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Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach

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ABSTRACT

The nutritional morphology, physiology and ecology of terrestrial isopods (Isopoda: Oniscidea) is significant in two respects. (1) Most oniscid isopods are truly terrestrial in terms of being totally independent of the aquatic environment. Thus, they have evolved adaptations to terrestrial food sources. (2) In many terrestrial ecosystems, isopods play an important role in decomposition processes through mechanical and chemical breakdown of plant litter and by enhancing microbial activity. While the latter aspect of nutrition is discussed only briefly in this review, I focus on the evolutionary ecology of feeding in terrestrial isopods.

Due to their possessing chewing mouthparts, leaf litter is comminuted prior to being ingested, facilitating both enzymatic degradation during gut passage and microbial colonization of egested faeces. Digestion of food through endogenous enzymes produced in the caeca of the midgut glands (hepatopancreas) and through microbial enzymes, either ingested along with microbially colonized food or secreted by microbial endosymbionts, mainly takes place in the anterior part of the hindgut. Digestive processes include the activity of carbohydrases, proteases, dehydrogenases, esterases, lipases, arylamidases and oxidases, as well as the nutritional utilization of microbial cells. Absorption of nutrients is brought about by the hepatopancreas and/or the hindgut epithelium, the latter being also involved in osmoregulation and water balance. Minerals and metal cations are effectively extracted from the food, while overall assimilation efficiencies may be low. Heavy metals are stored in special organelles of the hepatopancreatic tissue. Nitrogenous waste products are excreted *via* ammonia in its gaseous form, with only little egested along with the faeces. Nonetheless, faeces are characterized by high nitrogen content and provide a favourable substrate for microbial colonization and growth. The presence of a dense microbial population on faecal material is one reason for the coprophagous behaviour of terrestrial isopods. For the same reason, terrestrial isopods prefer feeding on decaying rather than fresh leaf litter, the former also being more palatable and easier to digest. Acceptable food sources are detected through distance and contact chemoreceptors. The 'quality' of the food source determines individual growth, fecundity and mortality, and thus maintenance at the population level. Due to their physiological adaptations to feeding on and digesting leaf litter, terrestrial isopods contribute strongly to nutrient recycling during decomposition processes. Yet, many of these adaptations are still not well understood.

Key words: ecophysiology, evolutionary ecology, Isopoda, nutrition, Oniscidea, terrestrialization, woodlice.

CONTENTS

I. INTRODUCTION

Within the Crustacea, the taxon Oniscidea (Isopoda) is the only suborder that includes, and essentially consists of, species inhabiting terrestrial environments – only a few species of this suborder inhabit aquatic environments, possibly secondarily. Several excellent reviews on morphological (e.g. Schmalfuss, 1984*a*) and ecophysiological (e.g. Wieser, 1984; Carefoot, 1993) adaptations to the terrestrial environment (Edney, 1954, 1968; Warburg, 1987) have appeared. However, relatively little attention has been paid to nutritive aspects of ecophysiology, in these reviews.

Table 1. *Classification of terrestrial isopods (Isopoda: Oniscidea) as proposed by Erhard, 1998*

Oniscidea	Latreille, 1829
Diplocheta	Vandel, 1957
Ligiidae	Brandt, 1833
Holoverticata	Erhard, 1998
Tylida	Erhard, 1998
Tylidae	Milne-Edwards, 1840
Orthogonopoda	Tabacaru & Danielopol, 1996
Microcheta	Schmalfuss, 1989
Mesoniscidae	Verhoeff, 1908
Euoniscoida	Vandel, 1943
Synocheta	Legrand, 1946
5 families, e.g.	
Trichoniscidae	Sars, 1899
Crinocheta	Legrand, 1946
26 families, e.g.	
Oniscidae	(Linné, 1753) Sars, 1899
Porcellionidae	Brandt & Ratzeburg, 1831
Trachelipodidae	Strouhal, 1953
Armadillidiidae	Sars, 1899

Numerous studies have dealt with the most important aspects of nutrition (see below), but have revealed contrary results or controversial conclusions have been drawn. This may be because the investigated species represent different stages of adaptation to the terrestrial habitat. Thus, understanding the adaptive features of nutritive isopod biology to the terrestrial environment may reveal insight into prerequisites for the colonization of terrestrial habitats. This review aims to compare, summarize and integrate the available results on nutritive biology in as many species as possible. To this end (for systematics, see Table 1), the amphibious or semi-terrestrial species of the 'prototypal' (Schmalfuss, 1978, 1989; Carefoot & Taylor, 1995) Ligiidae Brandt & Ratzeburg, 1831 (Diplocheta Erhard, 1998) and the Tylidae Milne Edwards, 1840 (Tylida Erhard, 1998), mostly inhabiting marine shores, as well as the small, mostly endogean hygrophilic species of the

taxon Synocheta Legrand, 1946 (e.g. species of the Trichoniscidae Sars, 1899), and the 'fully terrestrial' species of Crinocheta Legrand, 1946 (e.g. species of Oniscidae Latreille, 1806, Porcellionidae Brandt & Ratzeburg, 1831, Trachelipodidae Strouhal, 1953, and Armadillidiidae Brandt, 1833) will be considered. The taxa Tylida and Synocheta have been considered very rarely, and, to my knowledge, no data are available on nutrition in Microcheta Schmalfuss, 1989 (family Mesoniscidae Verhoeff, 1908).

The ability of woodlice [also known as 'sowbugs', 'pillbugs' (for those species that roll up into a ball), 'potato beetles', and 'sea slaters' (for shore isopods of the genus *Ligia*)] to utilize leaf litter as food source (see sections IV–VI) probably facilitated their terrestrialization which possibly took place during the tertiary age, approximately 50 million years ago (Edney, 1968; Hessler, 1969), eons after other saprophagous soil animals had successfully colonized land (summarized in Piearce, 1989). Although the existence of terrestrial isopods during the carboniferous, approximately 300 million years ago, has been discussed (see Piearce, 1989), no fossil woodlice have been identified below the Upper Eocene, 35–40 million years ago (Hartenstein, 1968). However, in Baltic (see Weitschat & Wichard, 1998; M. Zimmer, personal observations) as well as Dominican (Schmalfuss, 1980, 1984*b*) amber (approximately 30 million years old), inclusions of a diverse woodlouse fauna can be found that strongly resembles the recent one. Thus, we can assume that successful colonization of land by a common ancestor and species diversification had occured long before the Eocene. The feeding and nutrition of terrestrial isopods and their digestive capabilities thus are significant from an evolutionary point of view. Of interest here is the ecophysiology of feeding, digestive processes and nutrition, and ecological interactions in the processes of decomposition, humification and nutrient recycling. This review will first summarize briefly the anatomical basis of ingestion (mouthparts), digestion and assimilation (alimentary tract), before digestion is described in detail, including gut microbiota and the digestive processes of assimilation, defecation and excretion. These features of isopod nutrition correspond with active food choice and foraging that, in turn, will influence individual fitness and the population dynamics of isopods. Different food qualities can be classified. Finally, a brief comment on the significance of isopod nutrition in the context of their contribution to decomposition processes will be given, and the significance of the nutritional preferences of isopods for their transition from water to land will be discussed.

II. ANATOMY

(1) Mouthparts

Most terrestrial isopods predominantly feed on plant litter from plants growing in the surrounding habitat (grassland or forest ecosystems; henceforth, leaf litter) or in adjacent systems (seaweed wrack, in the case of shore isopods). Prior to the ingestion of food, woodlice use their chewing mouthparts to comminute the leaf litter material. The morphology of isopod mouthparts has been studied occasionally during the last hundred years (e.g. Lereboullet, 1853; Meinertz, 1932, 1934; Radu, 1951; Hassall, 1977*b*). The oral cavity is bordered by the labrum (anteriorly), by the mandibulae (laterally), and by the paragnathites (posteriorly) (Fig. 1). The labrum is connected to the head capsule *via* the clypeus. The mandibulae beneath the labrum have heavily sclerotized teeth and cutting edges. The right and left mandibulae are different in shape, as are those of many other Peracarida (Gordon, 1964), the teeth being more pronounced on the right mandible (Hassall, 1977*b*, in *Philoscia muscorum* Scopoli 1763, Philosciidae Kinahan, 1857). Behind the distal parts of the mandibulae, the cuticle projects to form a pair of flattened paragnathites. The smaller anterior lobe of the paragnathite is covered with small setae projecting into the cleft between the two paragnathites, and the main lobe is positioned ventrally.

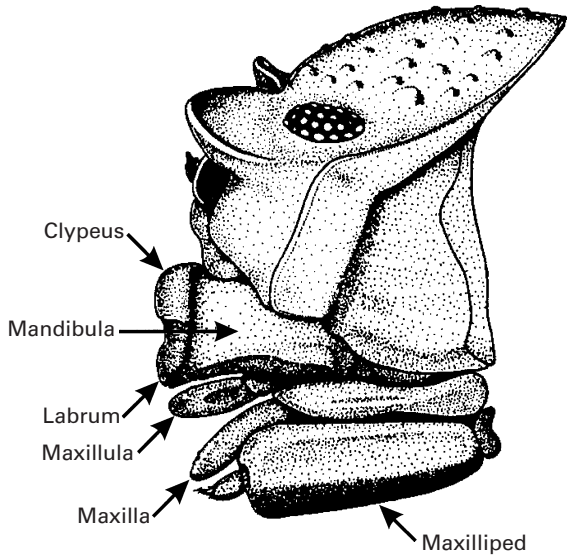

Fig. 1. Lateral view of the head capsule and the outer mouth parts of *Porcellio scaber* (Porcellionidae). Redrawn from Gruner (1993) by M. Lessens.

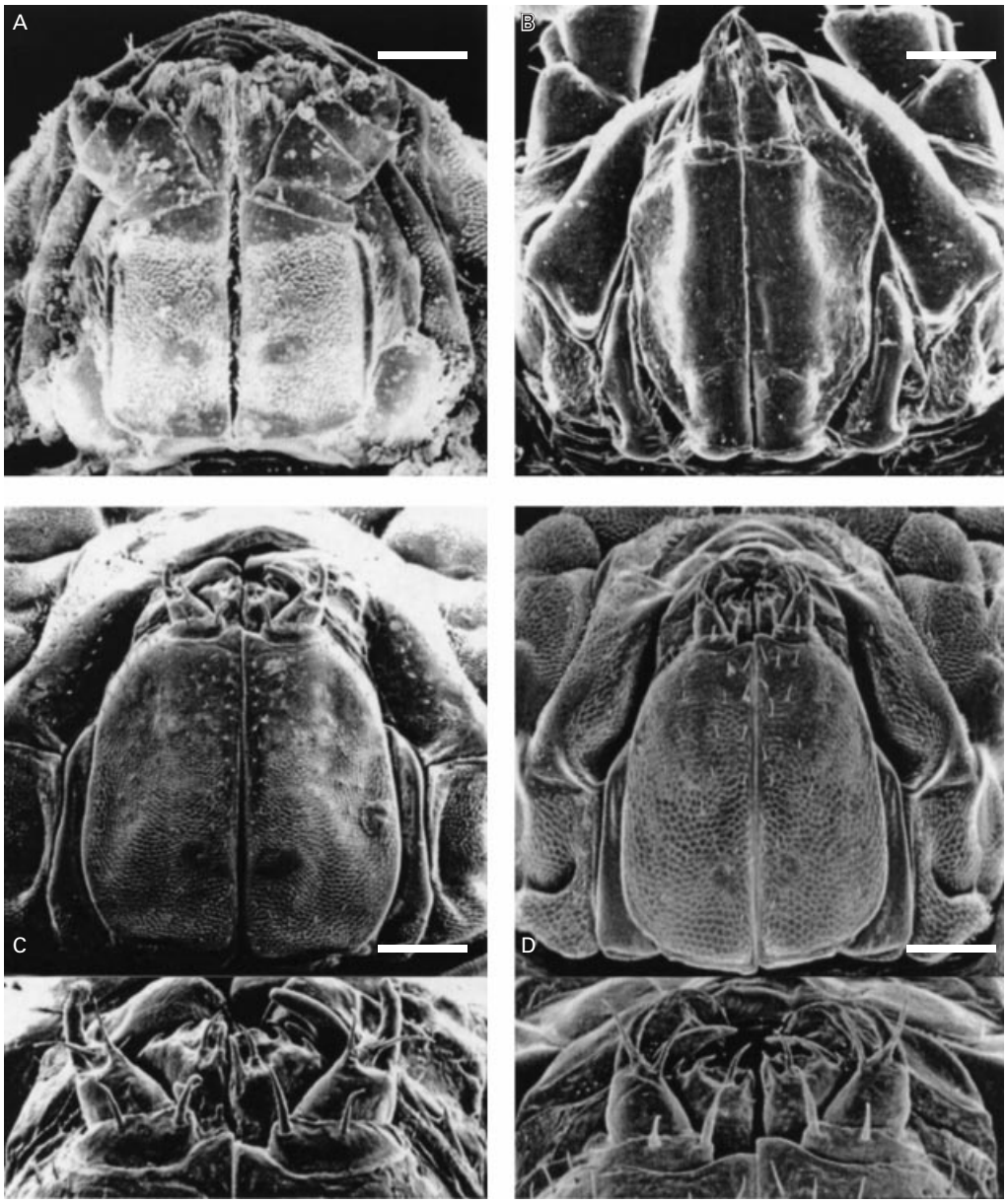

Fig. 2. Scanning electron micrographs of the outer mouthparts of A: *Ligia oceanica* (Ligiidae), B: *Trichoniscus pusillus* (Trichoniscidae), C: *Porcellio scaber* (Porcellionidae), D: *Armadillidium pictum* (Armadillidiidae). Details in C and D show the tips of the maxillulae, the maxillae and the mandibulae. Scale bars: A = 500 μm; B = 150 μm; C = 400 μm (inset: 200 μm); D = 300 μm (inset: 150 μm).

More posteriorly, a pair of two-lobed maxillulae, the small inner endite being called the scaphognathite, and a pair of delicately flattened maxillae project from the head capsule. The scaphognathites bear distal brushes that project into the cleft between the paragnathites, while the broad and strong outer endites are characterized by stout spines at their tip. The maxillipeds, derived from the appendages of the original first thoracic segment, insert most posteriorly, and cover the oral aperture hiding all but the labrum and the tips of the maxillulae, the maxillae and the mandibulae from direct view (see Fig. 2). The interactions among the mouthparts during feeding have been described extensively by Hassall (1977*b*), to whom the interested reader is referred.

