

5 Intestinal Microbiota of Terrestrial Isopods

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5.1 Introduction

Isopods are a cosmopolitan group of crustaceans, which inhabit marine environments ranging from deep-sea to intertidal areas, surface and underground freshwaters and terrestrial environments from high humidity to dry habitats, including deserts. More than one third of the described isopodan species (approximately 9000) belong to the terrestrial Oniscidea or woodlice (slaters, sowbugs and pillbugs; Schamlfuss 2003). The phylogeny and systematics of Oniscidea were analysed and presented by several authors (Schmalfuss 1989; Erhard 1998; Tabacaru and Danielopol 1999). In general, Oniscidea are assigned to five sections, namely Diplocheta, Tylida, Microcheta, Synocheta and Crinocheta, with 33 families altogether (Erhard 1998). Amphibious species of the family Ligiidae (slaters) and members of Mesoniscidae represent only approximately 50 of the described species, the rest belonging to the higher oniscideans, mostly to troglobiontic Synocheta and “truly terrestrial” Crinocheta.

Terrestrial isopods are effective herbivorous scavengers feeding predominantly on decayed plant material, fungi and algae, thus participating in decomposition and cycling of energy and organic matter in the terrestrial environments (Hopkin 1991; Zimmer and Topp 1997). Due to their significant ecological role and their ability to survive in polluted environments, a substantial amount of research was focused on these organisms, and as a result a comprehensive knowledge accumulated on their biology. Species like *Porcellio scaber* and *Oniscus asellus*, for example, are among the most studied organisms in terrestrial ecophysiology and ecotoxicology (Hopkin 1989; Drobne 1997). Terrestrial isopods have diverse feeding strategies including coprophagy and occasional cannibalism. The nutritional importance and significance of coprophagy in the field was not demonstrated

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(Carefoot 1993; Slavecz and Maiorana 1998). However, there is some evidence supporting the importance of coprophagy for development of juveniles (Wieser 1966; Hassall and Rushton 1984).

The food consumption of terrestrial isopods varies according to species (Warburg 1987) and is approximately 0.4 mg dry food per mg dry wt. of animal per day (own observ.). Food assimilation efficiency is between 30 and 50% in *P. scaber* (Nair et al. 1994; Drobne and Hopkin 1995). Food can remain in the gut for 4–17 h (Hartenstein 1964) and is digested and absorbed in a 24 h digestive cycle (Hames and Hopkin 1991). When the feeding rate is lower, food remains in the gut for a longer time. Animals produce 10–35 faecal pellets per day and one pellet is about 1.5 ± 0.2 mm long. About five to seven pellets fill the entire gut. Daily faecal production is independent of the animal's size (own observ.).

The role of isopods as decomposers in terrestrial environments is mainly indirect. They promote microbial activity by fragmentation of the substrate, by increasing the number of some of the ingested microbes in their gut and the distribution of microorganisms in the terrestrial ecosystem (Hanlon 1981a; Hassall et al. 1987; Neuhauser and Hartenstein 1978; Gunnarsson et al. 1988; van Wensem et al. 1993). At the same time, isopods utilise the ingested microorganisms as a source of nutrients, enzymes and vitamins (Neuhauser et al. 1974; Hassall and Jennings 1975; Neuhauser and Hartenstein 1976; Kozlovskaia and Striganova 1977; Kaplan and Hartenstein 1978; Carefoot 1984; Gunnarsson and Tunlid 1986; Kukor and Martin 1986; Ullrich et al. 1991).

5.2

Structure and Function of the Digestive System

The oniscidean digestive system has been extensively studied and well described in both slaters and sowbugs (Hames and Hopkin 1989; Štrus et al. 1995). The tripartite digestive system of terrestrial isopods (Fig. 5.1) consists of a foregut comprising oesophagus and stomach (proventriculus), a midgut presented mainly by tubular midgut glands (hepatopancreas) and a hindgut. The latter consists of two anatomically and functionally different parts; an anterior chamber and a papillate region with rectum, which are innervated by separate nerves (Molnar et al. 1998).

