Soc Lond 53 : 247–265

Wieser W, Oberhauser C (1984) Ammonia production and oxygen consumption during the life cycle of *Porcellio scaber* (Isopoda, Crustacea). Pedobiologia 26 : 415–419

Wieser W, Schweizer G (1970) A re-examination of the excretion of nitrogen by terrestrial isopods. J Exp Biol 52 : 267–274

Wieser W, Schweizer G (1972) Der Gehalt an Ammoniak und freien Aminosäuren, sowie die Eigenschaften einer Glutaminase bei *Porcellio scaber* (Isopoda). J Comp Physiol 81 : 73–88

Wieser W, Schweizer G, Hartenstein R (1969) Patterns in the release of gaseous ammonia by terrestrial isopods. Oecologia (Berl) 3 : 390–400

Wieser W, Busch G, Büchel L (1976) Isopods as indicators of the copper content of soil and litter. Oecologia (Berl) 23 : 107–114

Wieser W, Dallinger R, Busch G (1977) The flow of copper through a terrestrial food chain. II. Factors influencing the copper content of isopods. Oecologia (Berl) 30 : 265–272

Williams WD (1983) On the ecology of *Haloniscus searlei* (Isopoda, Oniscoidea), an inhabitant of Australian salt lakes. Hydrobiologia 105 : 137–142

Williams T, Franks NR (1988) Population size and growth rate, sex ratio and behaviour in the ant isopod, *Platyarthrus hoffmannseggii*. J Zool Lond 215 : 703–717

Willows R (1984) Breeding phenology of woodlice and oostegite development in *Ligia oceanica* (L.) (Crustacea). Symp Zool Soc Lond 53 : 469–485

Willows RI (1987a) Population dynamics and life history of two contrasting populations of *Ligia Oceanica* (Crustacea: Oniscidea) in the rocky supralittoral. J Anim Ecol 56 : 315–330

Willows R (1987b) Intrapopulation variation in the reproductive characteristics of two populations of *Ligia oceanica* (Crustacea: Oniscidea). J Anim Ecol 56 : 331–340

Willows R (1987c) Population and individual energetics of *Ligia oceanica* (L.) (Crustacea: Isopoda) in the rocky supralittoral. J Exp Mar Biol Ecol 105 : 253–274

Wilson WJ (1970) Osmoregulatory capabilities in isopods: *Ligia occidentalis* and *Ligia pallasii*. Biol Bull (Woods Hole) 138:96–108

Wood S, Griffith BS (1988) Bacteria associated with the hepatopancreas of the woodlice *Oniscus asellus* and *Porcellio scaber* (Crustacea, Isopoda). Pedobiologia 31:89–94

Wood S, Russell JD (1987) On the nature of the calcium carbonate in the exoskeleton of the woodlouse *Oniscus asellus* L. (Isopoda, Oniscoidea). Crustaceana 53:49–53

Wright JC, Machin J (1990) Water vapour absorption in terrestrial isopods. J Exp Biol 154:13–30

York H (1973) Stoffwechselbesonderheiten und Aktivitätsperiodik bei *Helleria brevicornis* (Crustacea, Isopoda). Pedobiologia 13:214–226

Zahid ZR, Al-Hamood MH, Agha AH (1982) The neurosecretory system of the terrestrial isopod *Porcellio evansi* (Oniscoidea). Crustaceana 43:241–248

Zar JH, White JJ (1969) Seasonal variation in the fatty acid composition of the woodlouse, *Tracheoniscus rathkei* Brandt. Trans Ill State Acad Sci 62:410–412

Zimka JR (1974) Predation of frogs, *Rana arvalis* Nilss., in different forest site conditions. Ekol Pol 22:31–63

# Species Index

# Subject Index

# Springer-Verlag and the Environment