Størmer (1977) suggested that the preoral cavity formed by the 'basal portions of head appendages' was important during terrestrialization. Since the structure of the mouthparts reflects the type of diet utilized (Jones, 1972; Hassall, 1977*b*), further comparative information on their functional mor-

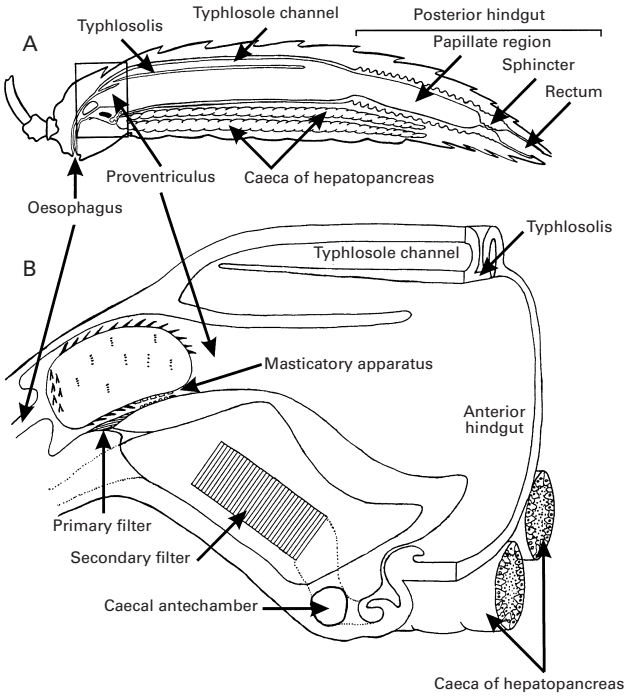

Fig. 3. Schematic section of the digestive tract of terrestrial isopods (Crinocheta). A: whole gut; B: details of the foregut-midgut region. Simplified and combined after Hassall (1977*b*; *Philoscia muscorum*, Philosciidae) and Hames & Hopkin (1989; *Oniscus asellus*, Oniscidae); drawings by M. Lessens.

phology in different isopod species should reveal information on nutritive adaptations during the process of terrestrialization.

(2) Alimentary tract

The alimentary tract of terrestrial isopods is a straight tube between the oral aperture and the anus. It can be subdivided into a small foregut (stomach), a junction with two or three pairs of midgut glands (hepatopancreas), and a large hindgut that comprizes approximately 80–90% of the total length of the digestive system (Fig. 3A). The morphology and, later, the ultrastructure of the digestive system has been investigated in detail for more than a hundred years (e.g. Lereboullet, 1853; Huet, 1883; Frenzel, 1884; McMurrich, 1898; Schönichen, 1898; Nussbaum-Hilarowicz, 1921; Patrick, 1926; Patané, 1934; Cicero, 1964; Alikhan, 1968, 1969, 1972*c*; Schmitz & Schultz, 1969; Smith, Witkus & Grillo, 1969; Witkus, Grillo & Smith, 1969; Clifford & Witkus, 1971; Hassall & Jennings, 1975; Holdich & Mayes, 1975; Hassall, 1977*b*; Hryniewiecka-Szyfter & Tyczewska, 1978, 1979; Storch & Lehnert-Moritz, 1980; Storch, 1984, 1987; Štrus, Burkhardt & Storch, 1985; Štrus, Drobne & Ličar, 1995; Hryniewiecka-Szyfter & Storch, 1986; Lane, 1988; Hames & Hopkin, 1989). By contrast, nervous control of the hindgut and digestive processes have been studied only very recently (Molnár *et al.*, in press; Pollák *et al.*, in press).

The ectodermal foregut consists of an oesophagus and a proventriculus (Goodrich, 1939; Schmitz & Schultz, 1969; Hassall, 1977*b*; Storch, 1987; Lane, 1988; Hames & Hopkin, 1989). The former is a short simple tube, while the latter is characterized by complex chitinous wall protuberances (Schmitz & Schultz, 1969; Hassall, 1977*b*; Hames & Hopkin, 1989, and references therein) that function in preventing regurgitation of food into the oesophagus, and in pressing and masticating the food material (Hassall, 1977*b*; Storch, 1987; Hames & Hopkin, 1989). For this, musculature surrounds the foregut and connects it to the exoskeleton (Lane, 1988; Hames & Hopkin, 1989).

The most prominent part of the proventricular foregut is the combination of two filter systems that separate solid and fluid components of the ingested food (see Fig. 3B), and channel the former into the hindgut lumen, while the latter are drawn to the lumen of the midgut glands that adjunct the alimentary tract ventrally at the proventriculus (Fig. 3A). According to Wood & Griffiths (1988), these filters prevent the influx of particles larger than 1.17 μm, but Hames & Hopkin (1989) described their mesh size to be only 40–50 nm.

In contrast to marine isopod species, the proventriculus of terrestrial isopods does not function in enzymatic food degradation (Hassall, 1977*b*, but see Štrus *et al.*, 1995). Rather, the food material is ground in a proventricular masticatory apparatus before it is passed forward to the anterior hindgut (Storch, 1987; Hames & Hopkin, 1989). During this, digestive fluids from the midgut glands are mixed with the food (Hassall & Jennings, 1975; Hames & Hopkin, 1989). In the ligiid species, *Ligia italica* Fabricius 1798 and *Ligidium* (*Oniscus*) *hypnorum* (Cuvier 1792) (both Ligiidae), there is no masticatory apparatus, rather the food material is pressed by cushion-like protrusions prior to passing the filter systems [Štrus *et al.*, 1995; see Nicholls, 1931, for *Ligia* (*Oniscus*) *oceanica* (Linnaeus 1767), Ligiidae]. Kensley (1974) described a 'gastric mill' in the foregut of *Tylos granulatus* Krauss 1843 (Tylidae). Tabacaru & Giurginca (in press) presented a detailed comparison of stomach structures in numerous isopod species. They found

similarities between aquatic species and basal groups of oniscid isopods, while the 'fully terrestrial' Crinocheta appear to differ remarkably in this respect. Obviously, the mastication of food is adaptive to terrestrial food sources.

The midgut is restricted (see Holdich, 1973) to a small ring of cells between the posterior proventriculus and the anterior hindgut in the prototypal species *Ligia italica* and *Ligidium hypnorum* (Štrus *et al*., 1995), but there are no endodermal midgut cells in the alimentary tract of *Oniscus asellus* Linnaeus 1758 (Oniscidae), *Porcellio scaber* Latreille 1804 (Porcellionidae), *Trachelipus illyricus* Verhoeff 1901 (Trachelipodidae), and *Armadillidium vulgare* (Latreille 1804) (Armadillidiidae) (Palackal *et al*., 1984; Bettica *et al*., 1987; Štrus *et al*., 1995). In general, the existence of a true midgut has been doubted in terrestrial isopods by Holdich & Mayes (1975, in the genus *Porcellio*) and Brecko *et al*. [1991, in *Cylisticus convexus* (De Geer 1778), Cylisticidae Verhoeff, 1949]. In 'fully terrestrial' species, the midgut is restricted to the hepatopancreas (digestive midgut glands) (Holdich, 1973; Hassall & Jennings, 1975; Hassall, 1977*b*; Hames & Hopkin, 1989) that comprises two pairs of caeca in terrestrial species, but three pairs in *Tylos europaeus* Arcangeli 1938 (Tylidae) (Hames & Hopkin, 1989), *Ligia oceanica* (Hewitt, 1907; Nicholls, 1931; Hames & Hopkin, 1989; Erhard, 1997) and *Ligidium hypnorum*, with the latter, as well as *Tylos latreilli* Audouin 1826 (Tylidae) having only a rudimentary third pair of caeca (Vandel, 1943; Erhard, 1997). The caeca of the hepatopancreas lie freely in the body cavity, closely associated ventro-laterally with the hindgut, and terminate in the last pereion segment (e.g. Hartenstein, 1964*b*; Lane, 1988; Fig. 3A). The evolutionary significance of the reduction in lobe number is not yet understood, but is likely to be related to the terrestrial habitat and the food source (cf. Hassall & Jennings, 1975; Zimmer *et al*., in press) (section V.3), as is the evolutionary reduction of the midgut.

The hepatopancreas functions as a true midgut by being involved in the secretion of digestive enzymes and the absorption of nutrients (e.g. Clifford & Witkus, 1971; Hassall & Jennings, 1975; Bettica *et al*., 1984; Hopkin & Martin, 1984; Lane, 1988). Thin sheets of musculature running obliquely around the caeca change their length and diameter and make the flux of fluids from and into the hepatopancreas possible (Hassall & Jennings, 1975; Hopkin & Martin, 1982*a*; Hames & Hopkin, 1989). Two types of cells have been described in the hepatopancreatic tissue (named after Frenzel, 1884), large 'B cells' that project into the lumen of the hepatopancreas and small conoidal 'S cells' (Alikhan, 1969; Clifford & Witkus, 1971; Hryniewiecka-Szyfter, 1972; Hopkin & Martin, 1984; Prosi, Storch & Janssen, 1983; Marcaillu, Truchet & Martoja, 1986; Witkus *et al*., 1987; Hames & Hopkin, 1989; R- and F-cells according to Lane, 1988, to conform with the terminology frequently used in Crustacea). B cells are involved in both secretion and absorption, while S cells mainly function in absorption (Clifford & Witkus, 1971; Bettica *et al*., 1984; Hopkin & Martin, 1984). In the aquatic isopods, *Lirceus* (*Mancasellus*) *brachyurus* (Harger 1876) (Asellota Latreille, 1803: Asellidae Rafinesque-Schmaltz, 1815), and *Asellus intermedius* Forbes 1876 (Asellota: Asellidae), similar functions have been ascribed to these different cell types, with S cells additionally being involved in storage (Steeves, 1963; Smith, Nadakavukaren & Hetzel, 1975). In terrestrial isopods, glycogen and lipids are stored in B cells (Patané, 1934; Szyfter, 1966; Alikhan, 1972*a*; Storch, 1982). An alternative point of view is that these two cell types merely reflect different stages of cell differentiation (Jones, Babbage & King, 1969; Schmitz & Schultz, 1969; Moritz, Storch & Buchheim, 1973; Lane, 1988) during which they switch from an initial absorptive phase to their mature, predominantly secretory, function (Hassall & Jennings, 1975). Proliferation of cells mainly takes place at the distal blind end of the caeca, and differentiation is associated with a relative movement to the proximal part (Donadey & Besse, 1972; Prosi *et al*., 1983).

S cells are sites of extensive copper storage (Wieser, 1968; Alikhan, 1972*b*; Hopkin & Martin, 1982*a*, *b*; Prosi *et al*., 1983; Storch, 1984; Dallinger & Prosi, 1988; Prosi & Dallinger, 1988) in special organelles (Alikhan, 1972*b*; Alikhan & Storch, 1990), the cuprosomes (Wieser & Klima, 1969) (see section V.1). Cuprosomes also contain sulphur (Hopkin & Martin, 1982*a*), indicating an involvement of metallothionins in copper storage (see Hopkin & Martin, 1984). The accumulation of copper in hepatopancreatic tissue results in hepatopancreatic copper concentrations that are twice to four times higher than in the haemolymph (Wieser & Wiest, 1968; Alikhan, 1972*b*), or even up to ten fold as high compared to the rest of the body (Hopkin & Martin, 1982*a*, *b*, 1984; Hopkin *et al*., 1985, 1986; Alikhan & Storch, 1990; Hopkin, 1990), this being among the highest levels reported for biotic systems (Hopkin & Martin, 1982*a*, *b*). By contrast, the copper content of

the haemolymph is remarkably low in terrestrial isopods compared to many other Crustacea (see Alikhan, 1972*b*). The physiological reasons for the accumulation of copper in the hepatopancreas have been the subject of considerable debate (cf. Zimmer & Topp, 1998*c*), and will be discussed later in this review (section V.1). Hassall & Jennings (1975) found iron in hepatopancreatic cytoplasm, located in granules of the B cells (Hryniewiecka-Szyfter, 1972; Hopkin & Martin, 1982*a*).

B cells undergo ultrastructural changes during starvation and moulting (Wieser, 1965, 1968; Alikhan, 1972*a*; Storch & Lehnert-Moritz, 1980; Storch, 1982, 1984), and also alter in response to changing food sources (Štrus *et al*., 1985). By contrast, only minor changes occur in S cells during starvation (Prosi *et al*., 1983). More recent studies by Hames & Hopkin (1990) presented evidence for normal diurnal changes in the ultrastructure of these cells that correspond with cycles of lipid accumulation and secretion.

The midgut glands contain large numbers of obligately endosymbiotic bacteria, at least in some species (Donadey & Besse, 1972; Hopkin & Martin, 1982*a*; Wood & Griffiths, 1988; Hames & Hopkin, 1989; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999; Zimmer *et al*., 2001) (see section III.2). As stated above, the hepatopancreas is prevented from influx of solid particles by a complex filter system (Hassall, 1977*b*; Storch, 1987; Hames & Hopkin, 1989; Fig. 3B), and only fluids and extremely small particles appear to pass through this filter system towards the hepatopancreatic caeca (Storch, 1987). However, as will be discussed later, hepatopancreatic bacteria are thought to be capable of passing through the filter system (Zimmer & Topp, 1998*b*), and Storch (1987) discussed the possibility of actively changing the mesh size of the proventricular filters.

Despite dense bacterial populations, the hepatopancreatic lumen is clearly oxic (M. Zimmer & A. Brune, in preparation). Two explanations are possible. First, hepatopancreatic bacteria may be anaerobic, i.e. not consuming oxygen as terminal electron acceptor, but aero-tolerant. Second, influx of oxygen from the surrounding haemolymph may be sufficient to meet oxygen consumption.

The pH level of the hepatopancreatic lumen shows little variation between species as well as intraspecifically, ranging from a mean value of 6.1 to 6.5 in *Trichoniscus pusillus* Brandt 1833 (Trichoniscidae), *Oniscus asellus*, *Porcellio scaber*, *Trachelipus* (*Porcellio*) *rathkii* (Brandt 1833) (Trachelipodidae) (M. Zimmer & A. Brune, in preparation), and *Tylos granulatus* (Kensley, 1974). By contrast, Wood & Griffiths (1988) presented pH ranges of 4.7–5.4 and 5.4–6.1 in *Oniscus asellus* and *Porcellio scaber*, respectively.

The main site of digestive processes is the tube-like hindgut (see Fig. 3A) (Hassall & Jennings, 1975; Hames & Hopkin, 1989; Štrus *et al*., 1995). Because the gut provides the best-suited exchange organ with the environment in terrestrial habitats, the hindgut epithelium is also involved in water and ion balance (see section V.1). Due to its size and its central position in the body cavity (Fig. 3A), the anterior part of the hindgut was erroneously assumed to be the midgut for a long time (e.g. Schmitz & Schultz, 1969; Alikhan, 1968, 1969, 1972*c*; cf. Holdich, 1973). However, early embryological and developmental studies (Goodrich, 1939; Strömberg, 1965), as well as ultrastructural investigations (Holdich & Mayes, 1975) clearly proved its ectodermal origin, and thus demonstrated its status as hindgut.