Frequent moulting is an important characteristic of juvenile and adult oniscideans and is related to growth, renewal of the cuticle and reproduction in mature females. Adult sowbugs and pillbugs moult once monthly, slaters twice monthly. The cuticles of the foregut and hindgut are completely renewed during exuviation (Štrus and Blejec 2001). In contrast to

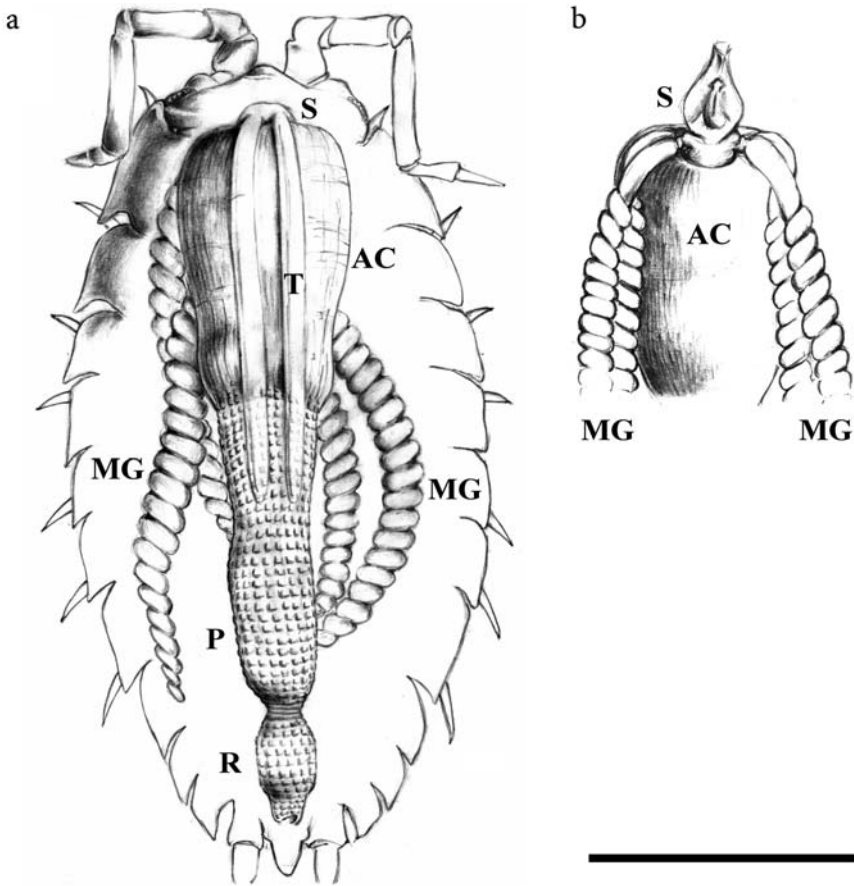


Fig. 5.1. Anatomy of the digestive system of *Porcellio scaber*. **a** Dorsal view of stomach (S), midgut glands (MG) and hindgut consisting of anterior chamber (AC) with typhlosole (T), papillate region (P) and rectum (R). **b** Ventral view of anterior chamber of the hindgut (AC) and the midgut glands (MG) connected to the stomach (S). Scale bar 5 mm

all other crustaceans, terrestrial isopods consume their old cuticle (external and gut) soon after exuviation.

The food is ground and taken up by mouthparts. Fragments of food pass via the oesophagus through the stomach where they are processed mechanically before passing into the anterior chamber of the hindgut. During this process the food is mixed with a secretion derived from the hepatopancreas. The anterior chamber of the hindgut has a pair of typhlosole channels on the dorsal part. When the hindgut is filled with food, contraction of the muscles surrounding the gut forces liquids and fine food particles back into the stomach via the typhlosole channels. This material

is filtered in the stomach and passed into the lumen of the hepatopancreas where the absorption of nutrients takes place (Hames and Hopkin 1989). The absorption of food in the hindgut is limited due to the cuticular lining. However, some absorption of nutrients was reported in the anterior chamber of the hindgut (Hryniewiecka-Szyfter and Storch 1986). Water and ions are absorbed in the papillate region and undigested food is passed into the rectum (Hames and Hopkin 1989). Dry faecal pellets are formed in the rectum and excreted through the anus.