The hindgut can be subdivided into a large anterior part with a conspicuous dorsal structure of invaginations forming a pair of separated tubes that extend dorsally above the hindgut lumen (Fig. 4A), and a shorter posterior part, consisting of a 'papillate region' (although there are no papillae in *Porcellio scaber*: Lane, 1988) (Fig. 4C), a 'sphincter' (Fig. 4D), and the 'rectum' (Vernon, Herold & Witkus, 1974; Hassall & Jennings, 1975; Holdich & Mayes, 1975; Palackal *et al*., 1984; Lane, 1988). The hindgut is surrounded by two layers of musculature, an inner layer of circular muscles and an outer layer of longitudinal muscle bands (Schmitz & Schultz, 1969; Alikhan, 1972*c*; Holdich & Mayes, 1975; Palackal *et al*., 1984; Lane, 1988; Fig. 4C, D), with the longitudinal bands lacking in the dorsal region of invaginations (Hames & Hopkin, 1989; Fig. 4A). The hindgut musculature produces peristaltic movements of the hindgut (see Hartenstein, 1964*a*), and seals the invaginated tubes (Hames & Hopkin, 1989).

According to Murlin (1902), the structure separating the anterior hindgut from the tubes is called the typhlosolis, and the tubes are known as typhlosole channels (Alikhan, 1972*c*; Hassall & Jennings, 1975; Holdich & Mayes, 1975; Lane, 1988; Hames & Hopkin, 1989). The papillate region of the posterior hindgut is characterized by epithelial cells that project outwards into the surrounding haemolymph (Hassall & Jennings, 1975). These cells show characteristics of ion-transporting and water-resorbing epithelia (Smith *et al*., 1969; Lindqvist &

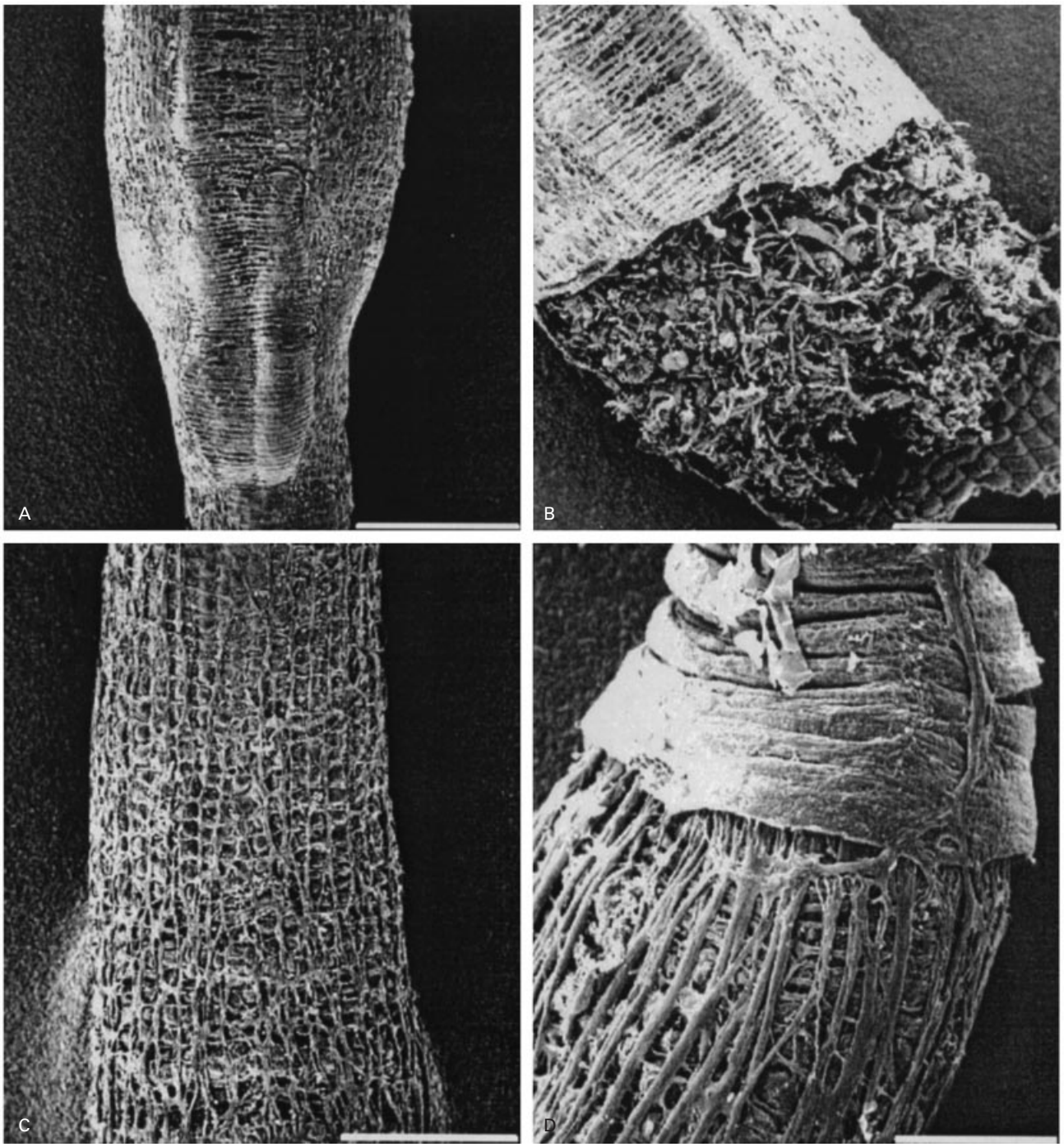

Fig. 4. Scanning electron micrographs of gut sections of *Porcellio scaber* (Porcellionidae). (A) junction of anterior and posterior hindgut, and (B) the lumen of the anterior hindgut (B), showing the external appearance of the typhlosole channels (A) and the cell-like structure of the cuticle lining the hindgut epithelium (B). (C) papillate region, and (D) sphincter, showing the layers of musculature as described in the text. Scale bars: A = 750 μm; B = 500 μm; C = 500 μm; D = 250 μm.

Fitzgerald, 1976; Palackal *et al.*, 1984; Hryniewiecka-Szyfter & Storch, 1986). However, the posterior hindgut has been described to participate in osmoregulation in *Armadillidium vulgare*, but not in *Oniscus asellus* (Coruzzi, Witkus & Vernon, 1982). The sphincter is formed by circular muscles surrounding the above-mentioned network of hindgut musculature (Hassall & Jennings, 1975; Holdich & Mayes, 1975; Palackal *et al.*, 1984; Fig. 4D), and may be used to seal off the papillate region from the

rectum (Hassall & Jennings, 1975). By periodic tight constriction of this region, premature loss of food and water from the digestive tract is prevented (Palackal *et al*., 1984), and compaction of faecal pellets may take place here prior to egestion (see Hames & Hopkin, 1989), although physical compression of faecal material and removal of water has also been attributed to the entire posterior hindgut (Smith *et al*., 1969; Witkus *et al*., 1969; Vernon *et al*., 1974; Lindqvist & Fitzgerald, 1976; Coruzzi *et al*., 1982).

Despite the external features characterizing the anterior and the posterior hindgut, the hindgut lumen can be considered a simple straight tube without internal compartmentalization (see Fig. 3A), except for the typhlosole channels. Nonetheless, differences in pH levels (Nicholls, 1931; Kensley, 1974; Zimmer & Topp, 1997*b*; M. Zimmer & A. Brune, in preparation) and enzymatic activities (Hartenstein, 1964*b*; Saleem & Alikhan, 1974; Hassall & Jennings, 1975; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999) of different sections of the hindgut have been described. The anterior hindgut is the site of digestion of leaf litter (Hassall & Jennings, 1975; Hames & Hopkin, 1989; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999) and microbial cells (Reyes & Tiedje, 1976; Coughtrey *et al*., 1980; Zimmer & Topp, 1998*b*), whereas the posterior hindgut is characterized by microbial proliferation and dense populations of microorganisms (Gunnarsson & Tunlid, 1986; Hassall, Turner & Rands, 1987; Zimmer & Topp, 1998*b*). Further, water resorption and osmoregulation are also features of the posterior hindgut (Smith *et al*., 1969; Coruzzi *et al*., 1982; Palackal *et al*., 1984; Hryniewiecka-Szyfter & Storch, 1986).

pH levels in the hindgut lumen are 6.0–7.2 in *Ligia oceanica* (Nicholls, 1931), 6.8–7.4 in *Tylos granulatus* (Kensley, 1974), 6.1–7.0 in *Trichoniscus pusillus* (M. Zimmer & A. Brune, in preparation), 6.4–6.8 (Hartenstein, 1964*a*), 4.7–5.4 (Wood & Griffiths, 1988) and 5.2–6.9 (M. Zimmer & A. Brune, in preparation) in *Oniscus asellus*, 6.5–7.1 (Kukor & Martin, 1986) to 5.6–6.5 (M. Zimmer & A. Brune, in preparation) in *Trachelipus rathkii*, and 5.5–6.5 in *Porcellio scaber* (Zimmer & Topp, 1997*b*; M. Zimmer & A. Brune, in preparation), most species – but not *Tylos granulatus* and *Trichoniscus pusillus* – exhibiting a pH gradient from the more strongly acidic anterior to the slightly acidic posterior hindgut (M. Zimmer & A. Brune, in preparation). Thus, the lumen of the anterior hindgut exhibits pH levels that provide optimal conditions for the enzymatic activities necessary to digest terrestrial leaf litter (section IV.2), while the pH in the posterior hindgut is appropriate for bacterial proliferation (section III.1) (Zimmer & Topp, 1998*b*, in *Porcellio scaber*).

The small, but significant pH difference between anterior and posterior hindgut is homeostatically maintained as long as the food pH does not drop below 4.0 (Zimmer & Topp, 1997*b*). From comparative studies of axial pH gradients and K^+ concentrations in the hindgut lumen of *Porcellio scaber*, we may conclude that K^+ in- and efflux, promoted by K^+-ATPases, may serve as pH-regulating mechanism (M. Zimmer & A. Brune, in preparation), as has been described in Lepidopteran larvae (Dow, 1992). Hartenstein (1964*a*) did not detect any axial changes in pH by using staining techniques *in vivo*, but from small differences in redox potential he concluded that there might be different pH levels in different hindgut regions, with the papillate region exhibiting the highest pH values. By contrast, M. Zimmer & A. Brune (in preparation) failed to find redox gradients in the hindgut lumina of several species using micro-electrodes.

Due to oxygen-consuming processes (i.e. digestion, and microbial metabolism and proliferation), the radial centre of the entire hindgut is anoxic, while the influx of oxygen from the haemolymph *via* epithelial cells is sufficient to maintain a small peripheral ring of the lumen oxic (M. Zimmer & A. Brune, in preparation). The conditions of different regions of the hindgut lumen, e.g. oxygen saturation and pH level, can be expected to have considerable effects on digestive processes (section IV.2) and hindgut microbiota (section III.1).

The function of the typhlosolis (*sensu* Murlin, 1902) has been subject to considerable debate. The typhlosole channels probably do not merely enhance the surface area available for ion exchange with the haemolymph (as suggested by Alikhan, 1972*c*), but also channel digestive fluids back and forth to ensure mixing of food and digestive enzymes (Hartenstein, 1964*a*), transport nutrients to the absorptive hepatopancreas (Hames & Hopkin, 1989), and/or protect ingested microbiota from being digested during the passage through the anterior hindgut before their enzymes can be utilized for digestive processes in the papillate region of the posterior hindgut; digestive enzymes are transported from the hepatopancreas inside the typhlosole channels to the posterior hindgut (Hassall & Jennings, 1975). Typhlosole channels are only known from oniscid isopods; they are not present in any marine or freshwater isopod species of other suborders, investigated so far (cf. Hames & Hopkin, 1989). These authors mentioned rudimentary typhlosole structures in the semi-

terrestrial *Ligia oceanica* and *Tylos europaeus* (Hames & Hopkin, 1989). Arguing that the typhlosole channels are involved in recycling fluids, Hames & Hopkin (1989) discuss the possible significance of this structure for the transition from water to land. Typhlosole channels had previously been found in *Ligia exotica* Roux 1828 (Ligiidae) (Chandy, 1939) and *Ligia oceanica* (Hewitt, 1907), while neither Nicholls (1931) nor Kensley (1974) presented evidence for this structure in the shore-inhabiting *Ligia oceanica* or *Tylos granulatus*, respectively. Further, Štrus *et al.* (1995) did not find evidence for rudimentary typhlosole channels in the ligiids, *Ligia italica* and *Ligidium hypnorum*. Obviously, Tylidae and Ligiidae represent evolutionary stages of terrestrialization at which typhlosole channels evolved (see Hames & Hopkin, 1989). The typhlosolis, as well as the reduction of the endodermal midgut (see above), has probably been important for the evolutionary transition from amphibious to more terrestrial habitats (Štrus *et al.*, 1995).

Lindqvist & Fitzgerald (1976) investigated the osmoregulatory movement of fluids between the gut lumen and the haemolymph. They suggested the foregut or the hepatopancreas to be involved in this process. By contrast, osmoregulatory activity of the hindgut epithelium has been described in intertidal (Holdich & Ratcliffe, 1970) and terrestrial (Smith *et al.*, 1969; Coruzzi *et al.*, 1982; Palackal *et al.*, 1984) isopods, and prevention of water loss has been ascribed both to the hindgut epithelium (Palackal *et al.*, 1984; Hryniewiecka-Szyfter & Storch, 1986) and to the typhlosolis (Hames & Hopkin, 1989; see above). The uptake of water *via* the hindgut from moist substrata has been suspected (Spencer & Edney, 1954; Kuenen, 1959); the watered hindgut was thought to be used to lubricate the cuticle *via* the mouth and anus in desiccated animals (Holdich & Mayes, 1975).

Due to its cellular ultrastructure and some histochemical properties, the hindgut epithelium has been suspected to be involved in the absorption of digestively released nutrients (Holdich & Mayes, 1975, based on results from Alikhan, 1969, 1972*c*). The ultrastructure of epithelial hindgut cells changes during starvation (Hryniewiecka-Szyfter & Storch, 1986). Alikhan (1969, 1972*c*) also proposed digestive enzymes to be secreted by the hindgut epithelium, but McMurrich (1898), Vernon *et al.* (1974) and Hassall & Jennings (1975) did not find evidence for enzyme secretion by the hindgut epithelium; its secretory activity is probably related to secretion of the hindgut cuticle (Lane, 1988; see section II.3). Both secretory and absorptive activity might also indicate ion and water transport (Smith *et al.*, 1969; Witkus *et al.*, 1969; Vernon *et al.*, 1974; Holdich & Mayes, 1975; Lindqvist & Fitzgerald, 1976; Coruzzi *et al.*, 1982; Palackal *et al.*, 1984; Lane, 1988). Lindqvist & Fitzgerald (1976) stressed the adaptive significance of water storage inside the hindgut for survival in the terrestrial habitat.

(3) Peritrophic envelope or hindgut cuticle?

In insects, midgut cells secrete peritrophic membranes consisting of chitin fibres in a gel-like matrix of acid mucopolysaccharides (summarized in Peters, 1992). The functions of peritrophic membranes include protection of the epithelium from mechanical abrasion by lumen contents, the removal of electrolytes excreted into the gut, assistance in gut irrigation by retaining the faecal mass centrally during anal drinking (Dall & Moriarty, 1983), and assistance in absorption (Fawcett, 1965).

In terrestrial isopods, the foregut (Hartenstein, 1964*a*) and the hindgut (Holdich & Ratcliffe, 1970; Hassall & Jennings, 1975; Palackal *et al.*, 1984; Hryniewiecka-Szyfter & Storch, 1986; Lane, 1988) are lined by a thick intima (cuticle) that contains chitin and acid mucopolysaccharides and is secreted by tegumental glands (Lane, 1988). This intima appears to be composed similarly to peritrophic membranes described in other crustaceans (Georgi, 1969) and in insects (summarized in Peters, 1992), and apparently fulfils similar functions. Presumably, the foregut intima protects against abrasion (see Hartenstein, 1964*a*), while that of the hindgut is rather associated with osmoregulation and water budgeting (Palackal *et al.*, 1984; Hryniewiecka-Szyfter & Storch, 1986; Lane, 1988).

The endodermal midgut, if present (section II.2), is characterized by a break between the cuticles of the ectodermal foregut and the hindgut (Goodrich, 1939). Lane (1988) hinted at an intima inside the caeca of the hepatopancreas, but did not give any information on its origin or chemical composition. Since the hepatopancreas clearly consists of endodermal midgut tissue (Hames & Hopkin, 1989), Hryniewiecka-Szyfter & Storch (1986) were, however, right to reject the existence of a hepatopancreatic intima.

In marine isopods, midgut cells appear to secrete peritrophic membranes (Holdich & Ratcliffe, 1970) that enclose the ingested food. In terrestrial isopods, the food bolus is stuck together by mucopolysaccharides secreted by the cephalic tegumental glands

into the foregut, and mixed with the food (Stevenson & Murphy, 1967). Thus, Holdich & Mayes (1975) noted that peritrophic membranes as such are unnecessary in terrestrial isopods: Vernon *et al.* (1974) concluded from their results that, in contrast to some aquatic isopods they examined, there are no peritrophic membranes in *Armadillidium vulgare* (cf. Palackal *et al.*, 1984). Georgi (1969) did not find any evidence for the existence of peritrophic membranes in *Porcellio scaber*, and Hopkin & Martin (1984) and Hames & Hopkin (1989) did not find peritrophic membranes in *Oniscus asellus* and *Porcellio scaber*. The absence of peritrophic membranes in *Oniscus asellus* was also reported by Hartenstein (1964*a*), but he occasionally observed a 'very thin sheath' that was 'separated from the lumen of the tract upon withdrawal of the latter from the body'. Alikhan (1972*c*) described a 'chitinous membrane' lining the 'midgut' (the hindgut was erroneously taken for the midgut; cf. Holdich & Mayes, 1975) of *Porcellio laevis* Latreille 1804 (Porcellionidae) that was thought to be secreted by the 'midgut epithelium' (Schmitz & Schultz, 1969; Alikhan, 1972*c*), and Warburg (1993) mentioned the existence of peritrophic membranes in terrestrial isopods (citing Bettica *et al.*, 1987; Lane, 1988; Brecko *et al.*, 1991). Warburg (1993) probably referred to the chitinous intima of the gut containing acid mucopolysaccharides, this being a cuticle rather than a peritrophic membrane (Holdich & Mayes, 1975) – the hindgut cuticle of terrestrial isopods is secreted by the hindgut cells (Holdich & Mayes, 1975; Lane, 1988). Furthermore, while peritrophic membranes are secreted continuously and surround the egested faeces (Peters, 1992), the chitinous intima remains in the gut and is only renewed when moulting (Georgi, 1969), and there is no evidence for membranes surrounding the faeces of terrestrial isopods (M. Zimmer, unpublished observations from scanning electron micrographs). Besides the costs of continuous production, no disadvantages of producing peritrophic membranes are obvious. The reasons for the loss of this structure during terrestrialization remain unclear.

III. GUT MICROBIOTA

(1) Hindgut microbiota

A number of studies have investigated microbiota in the leaf litter, the hindgut and faeces of different species of isopods (e.g. Wieser, 1968; Donadey & Besse, 1972; Hassall & Jennings, 1975; Reyes & Tiedje, 1976; Coughtrey *et al.*, 1980; Hopkin & Martin, 1982*a*; Márialigeti *et al.*, 1984; Hassall & Rushton, 1984; Griffiths & Wood, 1985; Ineson & Anderson, 1985; Kukor & Martin, 1986; Gunnarsson, 1987; Hassall *et al.*, 1987; Ullrich, Storch & Schairer, 1991; Drobne, 1995; Kayang, Sharma & Mishra, 1996; Zimmer & Topp, 1998*b*; Zimmer, 1999). Several authors cultivated approximately $5 \times 10^7 - 5 \times 10^8$ bacteria per gut in *Trachelipus rathkii Oniscus asellus*, *Ligia pallasii* Brandt 1833 (Ligiidae) and *Porcellio scaber* (Reyes & Tiedje, 1976; Coughtrey *et al.*, 1980; Carefoot, 1984*a*, *b*; Zimmer & Topp, 1998*b*, respectively) on agar plates. However, the numbers of bacteria and fungi that can be cultivated in artificial media range only between 0.01 and 1% of the total numbers of gut microbiota (Zimmer & Topp, 1998*b*). While the anterior hindgut was only sparsely colonized, dense populations were observed in the posterior hindgut of *Porcellio scaber* by Drobne (1995). However, this was not true for *Ligidium hypnorum*, which showed a homogeneously colonized hindgut cuticle (Drobne, 1995). Boyle & Mitchell (1978) – in contrast to Coughtrey *et al.* (1980) and Ullrich *et al.* (1991) – did not find bacteria in the alimentary system of *Oniscus asellus*, and no hindgut bacteria were found in *Hyloniscus riparius* (Koch 1835) (Trichoniscidae) (Drobne, 1995) or the marine wood-boring *Limnoria lignorum* (Rathke 1799) [Sphaeromatidea Wägele, 1989 ('Flabellifera' Sars, 1882): Limnoriidae Harger, 1879] (Ray & Julian, 1952; Ray, 1959) and *Limnoria tripunctata* Menzies 1951 (Sleeter *et al.*, 1978).

The most numerous of the hindgut bacteria characterized so far are coryneform Micrococcaceae – common saprotrophic forms, forming white colonies – *Arthrobacter*-like coccoid cells and rods (Ullrich *et al.*, 1991, in *Oniscus asellus*). Some of these microbiota could not be found in decaying leaf litter, but the microbial gut community appears to be very similar to that of faeces (Reyes & Tiedje, 1976; Ullrich *et al.*, 1991). By contrast, litter-colonizing fungi could be isolated from the hindgut of *Trachelipus rathkii*, but not from faeces (Reyes & Tiedje, 1976). Beerstecher *et al.* (1954*b*) isolated *Azotobacter agilis* from the hindgut of a pillbug they named *Oniscus asellus* (see section V.1). Coughtrey *et al.* (1980), Griffiths & Wood (1985) and Márialigeti *et al.* (1984) stressed the presence of fungi and actinomycetes, the latter being important for nutrition (Coughtrey *et al.*, 1980). Márialigeti *et al.* (1984) proposed actinomycetes to be passive survivors of the gut passage instead of members of the

typical gut microbiota (cf. Griffiths & Wood, 1985). Facultative anaerobic actinomycetes (Márialigeti *et al*., 1984), other bacteria or fungi (Zimmer & Topp, 1998*a*) are probably the most stable members of the transient gut microbiota community, because 'low oxygen conditions due to restricted gas transport and active respiration' (Reyes & Tiedje, 1976) are likely. Large parts of the hindgut lumen have been shown to be anoxic (M. Zimmer & A. Brune, in preparation), although Márialigeti *et al*. (1984) stated that it is 'not constantly anaerobic'.

Several antibiotics have been used to reduce the number of gut microbiota experimentally (e.g. Reyes & Tiedje, 1976; Carefoot, 1984*a*, *b*; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999), but the susceptibility of these microbiota to the tested antibiotics varied markedly between studies. While Reyes & Tiedje (1976) succeeded in strongly reducing the number of (platable) microbiota in the gut of *Trachelipus rathkii* with tetracycline and chlortetracycline by factor of 10^3, Carefoot (1984*a*, *b*) only obtained a reduction by less than two orders of magnitude in *Ligia pallasii* when feeding with ampicillin, neomycin and penicillin, or even less, when using other antibiotics. Similarly, Zimmer & Topp (1998*b*, *c*) and Zimmer (1999) reduced the number of platable as well as non-platable bacteria in the gut of *Porcellio scaber* by 75–99 % and 68–97 %, respectively, with a mixture of amphotericin, penicillin and streptomycin, and terramycin® (oxytetracyclin), tegosept®, dithan® and sorbic acid. Fungi and actinomycetes were less susceptible to these antibiotics (Zimmer & Topp, 1998*b*).

Leaf-litter-colonizing microbiota are ingested along with the food. In the anterior hindgut (Zimmer & Topp, 1998*b*), these microbiota are digested and their number is strongly reduced (Reyes & Tiedje, 1976; Beck & Friebe, 1981; Márialigeti *et al*., 1984; Gunnarsson & Tunlid, 1986; Zimmer & Topp, 1998*b*). Several authors expected ingested fungi to be utilized as food (Hanlon & Anderson, 1980; Beck & Friebe, 1981; Kayang, Sharma & Mishra, 1994, 1996; cf. Coughtrey *et al*., 1980). The potential of the ingested microbiota to contribute to nutritional requirements (Beerstecher *et al*., 1954*b*; Carefoot, 1984*a*, *b*) or to provide digestive enzymes (Hassall & Jennings, 1975; Kaplan & Hartenstein, 1978; Kukor & Martin, 1986; Zimmer, 1999) will be discussed in sections IV.2 and V.1.

Multiplication of those bacteria that survive the passage of the anterior hindgut – particularly coryneform bacteria (Ullrich *et al*., 1991) – results in an increase in their number in the posterior hindgut (Kozlovskaja & Striganova, 1977; Coughtrey *et al*., 1980; Gunnarsson & Tunlid, 1986; Hassall *et al*., 1987; Zimmer & Topp, 1998*b*), while fungal proliferation appears to be less extensive (Kozlovskaja & Striganova, 1977; Zimmer & Topp, 1998*b*). It is only by growth and proliferation of ingested bacteria and fungi that gut microbiota can maintain high densities in the gut of woodlice, and favourable growth conditions in food-filled guts are necessary for gut microbiota to maintain their numbers against losses from digestion and elimination (Reyes & Tiedje, 1976). The posterior hindgut is characterized by pH levels of 6.0–6.5 (Zimmer & Topp, 1997*b*; M. Zimmer & A. Brune, in preparation), revealing optimal conditions for intense proliferation of bacteria, although less suitable for fungal growth (Zimmer & Topp, 1998*b*). Thus, besides selective nutritive utilization of bacteria and fungi, differential proliferation may be responsible for changes of their numbers during gut passage.

Although Hassall & Jennings (1975, in *Philoscia muscorum*) rejected the existence of a permanent microbiota in the hindgut, some bacteria have been considered resident by others (Ineson & Anderson, 1985; Gunnarsson & Tunlid, 1986; Ullrich *et al*., 1991; Konstanjšek *et al*., in press). Ullrich *et al*. (1991) made the criticism that studies suggesting resident microbial inhabitants of isopod guts did so either indirectly or did not distinguish between ingested and resident microbiota. As stated above, Reyes & Tiedje (1976) observed differences between the leaf litter and faeces with respect to the species of microbiota isolated, indicating either selective digestion and growth of microbial cells, or a resident gut microbiota. Similar results were obtained by M. Spence (unpublished, cited in Carefoot, 1984*a*) in *Ligia pallasii*, two of 21 colony-forming bacteria being restricted to the gut, while others were also found colonizing the seaweed diet. Generally, some gram-positive bacteria are thought to represent specific intestinal microbiota of *Oniscus asellus* (Gunnarsson & Tunlid, 1986) and typically to be coprophilous (Ullrich *et al*., 1991). The latter authors expected coryneform bacteria to be dominant in the hindgut of this species. Recently, Konstanjšek *et al*. (in press) used molecular techniques to identify bacteria that they found attached to the hindgut cuticle in *Porcellio scaber*. Hassall *et al*. (1987) isolated a *Cytophaga* species from faeces that could not be detected in the litter. The density of gut bacteria decreases strongly during starvation (Reyes & Tiedje, 1976; Beck & Friebe, 1981; Ineson &

Anderson, 1985) and when feeding on sterile artificial diets (Zimmer & Topp, 1998*b*; Zimmer, 1999), both arguing against a resident population of hindgut bacteria. By contrast, Carefoot (1984*b*) did not observe changes in gut microbiota of *Ligia pallasii* after feeding on an artificial diet for up to 5 weeks. In numerous marine, freshwater and terrestrial isopod species, symbiotic fungi (Trichomycetes) of the genera *Alacrinella*, *Palavascia*, *Amoebidium*, *Asellaria*, *Eccrinopsis*, *Eccrinoides*, *Parataeniella*, and *Nodocrinella* are found attached to the hindgut cuticle (Lichtwardt, 1986).

(2) Hepatopancreatic microbiota

Several authors have described bacterial obligate endosymbionts (Wood & Griffiths, 1988) in the lumen of the hepatopancreas of *Porcellio dilatatus* Brandt and Ratzeburg 1833 (Porcellionidae) (Donadey & Besse, 1972), *Porcellio scaber* (Wood & Griffiths, 1988; Hames & Hopkin, 1989; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999), *Oniscus asellus* (Hopkin & Martin, 1982*a*; Wood & Griffiths, 1988; Hames & Hopkin, 1989) and *Ligia pallasii* (Zimmer *et al*., 2001). According to recent results (M. Zimmer & A. Brune, in preparation), these bacteria appear to be anaerobic, but aerotolerant (see section II.2).

Until recently, little attention has been paid to these endosymbiotic bacteria; they have been suggested to be involved in the hydrolysis of cellulose (Zimmer & Topp, 1998*b*), and the oxidative breakdown of lignins (Zimmer & Topp, 1998*c*) and tannins (Zimmer, 1999). In this way, hepatopancreatic endosymbionts of terrestrial isopods might enable these soil animals to digest leaf litter and to contribute directly to litter decomposition, rather than merely indirectly influencing litter breakdown through enhancing microbial activity (see section VII). Thus, their relationship to the isopod may be truly mutualistic (see section IV.3). Hence, the cultivation and characterization of these bacteria is of considerable interest. A first step towards this aim was recently successfully undertaken (M. Zimmer, A. Kappler & A. Brune, unpublished data). We cultivated two strains from hepatopancreas homogenates of both *Oniscus asellus* and *Porcellio scaber* that formed yellow (weakly gram-positive, coccoid) and white (gram-negative, rod-shaped) colonies, respectively. Cells of the white colonies from both *Oniscus asellus* and *Porcellio scaber* exhibited significant phenol-oxidizing activities, but we have not yet detected cellulase activity in cell suspensions (M. Zimmer, A. Kappler & A. Brune, unpublished data). Biochemical and genetic characterization of these bacteria are in progress.