Data on physicochemical conditions in the gut of woodlice were reviewed by Zimmer (2002). The pH levels in the digestive system vary from acidic in the midgut glands and anterior chamber of the hindgut to slightly acidic in the posterior part (reviewed in Zimmer 2002), which should be in accordance with conditions suitable for enzymatic degradation of litter in the anterior chamber and bacterial proliferation in the papillate region. The presence of Na^+/K^+ -ATPases, known to regulate pH in the invertebrate gut (Dow 1992), was demonstrated in the apical part of the epithelial cells in the hindgut of *P. scaber* (Warburg and Rosenberg 1989; Štrus et al. 2002), although direct measurements of pH in the isopod gut were not performed in these studies.

The presence of an anaerobic zone in the radial centre of the hindgut, as a result of the oxygen-consuming metabolism of the ingested facultative anaerobes, was suggested by Zimmer (2002). However, the large surface to volume ratio of the gut, its tube-like anatomy, the presence of air pockets in ingested food (Hames and Hopkin 1989) and the redox potential between +50 mV and +10 mV (Hartenstein 1964) indicate the prevalence of aerobic conditions in the gut, but anaerobic microhabitats cannot be excluded (Savage 1978).

In terrestrial isopods digestive juices are produced in the midgut glands and possibly also in the short endodermal part of the midgut in amphibious species (Štrus et al. 1995). The midgut glands are the central metabolic organs with absorptive, secretive, storage and excretive functions. The enzymatic composition of digestive juices produced in digestive glands was reviewed by Zimmer (2002). Possible existence of endogenous cellulases was not studied in isopods. They were described in nematodes (Yan et al. 1998), termites (Watanabe et al. 1998) and crayfish (Byrne et al. 1999; Xue et al. 1999). It is assumed that microbial enzymes ingested with food (Kozlovskaja and Striganova 1977, Kukor and Martin 1986; Ullrich et al. 1991) or produced by endosymbiotic bacteria in the midgut glands (Zimmer and Topp 1998a, b) are utilised for decomposition of ingested lignocellulose. Since the origin of cellulases and the role of microbiota in the digestive system of terrestrial isopods were not proved indisputably, mainly due to the shortcomings of the methods applied, this still remains to be elucidated.

5.3 The Microbiota of the Digestive System

As in other arthropods, the foregut of terrestrial isopods is generally poorly inhabited by microorganisms, while rich and varied flora is present in the tube-like hindgut, especially in its posterior part (Bignell 1984; Drobne 1995; Kostanjšek et al. 2003). According to Zimmer and Topp (1998b), the total number of gut microbiota vary from 300 to 700 million cells/mg of gut content, among which only 0.01 to 1% are cultivable (Reyes and Tiedje 1976a; Coughtrey et al. 1980; Carefoot et al. 1984; Griffiths and Wood 1985; Zimmer and Topp 1998b; Drobne et al. 2002).

Since terrestrial isopods prefer to feed on food colonised by microorganisms (Soma and Saito 1983; Gunnarsson 1987; Zimmer et al. 1996) and lack the gut compartments in which abundant resident microflora would develop, their gut microbiota consists mainly of ingested microbes (Hassall and Jennings 1975; Reyes and Tiedje 1976a; Ineson and Anderson 1985). However, the presence of resident bacteria has been suggested in the hindgut (Kostanjšek et al. 2002, 2003) and midgut glands (Wood and Griffiths 1988; Zimmer 2002). Part of the ingested microbiota, mainly fungi and Gram negative bacteria, are digested during passage through the digestive system (Reyes and Tiedje 1976b; Coughtrey et al. 1980; Hanlon and Anderson 1980; Hanlon 1981b; Gunnarsson and Tunlid 1986; Clegg et al. 1994, 1996; Kayang et al. 1994; Zimmer and Topp 1998b; Kostanjšek 2002). Some of the undigested bacteria seem to be passive transients through the gut (Márialigeti et al. 1984). The others, mainly Gram positive bacteria, can proliferate in the hindgut and subsequently in faeces (summarised in Table 5.1) (Reyes and Tiedje 1976a; Coughtrey et al. 1980; Hanlon and Anderson 1980; Ineson and Anderson 1980; Hassall et al. 1987; Hanlon 1981b; Gunnarsson and Tunlid 1986; Kayang et al. 1994).

5.3.1 Bacteria in the Gut

Although it has been assumed that bacteria in the gut consist mainly of ingested bacteria, it would appear likely that isopods possess and exploit resident gut bacteria in digestion, like other lignocellulose-feeding animals. Due to the gut anatomy, frequent renewal of the gut cuticle and short retention time of food, the gut of terrestrial isopods seems at the first glance a rather unsuitable environment for the development of resident microbiota (Hassall and Jennings 1975). However, reports based on traditional microbiological techniques (Reyes and Tiedje 1976a; Griffiths and Wood 1985; Ineson and Anderson 1985; Gunnarsson and Tunlid 1986; Hassall et al. 1987;

Table 5.1. Bacterial taxa from the digestive system of terrestrial isopods

Bacterial taxa	G	MG	F	Isopod	References
<i>Aeromonas</i> sp.	-	+	-	<i>Porcellio scaber</i>	Ullrich et al. (1993)
<i>Acinetobacter calcoaceticus</i>	-	-	-	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Arthrobacter</i> sp.	+	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Azotobacter agilis</i>	+	-	-	<i>Oniscus asellus</i>	Beerstecher et al. (1954)
<i>Bacillus</i> sp.	+	-	-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
<i>Bacillus cereus</i>	+	-	-	<i>Porcellio scaber</i>	Jorgensen et al. (1997)
	+			<i>Porcellio scaber</i>	Margulis et al. (1998)
<i>Bacteroides</i> sp.	+	-	-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
<i>Chromobacterium violaceum</i>	-	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Citrobacter freundii</i>	-	+	-	<i>Oniscus asellus</i>	Ullrich et al. (1993)
		+		<i>Porcellio scaber</i>	Ullrich et al. (1993)
Corynebacteriaceae	+	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Corynebacterium</i> sp.	+	-	-	<i>Oniscus asellus</i>	Ineson and Anderson (1985)
<i>Cytophaga</i> sp.	-	-	+	<i>Oniscus asellus</i>	Hassall et al. (1987)
			+	<i>Porcellio scaber</i>	Hassall et al. (1987)
			+	<i>Armadillidium vulgare</i>	Hassall et al. (1987)
<i>Desulphotomaculum ruminis</i>	+	-	-	<i>Porcellio scaber</i>	Lapanje et al. (2003); Kostanjšek et al. (2004a)
Enterobacteriaceae		+	-	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Enterobacter agglomerans</i>	+		-	<i>Oniscus asellus</i>	Griffiths and Wood (1985)
		+	-	<i>Porcellio scaber</i>	Ullrich et al. (1993)
<i>Enterobacter intermedium</i>	-	+	-	<i>Porcellio scaber</i>	Ullrich et al. (1993)
<i>Enterococcus faecium</i>	+	-	-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
<i>Enterococcus</i> sp.	+	-	-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
<i>Flavobacterium</i> sp.	+	-	+	<i>Tracheoniscus rathkei</i>	Reyes and Tidje (1976a)
<i>Klebsiella pneumoniae</i>	+		+	<i>Oniscus asellus</i>	Ineson and Anderson (1985)
		+		<i>Porcellio scaber</i>	Ullrich et al. (1993)
Micrococcaceae	+	-	-	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Mollicutes</i>	+	+	+	<i>Porcellio scaber</i>	Kostanjšek (2002); Kostanjšek et al. (2004a)
Mycobacteriaceae	-	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Neisseria</i> sp.	+	-	-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
<i>Paracoccus</i> sp.	+	-	-	<i>Porcellio scaber</i>	Own observation
<i>Plesiomonas</i>	+	-	-	<i>Oniscus asellus</i>	Griffiths and Wood (1985)