Ullrich *et al*. (1991) isolated gram-negative, facultatively anaerobic rod-shaped Enterobacteriaceae from the hepatopancreas of *Oniscus asellus*. Furthermore, they found Corynebacteriaceae and Mycobacteriaceae in the faeces of this species that were not detectable in the leaf litter (Ullrich *et al*., 1991). These gram-positive, coryneform bacteria produced orange pigment and formed filamentous rods of up to 12 μm and 30 μm length, respectively (Ullrich *et al*., 1991). Gram-positive hepatopancreatic bacteria (Wood & Griffiths, 1988; M. Zimmer, A. Kappler & A. Brune, unpublished data) are probably also coryneform bacteria (Ullrich *et al*., 1991). Wood and Griffiths (1988) described 'very few different types of microorganisms (…) in the hepatopancreas' of *Oniscus asellus* and *Porcellio scaber*, in the form of rod-shaped (cf. Zimmer *et al*., 2001, in *Ligia pallasii*) and filamentous cells. Zimmer (1998) observed predominantly filamentous bacteria together with rod-shaped and coccoid forms in the hepatopancreas of *Porcellio scaber*. Rod-shaped bacteria adhering to the cuticle of the papillate hindgut region have been described by Griffiths & Wood (1985) and by Konstanjšek *et al*. (in press). In *Trachelipus rathkii*, Reyes & Tiedje (1976) found bacterial species of the genera *Pseudomonas* and *Flavobacterium* that did not belong to the dominant litter microbiota. They may have isolated the same species as Griffiths & Wood (1985), or have identified hepatopancreatic bacteria as being present in the hindgut lumen (cf. Zimmer & Topp, 1998*b*) – Reyes and Tiedje (1976) presented evidence for these bacteria being digested during gut passage.

Recently, Drobne *et al*. (1999) described intracellular bacteria in the hepatopancreas of *Porcellio scaber*. However, these *Rickettsiella*-like bacteria were proposed not to be symbiotic, but to be lethally infectious (Drobne *et al*., 1999).

If endosymbionts facilitate the digestion of leaf litter in terrestrial isopods (Zimmer & Topp, 1998*b*, *c*), the existence of hepatopancreatic bacteria might have aided the colonization of terrestrial habitats, representing another example of endosymbiosis acting as an evolutionary motor (cf. Margulis, 1981). Recently, Zimmer *et al*. (2001, in press) compared intertidal isopod species of the suborders Valvifera Sars, 1882 and Sphaeromatidea Wägele, 1989 ('Flabellifera' Sars, 1882) and the prototypal oniscid, *Ligia pallasii*, with respect to hepatopancreatic bacteria and their possible contribution to digestive processes. *Ligia pallasii* contained high densities of

bacteria in the hepatopancreas (Zimmer *et al*., 2001) that appeared to contribute to cellulose hydrolysis (Zimmer *et al*., in press), while no such bacteria were found in *Idotea wosnesenskii* Brandt 1851 (Valvifera: Idoteidae Samouelle 1819) and *Gnorimosphaeroma oregonense* (Dana 1853) (Sphaeromatidea: Sphaeromatidae Milne Edwards 1840) (Zimmer *et al*., 2001).

If hepatopancreatic bacteria contributed to the woodlice's abilities to colonize terrestrial habitats (cf. Zimmer & Topp, 1998*b*; Zimmer *et al*. in press), it may be surprizing that the number of hepatopancreatic caeca have been reduced during the course of terrestrialization (Erhard, 1997; section II.2). However, on a dry mass basis the hepatopancreas contributes relatively more to the entire biomass in *Oniscus asellus* and *Porcellio scaber* than in *Ligia pallasii*, and the number of hepatopancreatic bacteria is higher in *Porcellio scaber* than in *Ligia pallasii* (Zimmer *et al*., in press). These observations agree with Lane's (1988) critique of the assumption that the hepatopancreatic caeca are reduced in terrestrial isopods. A relationship between the evolutionary differentiation of the hepatopancreas and the nutritive shift to feeding on leaf litter has been proposed by Hassall & Jennings (1975).

To provide the best nutritive conditions for their progeny, reproducing woodlice should invest in transferring hepatopancreatic bacteria to their offspring. This is an interesting topic; mutualistic symbiotic relationships are considered to have evolved from parasitic ones (Price, 1991), with parasites and host having conflicting interests as to whether or not the parasite is transferred to the host's offspring (cf. Yamamura, 1993). However, it is not known how this transfer might occur in isopods. There is evidence for bacteria of unknown identity or origin in the marsupial fluids of *Porcellio scaber* and *Oniscus asellus*, that form both yellow and white colonies when cultivated on agar (M. Stevens & M. Zimmer, unpublished data). Further studies on this topic are warranted. Another possible route for the inoculation of juveniles is by their feeding on the faeces of conspecific adults (Zimmer & Topp, 1998*b*; section V.2).

Whatever mechanism has evolved to allow for bacterial inoculation of mancae, early manca stages either have no hepatopancreatic filter, preventing the influx of solid particles into the caeca (section II.2), or they have a filter that allows the introduction of certain bacteria. Generally, this filter can be assumed to be a one-way device (cf. Fig. 1 in Hassall, 1977*b*) that allows surplus cells of an actively proliferating population of hepatopancreatic bacteria to be removed (Zimmer & Topp, 1998*b*). Hames & Hopkin (1989) described a direct, i.e. unfiltered, connection between the caecal antechamber and the hindgut (cf. Fig. 3B) allowing for particles to be voided. This connection may, at least in isopod mancae, also allow an influx of bacterial cells into the hepatopancreatic caeca *via* the antechamber and the foregut–hindgut junction (see Fig. 3B).

IV. DIGESTIVE PROCESSES

(1) Ingestion

During feeding, the proventriculus is filled with food particles that subsequently are passed forward to the hindgut. Generally, food is consumed at a slow pace (Lane, 1988, in *Porcellio scaber*); the proventricular chamber empties within 5–10 min and then is refilled with ingested food (in *Philoscia muscorum*: Hassall & Jennings, 1975). In starving juvenile *Porcellio scaber* and *Oniscus asellus*, however, Hames & Hopkin (1989) observed the passage of food through the foregut to never 'take more than two seconds'. After 30–240 min, the entire hindgut of previously starved *Oniscus asellus* is filled with ingested food (Hartenstein, 1964*a*).

Before the food enters the hindgut, liquids are squeezed out and passed to the midgut caeca (see above), and hepatopancreatic enzymes and bacteria are drawn into the proventriculus from where they are directed into the typhlosole channels (Hassall & Jennings, 1975; Hames & Hopkin, 1989). Simultaneously, digestive fluids from the hepatopancreas are mixed with the food (Hartenstein, 1964*a*; Hassall & Jennings, 1975) and passed along to the hindgut where they remain active for several hours (Hassall & Jennings, 1975). Channelling digestive enzymes to more posterior regions of the hindgut in the typhlosole channels may prevent ingested microbiota from being digested before their activity is used for digestive processes in the anterior hindgut (Hassall & Jennings, 1975).

Consumption rates, ranging from as little as 0.0004 mg mg^{-1} day^{-1} to up to 0.23 mg mg^{-1} day^{-1} (0.02–0.06 mg mg^{-1} day^{-1}, on average), vary between and within species as well as between different food sources, depending on numerous factors (Bakker, 1956; Gere, 1956; Biwer, 1961*a*, *b*; Wieser, 1965; Reichle, 1967, 1968; Shachak, Chapman & Steinberger, 1976; Dallinger & Wieser, 1977; Kozlovskaja & Striganova, 1977; Pobozsny, 1978;

Rushton & Hassall, 1983*a*; Dudgeon, Ma & Lam, 1990; Szlávecz & Maiorana, 1990; Ma *et al.*, 1991; Szlávecz, 1993; Uesbeck & Topp, 1995; Kautz *et al.*, in press; M. Zimmer, G. Kautz & W. Topp, in preparation; cf. section V.3). Relative to their size (biomass), juvenile and small adult isopods consume larger amounts of food than do large adults (Bakker, 1956; Gere, 1956; Wieser, 1965). Similar results were obtained when comparing species of different sizes (Biwer, 1961*a*, *b*: *Porcellio scaber* and *Armadillidium vulgare*). On artificial diets consumption rates are higher than on natural ones (Wieser, 1965; cf. Gere, 1956; but see Zimmer, 1999). Immediately before moulting and, in gravid females, prior to the release of marsupial mancae, feeding stops (Bakker, 1956; cf. Kozlovskaja & Striganova, 1977).

Although we might expect that 'high-quality' (see section VI) food would be consumed in larger amounts than 'low-quality' food when given a choice (see section V.3), in several cases a compensatory increase in consumption of 'low-quality' food has been observed (Wieser, 1965; Dallinger & Wieser, 1977; Rushton & Hassall, 1983*a*; Uesbeck & Topp, 1995; but see M. Zimmer, G. Kautz & W. Topp, in preparation). In addition to ingesting larger amounts of 'low-quality' food, the gain from such food sources may be increased by lengthening the gut retention time (Hubbel, 1971); although this would be achieved by slowing ingestion rates (for brief discussion see Wieser, 1984).

(2) Digestion

As for gut anatomy, digestive processes in terrestrial isopods were investigated early in the 20th century (e.g. Murlin, 1902; Nicholls, 1931), as well as during the last decades (Alikhan, 1969, 1972*c*; Hartenstein, 1964*a*, *b*, 1982; Saleem & Alikhan, 1974; Hassall & Jennings, 1975; Neuhauser & Hartenstein, 1978; Hames & Hopkin, 1989; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999). Digestive enzymes are produced in the hepatopancreas, and are secreted into the proventricular chamber of the foregut and the typhlosole channels to be mixed with the food (Hassall & Jennings, 1975; Lane, 1988; Hames & Hopkin, 1989; Fig. 5). Endogenous enzymes include different carbohydrases (Nicholls, 1931: amylase, invertase and glycogenase with pH optima at 5.5–6.0, proteases with pH optima at 6 and 9; Newcomer, 1956: amylase, α- and β-glucosidases, α-galactosidase, but no β-galactosidase, β-fructosidase or cellulase; Vonk, 1960: chitinase; Alikhan, 1969, 1972*c*: maltase; Beck & Friebe, 1981: optimal breakdown of several disaccharides at pH 5–6), dehydrogenases (Hartenstein, 1964*b*), esterases (Hartenstein, 1964*a*; Saleem & Alikhan, 1974; Hassall & Jennings, 1975), lipases [Hartenstein, 1964*a* – although Hassall & Jennings (1975) did not detect lipases or cholinesterases], arylamidases (Hassall & Jennings, 1975), oxidases (Hartenstein, 1982: peroxidase with pH optimum at approximately 7–8 in *Trachelipus rathkii*, aldehyde oxidase with pH optimum of 7.8 in *Oniscus asellus*), and a catalase (Hartenstein, 1982). Saleem & Alikhan (1974) and Hassall & Jennings (1975) distinguished acid phosphatases predominating in the hepatopancreas (in secretory B-cells *sensu* Frenzel, 1884) and alkaline phosphatases prevailing in the hindgut lumen. On a finer scale, Hassall & Jennings (1975) detected both phosphatases in the hepatopancreas, and in the anterior (typhlosole region) and posterior hindgut. They found only weak acid phosphatase activity in the papillate region and solely alkaline phosphatase in the sphincter region. Saleem & Alikhan (1974) proposed the acid phosphatases to be involved in digestion and autolytic degradation of animal tissue, while the alkaline phosphatases are active in phosphorylation of certain compounds prior to transport across membranes.

Due to high cellulolytic activities in the anterior hindgut that were thought to be of exogenous origin from microbiota ingested with the food (see section IV.3), Hassall & Jennings (1975) suggested that the ingested microbiota were not killed by the digestive enzymes of *Philoscia muscorum* (see section III.1), in part due to the typhlosole channels directing the endogenous enzymes to the papillate region of the posterior hindgut rather than to the anterior hindgut (cf. Murlin, 1902). Results presented by Zimmer (1999) suggest that ingested microbial enzymes hydrolytically detoxify ingested tannins (see section V.3) in the foregut and anterior hindgut, while their degradation by endogenous enzymes takes place at the transition from the anterior to the posterior hindgut. In accordance with this, Hassall & Jennings (1975) described endogenous enzymes as acting on the ingested food in the papillate region, after partial degradation by ingested microbial enzymes had already occurred in the anterior hindgut. Zimmer & Topp (1998*b*) localized the main site of litter digestion to be at the transition from the typhlosole region to the papillate region (cf. Fig. 5). Digestive enzymes must therefore be mixed with the ingested food prior to its passing the anterior hindgut. During the influx of hepatopan-

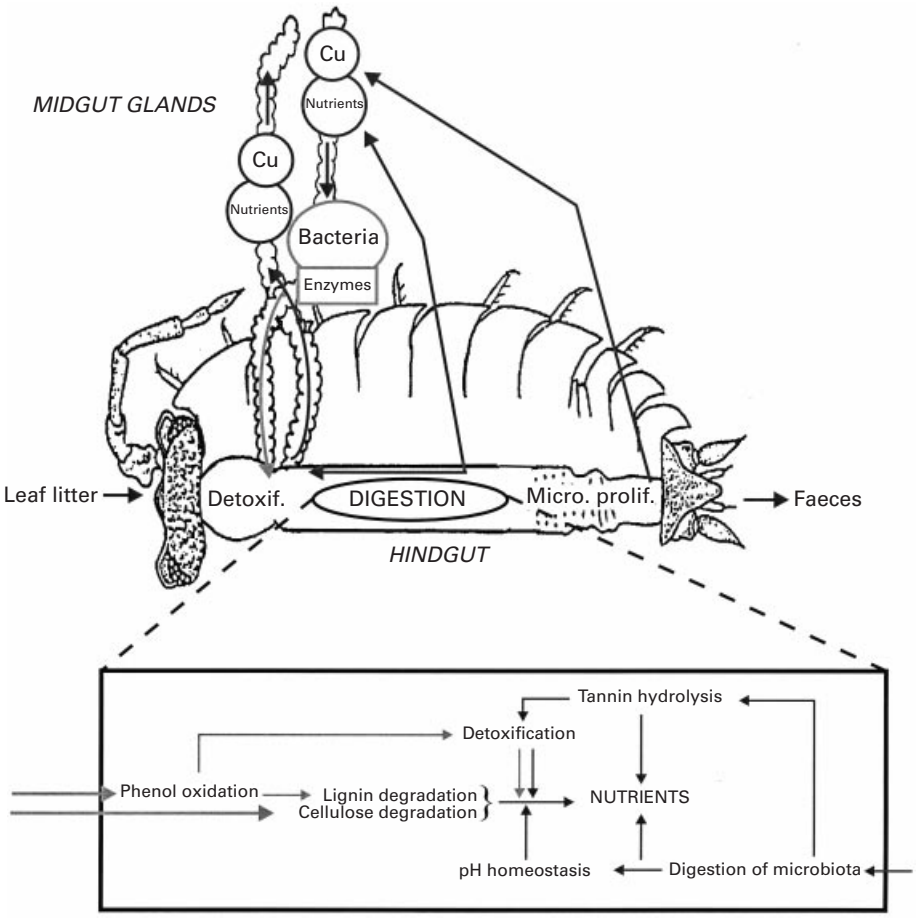

Fig. 5. Digestive processes in the hindgut of *Porcellio scaber* (Porcellionidae) (modified after Zimmer, 1998), including the ingestion of leaf litter, detoxification of ingestion phenolics (Detoxif.) in the foregut, digestion in the anterior hindgut through the activity of endogenous and bacterial enzymes, absorption of nutrients and copper, microbial proliferation (Microb. prolif.) in the posterior hindgut, and egestion of faeces. See text for further details.

creatic fluids into the proventricular chamber, the ingested food is probably inoculated with hepatopancreatic bacteria (Hames & Hopkin, 1989) (see sections II.2 and III.2). Through extracellular membrane-bound cellulases attached to these bacteria, cellulolytic activity may reach the anterior hindgut along with truly endogenous enzymes (Zimmer & Topp, 1998*b*).

The assimilation efficiency of natural diets depends on both the species and the food source (Table 2). On artificial diets (cf. Carefoot, 1984*a*, *b*) containing phenolic compounds, digestibility ranges between 10 and 86 % in *Porcellio scaber*, depending on whether leaf litter (23–65 %), artificial diet (reducing the number of hindgut microbiota: 17–86 % digestibility) or an antibiotic-containing diet (reducing the number of hepatopancreatic bacteria: 10–78 % digestibility) was fed prior to the experiment (Zimmer, 1999). Antibiotics strongly hindered the digestion in *Ligia pallasii* (Zimmer *et al*., 2001). Decreased digestibility after reduction of microbiota on the leaf litter (cf. Table 2), in the hindgut, or of hepatopancreatic bacteria, stresses the significance of each group of microbiota in digestive processes (see Hassall & Jennings, 1975; Reyes & Tiedje, 1976; Griffiths & Wood, 1985; Kukor & Martin, 1986; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999; Zimmer *et al*., 2001).

(3) Endogenous enzymes for litter degradation?

Leaf litter consists mainly of barely digestible, or even deterrent, compounds, such as cellulose, lignin and other phenolics, and nutrients are rather limited (e.g. Breznak & Brune, 1994). The ability to digest such compounds may have been an evolutionary

Table 2. *Estimates of digestibility of natural food sources in different species of terrestrial isopods as given in literature*

Species	Digestibility (%)	Food source	Reference
Ligia pallasii Brandt 1833 (Ligiidae)	< 75	Seaweed	Carefoot (1973)
Ligia pallasii Brandt 1833 (Ligiidae)	40–70	Seaweed	Zimmer *et al.* (2001)
Oniscus asellus Linnaeus 1758 (Oniscidae)	16	*Acer saccharum*	Hartenstein (1964*a*)
		Oak litter	
Oniscus asellus Linnaeus 1758	46	'sterilised'	Uesbeck & Topp (1995)
(Oniscidae)	72	inoculated	
		Birch litter	
Oniscus asellus Linnaeus 1758	46	'sterilised'	Uesbeck & Topp (1995)
(Oniscidae)	79	inoculated	
		Birch litter	
Porcellio scaber Latreille 1804 (Porcellionidae)	18	fresh	Hassall & Rushton (1982)
		Oak litter, different pH levels	
Porcellio scaber Latreille 1804	< 20	fresh	M. Zimmer, G. Kautz &
(Porcellionidae)	10–50	decomposed	W. Topp, in preparation
		Alder litter, different pH levels	
Porcellio scaber Latreille 1804	15–50	fresh	M. Zimmer, G. Kautz &
(Porcellionidae)	10–60	decomposed	W. Topp, in preparation
Protracheoniscus (*Porcellio*) *orientalis* (Uljanin 1875) (Trachelipodidae)	32	Mixed desert litter	Kozlovakaja & Striganova (1977)
		Oak litter	
Protracheoniscus (*Porcellio*) *politus*	4–12	fresh	Gere (1956)
(Koch 1841) (Trachelipodidae)	15–21	decomposed	
Trachelipus (*Porcellio*) *rathkii* (Brandt, 1833) (Trachelipodidae)	38–44	Yeast cells	Reyes & Tiedje (1973)
Hemilepistus cristatus Budde-Lund 1879 (Trachelipodidae)	79	Stems of desert forbs	Kozlovakaja & Striganova (1977)
Hemilepistus fedtschenkol Uljanin 1875 (Trachelipodidae)	46	Mixed desert litter	Striganova & Valiachmedov (1976)
Armadillidium vulgare (Latreille 1804) (Armadillidiidae)	< 20	Different food sources	Rushton & Hassall (1983*a*)

prerequisite for the nutritional utilization of terrestrial leaf litter. Although it has been long argued that saprophagous soil animals mostly lack enzymes for litter degradation, and thus, egest faeces that differ only slightly from the ingested leaf litter with respect to their chemical composition, woodlice are capable of degrading ingested cellulose (Hartenstein, 1964*a*, 1982; Hassall & Jennings, 1975; Kozlovskaja & Striganova, 1977; Kukor & Martin, 1986; Zimmer & Topp, 1998*b*) and oxidizing (Neuhauser & Hartenstein, 1976; Zimmer & Topp, 1998*a*; Zimmer, 1999) or hydrolyzing (Zimmer, 1999) ingested phenolics.

As early as 1964, Hartenstein suggested the existence of endogenous cellulases in *Oniscus asellus* [pH optima of approximately 5 in *Oniscus asellus* (Hartenstein, 1964*a*), and approximately 4.6 in *Oniscus asellus*, *Trachelipus rathkii*, and *Armadillidium vulgare* (Hartenstein, 1982)]. Later investigators observed that terrestrial isopods depend on the cellulolytic enzymes of ingested microorganisms (Hassall & Jennings, 1975; Kozlovskaja &

Striganova, 1977), or at least utilize acquired fungal cellulase (Kukor & Martin, 1986) for the digestion of ingested cellulose. Recently, Zimmer & Topp (1998*a*) observed contradictions between the activity of cellulolytic enzymes and the number of microbiota in the hindgut of *Porcellio scaber*: in studies on digestive processes, the anterior hindgut exhibited the highest cellulase activity (as had previously been described by Hassall & Jennings, 1975), but was characterized by low microbial counts. In contrast to Hassall & Jennings (1975), but in agreement with Hartenstein (1964*a*), cellulolytic activity was detected in the hepatopancreatic caeca that was 3–30-fold higher than that in the leaf litter (Zimmer & Topp, 1998*a*), and thus could not be attributed to the influx of ingested exogenous enzymes together with digestive fluids (cf. Hassall & Jennings, 1975). Zimmer & Topp (1998*b*) concluded that the cellulases active in the anterior hindgut mainly originate from hepatopancreatic bacteria (section III.2; Fig. 5) [as had been suggested on theoretical grounds by Hopkin & Martin (1982*a*)] that are drawn into the proventriculus and mixed with the food (cf. Hames & Hopkin, 1989; Zimmer & Topp, 1998*b*), or are even produced by the isopod itself (Hartenstein, 1964*a*). Zimmer & Topp (1998*b*) proposed these enzymes to be 'functionally endogenous'. Cellulases in the marine wood-boring *Limnoria lignorum* are believed to be of endogenous origin (Ray & Julian, 1952; Ray, 1959). Hassall & Jennings (1975) proposed favourable conditions for growth or enzyme production by ingested microbiota and utilization of their hydrolytic activities in the hindgut of *Philoscia muscorum*, since they measured an increase of cellulase activity during the incubation of food inside the hindgut.

This was also suggested by Neuhauser & Hartenstein (1976) with respect to ingested phenol-oxidizing microbiota. Since cellulose may be incorporated into lignocellulose, and lignins can only be degraded by oxidation (Breznak & Brune, 1994) the digestive degradation of cellulose will involve phenol oxidation. Zimmer & Topp (1998*c*) and Zimmer (1999) proposed that some of the copper-containing phenol oxidases active in the hindgut of *Porcellio scaber* are produced by hepatopancreatic bacteria that contain approximately 25 % of the hepatopancreatic copper (section V.1) (Zimmer & Topp, 1998*c*; but see Hopkin & Martin, 1982*a*). Zimmer & Topp (1998*b*, *c*) and Zimmer (1999) drew their conclusions based on correlations between enzymatic activities and bacterial numbers that had been reduced by antibiotics. Thus, these results have to be considered preliminary. The observed correlations may be due to the antibiotics independently influencing both the number of hepatopancreatic bacteria and enzymatic activities. Cultivation of these bacteria would provide important information on their enzymatic capabilities (see section III.2).

(4) Absorption

The site of nutrient absorption has been the subject of considerable debate for more than one hundred years. Three main possibilities have been discussed: (1) nutrients are absorbed by the hindgut epithelium (Murlin, 1902; Alikhan, 1969, 1972*c*; Saleem & Alikhan, 1974; Holdich & Mayes, 1975; Lane, 1988; Hames & Hopkin, 1989), (2) nutrients are absorbed by hepatopancreatic cells (McMurrich, 1898; Holdich & Ratcliffe, 1970; Clifford & Witkus, 1971), (3) nutrients are absorbed by both hindgut epithelium and hepatopancraetic tissue (Nussbaum-Hilarowicz, 1921; Nicholls, 1931; Chandy, 1939; Schmitz & Schultz, 1969; Kensley, 1974; Hassall & Jennings, 1975; Hryniewiecka-Szyfter & Storch, 1986; Hames & Hopkin, 1989).

McMurrich (1898) expected the properties of the hindgut cuticle to prevent absorption of nutrients by the hindgut epithelium, but Murlin (1902) showed the hindgut cuticle to be permeable to lipids and certain peptidic compounds. Food absorption through the hindgut cuticle is possible in the marine isopod *Cyathura* (*Anthura*) *carinata* (Krøyer 1847) (Anthuridea Leach 1814: Anthuridae Leach 1814) (Wägele, Welsch & Müller, 1981) and the terrestrial *Oniscus asellus* (Griffiths & Wood, 1985). The hindgut cuticle in terrestrial isopods may be permeable to various macromolecules (cf. Hryniewiecka-Szyfter & Storch, 1986), or permeability may be limited to molecules of the size of *tri*-galloyl-glucose in the anterior hindgut of *Porcellio scaber* (Zimmer, 1999). According to Zimmer (1999), these properties of the cuticle allow the absorption of digestive products up to the size of 1.9 nm, while larger molecules are prevented from passing (demonstrated by using hydrolyzable tannins: Zimmer, 1999). Thus, this section of the hindgut cuticle may serve as an ultrafilter (section II.2), allowing for compartmentalization of digestive processes (cf. section II.3). By contrast, the posterior hindgut is characterized by a cuticle impermeable to uncharged molecules of the size of glucose (approximatley 0.7 nm) in *Porcellio scaber* (Zimmer, 1999). Further, the epithelial infoldings forming the ectocuticular space are narrower in this region than in the anterior hindgut section

[Hryniewiecka-Szyfter & Tyczewska (1979) and Hryniewiecka-Szyfter & Storch (1986) in the marine *Saduria* (*Mesidotea*) *entomon* (Linnaeus 1758) (Valvifera: Chaetiliidae Dana, 1853)] or even are lacking in the most posterior part (Lane, 1988). Thus, absorption of digestively released nutrients in this hindgut section is unlikely; the inability to extract nutrients from the food in the posterior hindgut has been considered one reason for coprophagy (Wieser, 1978; section V.2). Hryniewiecka-Szyfter & Storch (1986) described absorption of glucose and amino acids by the epithelium of the anterior hindgut, while lipids reach the hindgut epithelium *via* the hepatopancreas and haemolymph. Glucose has been detected in the hepatopancreas (and the hindgut) in remarkable amounts (Hartenstein, 1964*a*; Zimmer & Topp, 1998*b*), but Lane (1988) did not detect lipids in the hindgut epithelium of *Porcellio scaber*. These findings together suggest that the hepatopancreas is the main site of nutrient absorption, but the evolutionary reduction of the hepatopancreas that accompanied the colonization of terrestrial habitats (but see Lane, 1988; Zimmer *et al*., in press) seems to contradict this conclusion.

How do digestive fluids containing nutrients digestively released in the hindgut reach the hepatopancreas, moving against the prevailing movement direction of the food bolus, to be absorbed there?

As described above (section II.2), the typhlosole channels may not only be used for passing endogenous hepatopancreatic enzymes to the posterior hindgut (Hassall & Jennings, 1975), but may also direct nutrients forward to the hepatopancreas (Hartenstein, 1964*a*; Hames & Hopkin, 1989). The actual function of these conspicuous structures in digestion and absorption is not yet fully understood.

In insects, peritrophic membranes are thought to allow for compartmentalization of the gut lumen with regard to digestive processes (Terra, Ferreirra & Branchi, 1979; Ferreirra & Terra, 1980; Santos & Terra, 1986; section II.3). Given that the hindgut cuticle of terrestrial isopods is permeable to digestively released nutrients (see above), an ectocuticular space between the cuticle and the epithelium, described by Holdich & Mayes (1975) as being formed by numerous 'microvilli-like structures' of the epithelial cells (cf. Hryniewiecka-Szyfter & Storch, 1986; Lane, 1988), may aid in compartmentalization of digestive fluids and transport of digestion products to the sites of absorption in the midgut glands (Zimmer, 1999; cf. section II.3 and Fig. 5). Further, given that the epithelium of the anterior hindgut is also involved in absorption of nutrients (see above), epithelial cells may supply nutrients directly to the hepatopancreatic epithelium *via* the haemolymph. These mechanisms, of course, are not mutually exclusive.

Whatever mechanisms are involved, nutrients reaching the hepatopancreas may be utilized as energy sources by hepatopancreatic bacteria (Zimmer & Topp, 1998*b*, *c*; section III.2), and are further digested intracellularly in hepatopancreatic tissue (Hassall & Jennings, 1975). However, Hartenstein (1964*b*) did not detect any activity of dehydrogenases involved in glycolysis or the Krebs cycle in hepatopancreatic tissue, further stressing our limited understanding of assimilation and absorption of nutrients in these animals.

(5) Excretion

Terrestrial isopods are essentially ammonotelic (Dresel & Moyle, 1950). The retention of ammonotelism probably offers energetic advantages, because terrestrial isopods do not perform the energetically expensive detoxification of nitrogenous end-products, but can get rid of ammonia directly; this might have facilitated the colonization of terrestrial habitats (Hartenstein, 1968).