Table 5.1. (continued)

Bacterial taxa	G	MG	F	Isopod	References
Pseudomonadaceae	+	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Pseudomonas fluorescens</i>	+	-	-	<i>Oniscus asellus</i>	Griffiths and Wood (1985)
<i>Pseudomonas</i> sp.	+		-	<i>Porcellio scaber</i>	Kostanjšek et al. (2002)
	+			<i>Tracheoniscus rathkei</i>	Reyes and Tidje (1976a)
		+		<i>Porcellio scaber</i>	Kostanjšek (2002)
<i>Rhabdochlamydia porcellionis</i>		+		<i>Porcellio scaber</i>	Kostanjšek et al. (2004b)
<i>Shevanella</i> sp.	+	-	-	<i>Porcellio scaber</i>	Own observation
Spirilaceae	-	-	+	<i>Oniscus asellus</i>	Ullrich et al. (1991)
<i>Streptomyces humidus</i>	-	-	+	<i>Protracheoniscus amoneus</i>	Márialigeti et al. (1984)
<i>Streptomyces moderatus</i>	-	-	+	<i>Protracheoniscus amoneus</i>	Márialigeti et al. (1984)
<i>Streptomyces nodosus</i>	-	-	+	<i>Protracheoniscus amoneus</i>	Márialigeti et al. (1984)
<i>Streptomyces pluricolorescens</i>	-	-	+	<i>Protracheoniscus amoneus</i>	Márialigeti et al. (1984)
<i>Streptomyces spadici</i>	-	-	+	<i>Protracheoniscus amoneus</i>	Márialigeti et al. (1984)

G, gut; MG, midgut glands; F, faeces

Ullrich et al. 1991) and molecular approaches applying 16S rRNA sequence analysis (Kostanjšek et al. 2002) indicated the possible presence of resident bacteria in the gut of terrestrial isopods. Moreover, long rod-like bacteria attached to the hindgut cuticle were observed in the posterior hindgut of *P. scaber* (Drobne 1995; Kostanjšek et al. 2003). Phylogenetic analysis based on 16S rRNA gene sequences grouped the latter in an independent and deeply branched cluster within *Mollicutes* (Kostanjšek et al. 2004a), while ultrastructural observations revealed a spherical attachment structure at the tip of these bacteria. Since such structures may be required for the specific attachment of bacteria to cuticular spines of the gut surface, thus revealing high adaptation to the digestive system, the attached bacteria might represent truly autochthonous gut bacteria of *P. scaber* (Kostanjšek et al. 2003).

Whereas a considerable part of resident gut bacteria colonises the gut via food (Reyes and Tiedje 1976a; Griffiths and Wood 1985; Ineson and Anderson 1985; Gunnarsson and Tunlid 1986; Ullrich et al. 1991), the presence of gut bacteria which cannot be detected in the soil or food (Hassall et al. 1987; Ullrich et al. 1991; Kostanjšek et al. 2002) indicates other possible ways of gut colonisation. This was supported by the discovery of attached rod-like bacteria on the newly-formed hindgut cuticle, still overlaid with

the old, intact cuticle (Kostanjšek 2002). Coprophagy and ingestion of the old hindgut cuticle as paths of gut recolonisation after exuviations may therefore not be the only and most important ways. It further indicates that rod-like bacteria somehow remain in the gut despite exuviation, enabling them to colonise the new gut cuticle soon after it has been formed (Kostanjšek 2002).