Urea could not be detected in terrestrial isopods (Dresel & Moyle, 1950; Hartenstein, 1968), but increasing amounts of uric acid have been found in *Porcellio scaber*, *Oniscus asellus* and *Armadillidium vulgare*, corresponding with a proposed gradient of physiological adaptation to truly terrestrial habitats; no uric acid was found in the prototypal *Ligia oceanica* (Dresel & Moyle, 1950). However, these authors ascribed the presence of uric acid rather to a reduced rate of excretion in the 'more terrestrial' species than to a significant interspecific difference. They concluded from their observations that excretion *via* ammonia is 'associated with aquatic prenatal life' (Dresel & Moyle, 1950) as terrestrial isopods bear their developing progeny in marsupial fluids.

Despite their habitats being mostly humid, terrestrial isopods lack free water to wash away the ammonia produced during digestive processes (Hartenstein, 1968). Thus, ammonia is excreted mainly in its volatile form (Dresel & Moyle, 1950; Hartenstein, 1968) in diurnally rhythmic pulses (Wieser, Schweizer & Hartenstein, 1969; Wieser & Schweizer, 1970), and in small quantitites *via* the faeces (Wieser & Schweizer, 1970). To excrete gaseous ammonia, it is first dissolved from the

maxillary glands (nephridia) (cf. Hoese, 1981; Kobusch, 1994) into the water conducting system (cf. Hoese, 1981) where it is volatilized due to alkalinization of the resulting fluid ('urine') (Hoese, 1981; Wright & O'Donnell, 1993). Recently, Carefoot *et al.* (2000) presented evidence for diurnal changes in the ammonia content of the haemolymph that correspond with proposed times of digestion and absorption in the field. These periodic changes of haemolymph ammonia levels coincide with changes in the maxillary urine and the pleon fluids that surround the gills (Wright & O'Donnell, 1993). The latter fluid, being mixed with fluids of the water conducting system, contains significantly more ammonia than the haemolymph, confirming the involvement of the water conducting system in ammonia excretion (Wright & O'Donnell, 1993).

Approximately 1.7 – 8.5 μg ammonia is excreted per individual *Oniscus asellus* per day, corresponding to a daily release of 0.27 μmol ammonia by a 53 mg (fresh mass) isopod (Hartenstein, 1968). In starving animals, which reduce their egestion rate (see sections IV.1 and IV.6), the amount of ammonia excreted in its volatile form is increased almost four times (Wieser & Schweizer, 1970). The level of protein in the diet correlates with the excretion rate of volatile ammonia, but not with the excretion rate of uric acid or the amount of faecal ammonia (Hartenstein, 1968).

(6) Egestion

Digestive processes (section IV.2) and the efficiency of absorbing nutrients (section IV.4), strongly depend on the duration of gut passage. In terrestrial isopods, gut passage takes approximately 13–17 h (Hartenstein, 1964*a*, in *Oniscus asellus*), 24 h (Hassall & Jennings, 1975, in *Philoscia muscorum*), 10–13 h (Alikhan, 1969, in *Porcellio laevis*), or 4–6 h (Grünwald, 1987, in several species). Easily digestible artificial diets (cf. Carefoot, 1984*a*, *b*) are passed through the gut more rapidly (see section IV.1), remaining for 5–7 h in the gut of *Porcellio scaber* (Zimmer, 1998), while starved animals keep the food inside their gut for up to 3 (Hames & Hopkin, 1989, in *Porcellio scaber* and *Oniscus asellus*) or even 7 days (Hassall & Jennings, 1975, in *Philoscia muscorum*). The efficiency of copper extraction from the food increases with increasing gut passage duration (Dallinger & Wieser, 1977), and, according to Hubbel (1971), the overall digestibility of the food also increases with the gut retention time. Thus, we expect food of lower nutritive value to be retained in the gut for longer than 'high-quality' (see section VI) food, but experimental data are mostly lacking (see Hubbel, 1971). This prediction, however, is contrary to the increased ingestion rates used to compensate for low nutritive value of food (Wieser, 1965; Dallinger & Wieser, 1977; Rushton & Hassall, 1983*a*; Uesbeck & Topp, 1995).

Due to the mechanical breakdown and comminution of litter material, the average particle size in faeces is reduced to 2–40 μm (Hartenstein, 1964*a*), resulting in a significantly increased surface area that, in turn, promotes microbial activity (Brown, Swift & Mitchell, 1978; Coughtrey *et al.*, 1980; Hartenstein, 1982; Márialigeti *et al.*, 1984; Hassall *et al.*, 1987). The significance of faeces of saprophagous animals as 'hot spots' (called 'biochora' by Sudhaus, 1981) of microbial activity and decomposition of certain leaf litter compounds will be discussed in sections V.2 and VI.

V. FOOD SOURCES

(1) Nutritional requirements

Like many other saprophagous animals, terrestrial isopods respond to spatial and temporal changes in the qualitative and quantitative availability of food by varying their feeding tactics (Hassall & Rushton, 1982). Nonetheless, little is known about the underlying nutritional requirements, mainly due to the heterogeneity of natural food sources (Carefoot, 1993), and probably the different levels of adaptation to terrestrial food sources.

The most reliable data are available for carbohydrates and minerals, which were examined by Carefoot (1984*a*, *b*) using chemically defined artificial diets. *Ligia pallasii* require starch, lactose, glucose, maltose, and sucrose, as well as the minerals, calcium, magnesium, phosphorus, copper, nickel, zinc, iron, manganese, sulphur, iodine, and silicon in decreasing order (Carefoot, 1984*a*, *b*). Whether or not the need for cellulose in the diet is due its role as roughage (as suggested by Carefoot, 1984*a*, *b*), is still open to debate (see section IV.3).

Beerstecher *et al.* (1954*b*) found that feeding a crinochete isopod they identified as *Oniscus asellus* (the authors described it as a common pillbug able to roll up into a ball; *O. asellus*, however, is not able to do this) but that was probably *Armadillidium vulgare* on pure cellulose acetate resulted in similar mortality and growth rates as starvation. These results suggest an inability to digest cellulose, in contradiction to the findings of Hartenstein (1964*a*), Hassall &

Jennings (1975), Kukor & Martin (1986), and Zimmer & Topp (1998*b*). Adding proteins or yeast extract increased growth and lowered mortality, while altering the fat content of the diet or the addition of vitamins did not affect growth or mortality (Beerstecher *et al*., 1954*b*). From studies using analogues of vitamins and amino acids, they concluded that there are high levels of metabolite synthesis in the gut of this species (Beerstecher *et al*., 1954*a*). Similarly, Carefoot (1973) did not find evidence for fat or vitamin requirements in the ligiid *Ligia pallasii*. Rather than extracting these compounds from ingested litter or seaweed, isopods appear to rely on their production by hindgut microbiota (Beerstecher *et al*., 1954*b*; Carefoot, 1973; Hartenstein, 1968; section IV.2). These results do not provide information on carbohydrate metabolism or metabolic sinks for minerals.

The storage of vast amounts of copper in the hepatopancreas (section II.2) has been the subject of numerous studies (Wieser, 1961, 1968, 1978; Wieser & Klima, 1969; Hayes, 1970; Alikhan, 1972*b*; Hryniewiecka-Szyfter, 1972; Coughtrey, Martin & Young, 1977; Dallinger, 1977; Dallinger & Wieser, 1977; Wieser, Dallinger & Busch, 1977; Debry & Lebrun, 1979; Hopkin & Martin, 1982*a*, *b*, 1984; Prosi *et al*., 1983; Hopkin *et al*., 1985, 1986; Hopkin, 1990; Zimmer & Topp, 1998*c*). The use of a haemocyanin as the respiratory pigment in isopods has been suggested as a reason for the storage of copper (Wieser, 1965); however, the storage capacity in hepatopancreatic tissue surpasses the physiological needs for haemocyanin by orders of magnitude (Dallinger & Wieser, 1977). Due to a strong correlation between environmental copper concentrations and hepatopancreatic copper content, Wieser, Busch & Büchel (1976), Wieser *et al*. (1977), Hopkin *et al*. (1986) and Hopkin, Hames & Bragg (1991*a*) suggested that terrestrial isopods could be used as bio-indicators for biologically available copper (and cadmium: Coughtrey *et al*., 1977), but remarkable individual (Prosi *et al*., 1983) and interspecific (Hopkin *et al*., 1985; Hopkin, 1990) variations in the content of copper and other metals suggest careful consideration of monitoring design.

Copper stored in hepatopancreatic S cells is not substantially depleted while feeding on a diet low in copper (Wieser *et al*., 1977; Coughtrey *et al*., 1980; Hopkin, 1990; but see M. Weißenburg & M. Zimmer, in preparation). Debry and Lebrun (1979) described an equilibrium between ingested and egested copper. Copper-deficient diets did not affect *Ligia pallasii* for up to 30 weeks (Carefoot, 1984*b*). However, loss of copper *via* the faeces forced isopods to compensate by extracting copper from the food (Wieser, 1966; Wieser & Wiest, 1968). A comparison of different species from the same contaminated sites revealed interspecific differences in metal extraction and retention among *Ligia oceanica*, *Porcellio scaber* and *Oniscus asellus* (Hopkin *et al*., 1985). These authors presented evidence for copper being extracted more efficiently than cadmium, lead and zinc, but it was previously shown that copper is retained less selectively than cadmium, being similar to lead and zinc in this respect (Martin, Coughtrey & Young, 1976). On the other hand, while copper was accumulated and retained over a 20 week experiment, other metals were lost during feeding on uncontaminated food, with *Porcellio scaber* and *Oniscus asellus* differing strongly from each other in this respect (Hopkin, 1990). After having fed on the same food source, individual *Oniscus asellus* contained much more hepatopancreatic cadmium and lead than specimens of *Porcellio scaber*; the latter showed significantly higher zinc contents (Hopkin, 1990). *Oniscus asellus* stores zinc in short-lived B cells, while *Porcellio scaber* stores zinc in long-lived S cells (Hopkin, Hames & Dray, 1991*b*). The reasons for these interspecific differences remain unclear. Hopkin (1990) observed high retention of copper and cadmium, being stored in the cuprosomes of S cells with long residence time in the hepatopancreas (Hopkin & Martin, 1982*a*; Dallinger & Prosi, 1988; Prosi & Dallinger, 1988), while those metals stored in B cell granules are apparently lost when these cells secrete digestive enzymes (Hopkin, 1990). Thus, metals such as copper (see Fig. 5) in digestive fluids may influence digestive processes.

Similar mechanisms have been proposed for the uptake and storage of copper and other heavy metals, e.g. cadmium and nickel (Martin *et al*., 1976; Wieser *et al*., 1977; Hopkin *et al*., 1985), while the ability to extract lead and zinc is much lower (Hopkin & Martin, 1984). Coughtrey *et al*. (1980) predicted the role of microbiota to be significant for metal uptake in general, but not for copper uptake, in *Oniscus asellus* (Oniscidae). In several terrestrial isopods (Hopkin & Martin, 1982*a*, *b*; Prosi *et al*., 1983), as well as in the aquatic *Asellus meridianus* (Brown, 1978), zinc and lead are stored in the cuprosomes together with copper, but only in the mature cells of the proximal part of the hepatopancreas (Prosi *et al*., 1983). In contaminated *Oniscus asellus*, zinc, cadmium and lead are stored in S cell cuprosomes as well as in B cell 'iron granules' (Hopkin & Martin, 1982*a*, 1984). The absorption

and storage of copper is adversely affected by nickel in the food, the latter also being stored in hepatopancreatic S cells (Alikhan & Storch, 1990). Since nickel inhibits isopod acid phosphatase (Saleem & Alikhan, 1974), this pollutant exhibits toxic effects by reducing membrane- and redox potentials (Alikhan & Storch, 1990), while copper and lead increase acid phosphatase activity in hepatopancreatic S cells (Prosi & Dallinger, 1988), resulting in higher membrane potentials (Alikhan & Storch, 1990). On the other hand, nickel is required to sustain muscular and neuronal action potentials (Alikhan, 1995). *Proasellus meridianus* (Racovitza 1919) (Asellota: Asellidae), a freshwater isopod, develops tolerance against copper (and lead) under certain environmental conditions (Brown, 1976, 1977), and several terrestrial species show increased cell metabolism as a mechanism of metal tolerance in highly contaminated sites (Alikhan, 1995). Some observations indicate that, despite being essential, copper may become toxic at high concentrations, decreasing reproduction (Farkas, Hornung & Fischer, 1996). In metal-contaminated areas (zinc and lead), adapted females of *Porcellio scaber* started to reproduce at lower age, i.e. smaller size, resulting in lower numbers of released mancae, but increased the mass of their offspring (relative to female mass) in an evolutionary response to metal contamination (Donker, Zonneveld & van Straalen, 1993).

The copper requirements of isopods are mediated *via* a water-soluble copper fraction (Wieser & Klima, 1969). Dallinger (1977) observed a preference for a copper-rich diet in copper-deficient *Porcellio scaber*, *Porcellio laevis* and *Oniscus asellus*, but detection mechanisms are not discussed in his paper. M. Weißenburg, M. Zimmer & K. Lunau (unpublished data) recently found preliminary evidence for *Porcellio scaber* being able to discriminate between copper-rich and copper-poor food, in sensory-ecological choice tests. Given that coprophilous microbiota are associated with copper assimilation by isopods (Wieser, 1966; Wieser & Wiest, 1968), this observation may, however, be due to olfactory detection of active microbial cells (Zimmer, Kautz & Topp, 1996), rather than copper itself (see also Hopkin & Martin, 1984). Whatever the detection mechanism involved, selective feeding on diets with different copper contents would enable terrestrial isopods to maintain a relatively constant body copper content (Dallinger, 1977), as has been found in marine and freshwater decapods (Bryan, 1968). Similarly, isopods from sites contaminated with copper and nickel show lower net assimilation rates of these metals than individuals of the same species [*Oniscus asellus*, *Porcellio scaber* and *Porcellionides* (*Metoponorthus*) *pruinosus* (Brandt 1833) (Porcellionidae)] from uncontaminated sites, suggesting either a saturation of uptake mechanisms or an increased metal-excretion rate (Alikhan, 1995). The same has been suggested for cadmium by Hopkin *et al.* (1986), and Hopkin (1990) suggested that hepatopancreatic cells serve as a buffer for physiologically optimal metal concentrations in body tissues.

Starvation results in an increase in hepatopancreatic copper concentration (Alikhan, 1972*b*), this being consistent with seasonal changes in hepatopancreatic copper concentrations, with higher values occuring during winter (Wieser *et al.*, 1977). These findings have been interpreted by Zimmer & Topp (1998*c*) as indicating the utilization of copper in digestive processes through copper-containing phenol oxidases, originating from hepatopancreatic bacteria. These authors estimated approximately 25 % of the hepatopancreatic copper to be localized in hepatopancreatic bacteria (but see Hopkin & Martin, 1982*a*; section IV.3). Considering the high content of lignins and phenolics in the natural food of terrestrial isopods that require phenol oxidases for their digestive breakdown (section IV.3), this is in agreement with findings that the efficiency of food assimilation increases with increasing copper concentration in the food (Dallinger & Wieser, 1977; Debry & Lebrun, 1979; Debry & Muyango, 1979).