Although the environment in the hindgut of terrestrial isopods is thought to be generally oxic, the mucopolysaccharides present in large amounts on the surface of the gut could provide microniches for anaerobic bacteria. Apart from slowing down the diffusion of oxygen, these biopolymers also enable bacterial attachment (Hartenstein 1964; Savage 1978). Several unsuccessful attempts to cultivate isopod gut microbes under anaerobic conditions were described (Reyes and Tiedje 1976a; Ullrich et al. 1991), but the presence of anaerobic bacteria was indirectly indicated by the detection of mercury methylation in the gut of *P. scaber* (Jereb et al. 2003). Since mercury can be biomethylated by sulfate-reducing bacteria (SRB), further work was focused on these bacteria in the digestive system of isopods (Kostanjšek et al. 2004a). Termites were the only arthropods in which SRBs were reported previously (Trinkerl et al. 1990; Ohkuma and Kudo 1996).

The SRB utilise various low molecular weight acids in the presence of sulfate and are major decomposers of organic matter in anaerobic environments (Santegoeds et al. 1998; Vester and Ingvorsen 1998). One of the side effects of SRB metabolic pathways is the methylation of mercury, where up to 95% of available mercury is transformed into highly toxic methyl mercury (Compeau and Bartha 1984, 1985; Pak and Bartha 1998a, b). Anaerobic culturing techniques were used successfully to enrich SRB from the substrate and gut samples, but not from the hepatopancreas and faeces. According to phylogenetic analysis based on 16S rRNA gene sequence these, first strictly anaerobic bacteria isolated from the gut of a terrestrial isopod, were identified as *Desulfotomaculum ruminis* (Lapanje et al. 2003).

Although oxygen influx from the surrounding haemolymph through the gut epithelium keeps the peripheral ring of the hindgut oxic (Zimmer 2002), the presence of strictly anaerobic SRBs (Lapanje et al. 2003) and the discovery of ribosomal genes from other anaerobic bacteria (Kostanjšek et al. 2002) on the hindgut cuticle indicate anaerobic microniches in the hindgut of terrestrial isopods (Kostanjšek et al. 2004a).

5.3.2 Fungi and Protozoa in the Gut

The concentration of fungi that can be cultivated in terrestrial isopods varies from 10^4 to 10^5 cells/mg of gut content (Coughtrey et al. 1980;

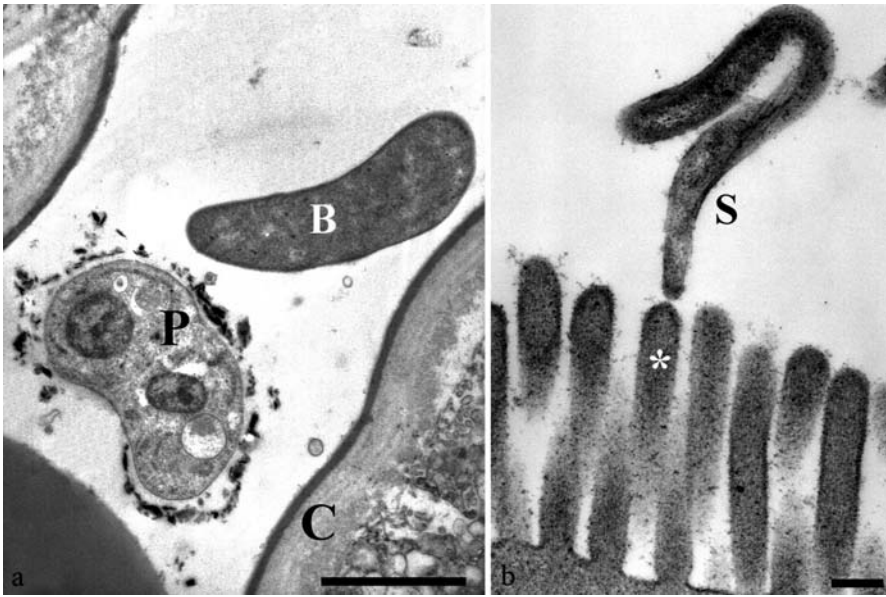


Fig. 5.2. Microorganisms in the digestive tract of terrestrial isopods. a Binucleate protist (P) and bacterium (B) above the hindgut cuticle (C) of *Ligia italica*. Scale bar 2 μm . b Spirochaeta (S) attached to microvillus (asterisk) of midgut gland cell of *Porcellio scaber*. Scale bar 200 m

Zimmer and Topp 1998b). However, the fungal flora of these animals is generally poorly known. Fungal genera observed in the isopod hindgut are *Penicillium*, *Trichoderma*, *Fusarium*, *Cladosporium*, *Aspergillus* and *Mucor* (Kayang et al. 1996). The symbiotic trichomycetes *Asellaria armadillidii*, *Parataeniella armadillidii*, *P. latrobi*, *P. dilatata*, *P. mercieri*, *P. scotonisci*, *Palavascia philosciae*, *Eccrinoides monticolae* and *E. helleriae* attached to the hindgut cuticle were reported in the gut as well (Lichtwardt et al. 2001). Although binucleate protist-like organisms were observed (Fig. 5.2) on the cuticular gut surface in the amphibious species *Ligia italica* and *Titanethes albus*, data on protozoa in the digestive system of isopods are scarce. However, some genera of trichomycetes described in the arthropod gut were found to be protists rather than fungi after detailed examination (Cafaro 2003).

5.3.3

Bacteria in the Midgut Glands

The entrance of microbes from the stomach into the digestive glands is supposed to be prevented by a system of chitinous filters (Hames and Hopkin 1989; Storch and Štrus 1989), allowing only fluids and particles smaller

than 40 nm to pass (Hames and Hopkin 1989). However, the presence of bacteria in the lumen of the digestive glands was observed in *Porcellio dilatatus* (Donadey and Besse 1972), *O. asellus* (Hopkin and Martin 1982; Wood and Griffiths 1988; Hames and Hopkin 1989, 1991; Ullrich et al. 1991; Clegg et al. 1996), *P. scaber* (Wood and Griffiths 1988; Hames and Hopkin 1989, 1991; Ullrich et al. 1991; Zimmer and Topp 1998a, b; Kostanjšek 2002) and *L. pallasii* (Zimmer et al. 2001) (Table 5.1). Ultrastructural investigations revealed the presence of various bacterial morphotypes in the digestive glands (Zimmer 2002). Among them rod-like hepatopancreatic bacteria described in *P. scaber* and *O. asellus* by Wood and Griffiths (1988) exhibit a high morphological resemblance to the *Mollicutes*-related bacteria attached to the hindgut cuticle of *P. scaber* (Kostanjšek 2002). Beside, the spirochetes attached to microvilli of gland cells and in the lumen of midgut glands were observed in *L. italica*, *T. albus* and *P. scaber* (Fig. 5.2).

In spite of abundant observations, the data on the occurrence of bacteria in the hepatopancreas may still be ambiguous. In some cases only the occasional presence of hepatopancreatic bacteria was observed in *P. scaber* and *O. asellus* (Wood and Griffiths 1988), contrary to observations from other authors, reporting their permanent presence and high bacterial counts in *P. scaber*, *O. asellus* and *L. pallasii* (summarised in Zimmer 2002). The latter led to the conclusion that the role of hepatopancreatic bacteria is crucial in the decomposition of complex organic compounds in the isopod diet (Zimmer 2002).

Our electron microscopic observations and results of the molecular detection of bacterial ribosomal genes (Kostanjšek 2002) supported the occasional presence of diverse bacteria in the digestive glands. Among hepatopancreatic bacteria genus *Pseudomonas* and rod-like *Mollicutes* commonly attached to the hindgut cuticle prevailed (Kostanjšek 2002). Since both these groups of bacteria are commonly found in the gut and are not always present in the hepatopancreas, it would be more likely that they occasionally invade the digestive glands from the gut, rather than being permanent hepatopancreatic endosymbionts (Wood and Griffiths 1988; Zimmer 2002).

5.3.4 Infections of the Digestive System

Tissues of terrestrial isopods are, like tissues of other crustaceans (Fryer and Lannan 1994), often invaded by intracellular bacteria (Federici 1984; Shay et al. 1985; Abd El-Aal and Holdich 1987; Bouchon et al. 1998; Drobne et al. 1999).

The first observed intracellular infection in terrestrial isopods was caused by *Rickettsiella grylli* (Weiss et al. 1984a; Roux et al. 1997). The infections were described in *Armadilidium vulgare* (Vago et al. 1970), *P. dilatatus* (Federici 1984), *Porcellio scaber* and *Oniscus asellus* (Abd El-Aal and Holdich 1987). The infection affected adipose tissue in haemocoel, muscular and connective tissue around the anal region, epidermis and tegumental glands (Fedrereici 1984; Abd El-Aal and Holdich 1987).

Another intracellular infection was described in the hepatopancreatic tissue of *P. scaber* (Shay et al. 1985; Drobne et al. 1999). In spite of certain similarities with *R. grylli*, the infection exhibits distinctive pathological changes in infected tissue and unique morphological features. In earlier descriptions different authors affiliated these bacteria with different bacterial taxa, despite the morphological and pathological similarities (Shay et al. 1985; Drobne et al. 1999). Phylogenetic analysis based on comparative 16S rRNA gene sequencing affiliated the infection agent to the ordo *Chlamydiales*, within which it forms an independent lineage, clearly distant from other known chlamydia. Due to the phylogenetic affiliation and distinctive morphology of the elementary bodies, the name '*Candidatus* Rhabdochlamydia porcellionis' was proposed (Kostanjšek et al. 2004b).

Beside the infections mentioned above, intracellular infection caused by bacteria from the genus *Wolbachia* also affects terrestrial isopods (Weiss et al. 1984b; O'Neill et al. 1997; Bouchon et al. 1998; Nyrö et al. 2002). The infection is transmitted maternally via egg cytoplasm and affects the host reproduction, enhancing the spread of the infectious agent (Rigaud and Rousset 1996; Bourtzis and O'Neill 1998). Although *Wolbachia* infection is generally focused on the gonads, it has also been detected in somatic tissues, including the digestive system of insects (Dobson et al. 1999) and terrestrial isopods (Martin et al. 1973; Rousset et al. 1992). The *Wolbachia* infection can alter the host's reproduction by male killing, parthenogenesis, cytoplasmic incompatibility and feminisation of genetic males (Bourtzis and O'Neill 1998). However, only the latter two alterations were detected in terrestrial isopods (Juchault et al. 1992; O'Neill et al. 1997).

5.4

Conclusions

Terrestrial isopods are decomposers of plant material in terrestrial environments. They promote microbial activity by trituration of plant material and distribution of microbes in the ecosystem. They preferentially feed on decayed plant material colonised by microorganisms, which are also utilised as source of nutrients and enzymes. Whereas some undigested mi-

croorganisms are passive transients, others proliferate in the hindgut and are distributed in the terrestrial environment with faeces.

The digestion of terrestrial isopods strongly depends on degradation of lignocellulose. The origin of cellulases in their digestive system still remains to be elucidated, however. Since the role of cellulolytic bacteria in the midgut glands is questionable, due to their only occasional presence in this organ, other sources of cellulases must be taken into account. The food preference of isopods indicates a potential role of ingested cellulolytic microbiota, but the presence of endogenous cellulases in the isopod digestive system cannot be excluded, either.

The gut of terrestrial isopods appeared for a long time to be an unsuitable environment for development of resident and anaerobic microbiota. The main arguments supporting this theory were its tube-like anatomy, the rapid passage of the food and frequent renewal of gut cuticle. However, the finding of bacteria attached to the hindgut surface with the ability to recolonise the gut cuticle after moulting indicates that some bacteria have adapted to this environment. The subsequent isolation of strictly anaerobic bacteria confirmed the presence of anaerobic microniches on the otherwise oxic hindgut surface. This shows the presence of microhabitats in the gut, which allow development of diverse resident microflora in the gut, in spite of its apparently unsuitable conditions.

In comparison to some other cellulose-feeding arthropods, data on microbiota in the digestive system of isopods are scarce, in spite of their importance as decomposers and reservoirs for various infections. However, previous work on this topic reveals that the digestive system of terrestrial isopods is a unique microbial environment, which remains an interesting field for further microbiological research.

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