The prototypal *Ligia oceanica* meets its mineral requirements entirely through its algal food, but the more terrestrial species face severe problems (Wieser, 1968). This may be either due to species-specific differences in requirements or to the physiological availability of minerals in different food sources (cf. Carefoot, 1984*b*, with respect to copper requirements in *Ligia pallasii*). Thus, Wieser (1968) assumed copper accumulation to represent an adaptation for terrestrialization, that is promoted when woodlice feed on faecal material rather than on leaf litter (Wieser, 1966). It has been proposed that microbial activity renders copper available in sufficiently high amounts in faecal pellets (Wieser, 1966; Wieser & Wiest, 1968; cf. section V.2). By contrast, Hassall & Rushton (1982) argued that copper is not a limiting nutrient for woodlice. However, given that copper is utilized during the oxidative degradation of lignins (Zimmer & Topp, 1998*c*) and phenolic compounds (Zimmer, 1999) of the leaf litter, having sufficient amounts of copper available would be essential from a nutritional point of view (see above). Thus, together with the need to transfer hepatopan-

creatic bacteria to their offspring (see section III.2), reproducing females should provide them with copper. Freshly released mancae of *Porcellio scaber* contain copper in concentrations of 0.1–0.4 μg mg^{-1} (Wieser & Wiest, 1968). Wieser *et al.* (1977) derived a similar value (0.13 μg mg^{-1}) from a regression of body mass against copper content of isopods collected in the field, and M. Stevens & M. Zimmer (unpublished data) detected 0.08 ± 0.05 μg per manca (mean $\pm$ S.D.; $N = 33$) in *Porcellio scaber* prior to exhibiting feeding activity, while Hopkin & Martin (1984) reported values of 0.04–0.1 μg mg^{-1} in mancae from mothers collected at both uncontaminated and copper-contaminated sites. The marsupial fluid contains copper in concentrations of 100 ± 77 μg μl^{-1} (mean $\pm$ S.D.; $N = 11$; M. Stevens & M. Zimmer, unpublished data), but cuprosomes (or 'iron granules') are not present in hepatopancreatic cells of young mancae (Hopkin & Martin, 1984).

The evolution of copper storage and accumulation (cf. Wieser, 1968), might have originated in mechanisms for extracting copper from copper-poor sea water *via* the digestive system in marine ancestors of terrestrial isopods. Whatever physiological requirements may have driven this development initially, these mechanisms have evolved to become highly efficient in terrestrial isopods, so that high quantities are extracted and stored even when only low concentrations are available in the food of terrestrial isopods. Detoxification of surplus copper is brought about by storage in specific cellular compartments and through the genesis of chelates with metallothionins rather than by energetically expensive excretion (for discussion see Hopkin & Martin, 1984). In accordance with this scenario, the intertidal semi-terrestrial isopod, *Tylos punctatus*, rather resembles marine isopods than terrestrial species, with respect to hepatopancreatic copper content and copper retention (Hayes, 1970).

Due to a shift from the gills to the gut as the main entry point for minerals in terrestrial isopods (section II.2), Wieser (1968) suggested that the ingested food is the main source of water and minerals in these animals. The storage capacity of the hepatopancreas, e.g. for copper, has been increased (see above), and toxicity of copper (and other heavy metals) has been reduced by compartmentalization (Wieser, 1968; Hopkin & Martin, 1982*a*; Hopkin, 1990). Further comparative studies are needed with respect to interspecific differences in the uptake and retention of essential (and non-essential, pollutant) metals and minerals before we can draw any valid conclusions with respect to the role of copper storage in terrestrial isopods during terrestrialization.

Besides copper, calcium is one of the principal elements to be found in large amounts in isopods (Wieser, 1966; Radu *et al.*, 1971). As suggested above for copper, calcium appears to be transferred from gravid females to their progeny *via* marsupial fluids (Beeby, 1980). Although calcium loss during moulting is reduced by ingesting the exuvia (e.g. Wieser, 1966) and by calcium recycling inside the body during the moult (Ziegler & Scholz, 1997), some calcium has to be replaced after moulting (e.g. Wieser, 1966). In *Ligia exotica*, approximately 25 % of the body calcium is lost while moulting (Numanoi, 1934), but calcium recycling due to mobilization of calcium deposits is remarkable in *Ligia pallasii* (Ziegler *et al.*, 2000). The ability to assimilate calcium from the food is more than sufficient to meet the animals' requirements (Radu *et al.*, 1971, in *Trachelipus balticus*). Thus, both calcium and copper accumulate with individual age (Wieser & Wiest, 1968; Alikhan, 1972*b*; Hopkin & Martin, 1984).

The assimilation of calcium is quantitatively correlated with the assimilation of lead in *Porcellio scaber* (Beeby, 1978). In gravid females of this species, the transfer of calcium to the marsupial mancae is suppressed by a high lead content of the food (Beeby, 1980). However, high lead concentrations did not affect female fertility, while toxic effects of lead on juvenile isopods were suggested (Beeby, 1980). Zinc has been described to be toxic to terrestrial isopods (Hopkin & Hames, 1994), although it is involved in the formation of calcium carbonate *via* carbonic anhydrase, and in other enzymatic reactions (Hopkin *et al.*, 1985). Both calcium and zinc are assimilated irrespective of coprophagy (Coughtrey *et al.*, 1980).

Isopods (*Oniscus asellus* and *Porcellio scaber*) do not selectively extract nitrogen from the ingested food (Wieser & Schweizer, 1970), but mostly utilize carbonic compounds (Biwer, 1961*a*, *b*), although proteins and amino acids have been proposed to serve as major food sources in crustaceans (Speck & Urich, 1969). Zimmer & Topp (2000) mentioned the dependence of *Porcellio scaber* and *Oniscus asellus* on a low C:N ratio of the available food source (i.e. high relative N content), and disproportionate increase in the content of carbonic compounds in faeces due to the digestion of nitrogenous compounds has been reported in *Ligia pallasii* (Zimmer *et al.*, 2001). Microbiota presumably provide a more easily utilizable nitrogen source (Reyes & Tiedje, 1976; Martin, 1984; Swift & Boddy, 1984; Gunnarsson &

Tunlid, 1986; Ullrich *et al*., 1991), however, interspecific differences with respect to the nutritional significance of leaf-litter-colonizing microbiota are clear from comparative studies on mortality, growth and reproduction in the sympatric *Porcellio scaber* and *Oniscus asellus* (Zimmer & Topp, 2000), and may thus be expected with respect to digestive capabilities and requirements. In the field, such differences between sympatric species may reduce interspecific competition (Zimmer, in press) and may result in species-specific ecosystem effects (Zimmer & Topp, 1999; section VII). Yet, both *Porcellio scaber* and *Oniscus asellus* can digest ingested microbiota (Coughtrey *et al*., 1980; Gunnarsson & Tunlid, 1986; Zimmer & Topp, 1998*b*; sections III.1 and IV.2). Further field studies and laboratory experiments are clearly required.

The ingestion of soil particles or sand grains (in *Ligia pallasii*) has been interpreted in terms of a 'gastric mill' (Carefoot, 1973) that is not present in Diplocheta (Ligiidae) but is found in Holoverticata (see Table 1; section II.2). Clays, as soil compounds ingested along with the food, may enhance digestive efficiencies by disrupting the formation of tannin–protein complexes (Waterman *et al*., 1980) and enhancing microbial phenol oxidase production (Claus & Filip, 1990), while others suppress phenol oxidase activity (Claus & Filip, 1988). Thus, ingested soil particles may be important with respect to digestive processes. Too little is known on this topic to draw any firm conclusion.

Although the digestion and nutritional utilization of ingested microbiota has been described (sections III.1 and IV.2), relatively little is known about the nutritional significance of these cells. Carefoot (1993) stated that 'to date, no successful demonstration of a nutritional role for gut bacteria' has been presented, and Hames & Hopkin (1989) noted that 'the role of microorganisms in digestion (…) [is] yet to be defined'.

According to Reyes & Tiedje (1976), the relative contribution of microbial activities to organic matter digestion by the isopod is minimal. The nutritive gain may, nonetheless, be high, due to lipids, vitamins (Beerstecher *et al*., 1954*a*, *b*; Carefoot, 1984*a*, *b*), or other essential nutrients (Ullrich *et al*., 1991) obtained from the digestion of microbial cells. Feeding terrestrial isopods with pure cultures of several bacteria provided evidence for bacteria being 'high-quality' food (Storch, 1984; Štrus *et al*., 1995). However, in long-term feeding experiments with bacteria as a basic food source, Ullrich *et al*. (1991) found no significant increase in biomass and concluded that terrestrial isopods benefit from ingesting and utilizing litter- or faeces-colonizing microbiota rather qualitatively than quantitatively, coryneform bacteria (see section III) being of particular significance (Ullrich *et al*., 1991). Coryneform bacteria, which may be resident in the hepatopancreas (section III.2), appear not to be affected by gut passage (Ullrich *et al*., 1991; cf. Zimmer & Topp, 1998*b*). In this context, Griffiths & Wood (1985) suggested that ingested bacteria are more important in terms of nutrition than resident bacteria adhering to the gut cuticle (Griffiths & Wood, 1985; Drobne, 1995), since the latter simply exploit digestively released nutrients but do not enhance the digestion of recalcitrant food compounds (Márialigeti *et al*., 1984). Coughtrey *et al*. (1980) proposed ingested (cf. Márialigeti *et al*., 1984) actinomycetes to be nutritionally important. Further, leaf-litter-colonizing fungi represent an important nutrient source (Reyes & Tiedje, 1973, 1976; Coughtrey *et al*., 1980; Hanlon & Anderson, 1980; Soma & Saito, 1983; Gunnarsson & Tunlid, 1986; Zimmer & Topp, 1998*b*), and thus, woodlice prefer microbially (Bauer & Christian, 1995; Daniel *et al*., 1997) and particularly fungally colonized leaf litter over weakly colonized litter (Soma & Saito, 1983; Gunnarsson, 1987; Stöckli, 1990), and selectively feed upon litter-colonizing fungi (Soma & Saito, 1983; Kayang *et al*., 1996). Densely colonized leaves are probably detectable by olfaction, due to air-borne microbial metabolites (Zimmer *et al*., 1996), and leaf-litter-colonizing microbiota may serve as an indicator of easily digestible food (M. Zimmer, G. Kautz & W. Topp, in preparation).

(2) Coprophagy

When given a choice, terrestrial isopods feed upon faeces dropped by themselves or by any other isopod (Wieser, 1968; Dallinger & Wieser, 1977; Hassall & Rushton, 1982, 1985; Ineson & Anderson, 1985; Gunnarsson & Tunlid, 1986; Hassall *et al*., 1987; Ullrich *et al*., 1991), and even by any other saprophagous soil animal (Szlávecz & Pobozsny, 1995), or by phytophagous insects (Zimmer & Topp, in press) – at least in the laboratory, while the occurrence of coprophagy in the field has been doubted (Hopkin & Martin, 1984). Although considerable effort has been invested into studies on isopods ingesting faeces, the nutritional significance of coprophagy is still unclear (Carefoot, 1993). There are several possibilities. (1) Coprophagy may be due to a need for copper (and other nutrients:

Wieser, 1978) that cannot be satisfied by feeding on leaf litter alone, due to an inability to extract these nutrients from plant tissue (Wieser, 1966, 1968; Dallinger & Wieser, 1977; Debry & Lebrun, 1979; for stronger evidence that coprophagy is not required to maintain a positive copper balance, see White, 1968; Coughtrey *et al*., 1980; Hassall & Rushton, 1982, 1985; Hopkin & Martin, 1984), or to absorb them in the posterior hindgut (Dallinger & Wieser, 1977; Wieser, 1978, 1984; cf. Zimmer, 1999). (2) Microbial activity of faeces may render them attractive as a source of (a) easily digestible nutrients, (b) microbial enzymes for the breakdown of recalcitrant compounds, or (c) microbial tissues which may provide essential nutrients (cf. Hassall & Rushton, 1982; Carefoot, 1984*a*, *b*; Ullrich *et al*., 1991; Drobne, 1995; Kautz *et al*., in press). Of course, these explanations are not mutually exclusive; their relative significance may depend on the physiology of the individual or species tested and/or the available food sources.

Wieser (1966) reported that populations of *Porcellio scaber* became extinct when access to faeces was denied in the laboratory, but this observation was not confirmed by Hassall & Rushton (1982), rearing woodlouse populations without access to faeces. Recently, Szlávecz & Maiorana (1998) and Kautz *et al*. (in press) failed to confirm marked nutritional benefits from coprophagy in *Porcellio scaber*. In earlier experiments, addition of cultured bacteria (including coryneform bacteria; see sections III and V.1) to faeces increased the survival rate of coprophagous *Oniscus asellus* as compared with those feeding on sterile faeces. Kautz *et al*. (in press) found the digestibility of 'low-quality' faeces (see section VI), to be increased by faeces-colonizing microbiota, while microbial colonization of faecal material became less significant with increasing quality of the leaf litter the faeces were derived from.

According to Hopkin & Martin (1984), coprophagy will rarely occur in the field due to the difficulty of finding faeces beneath the litter layer; however, given that microbially inoculated faeces represent 'hot spots' of microbial activity (section IV.6), olfactory orientation along gradients of airborne microbial metabolites (cf. Zimmer *et al*., 1996) may lead foraging isopod to this microbial 'hot spot'. Hassall & Rushton (1982) estimated coprophagy to account for less than 8% of total consumption in the field. The significance of this behaviour in the field is thus still unresolved (Carefoot, 1993).

Due to microbial colonization, faeces may serve as an important food source for woodlice, either due to the activity of microbial enzymes (the 'external rumen' proposed by Mason & Odum, 1969), or to microbial biomass (for discussion of the latter see Zimmer & Topp, 1998*c*, and Kautz *et al*., in press). Faeces have frequently been described to contain higher numbers of microbiota (Brown *et al*., 1978; Coughtrey *et al*., 1980; Hanlon & Anderson, 1980; Ineson & Anderson, 1985; Hassall *et al*., 1987; Ullrich *et al*., 1991) that are more active (Biwer, 1961*a*, *b*; Hassall *et al*., 1987) than in leaf litter. However, digestion of microbial cells occurs in the anterior hindgut, proliferation of bacteria only taking place subsequently in the posterior hindgut while the number of fungi does not increase (see section III.1); the number of fungi thus decreases during gut passage (Reyes & Tiedje, 1976; Coughtrey *et al*., 1980; Hanlon & Anderson, 1980), and freshly dropped faeces are, on average, not more densely colonized than the leaf litter (Gunnarsson & Tunlid, 1986; Fig. 6; M. Zimmer, unpublished data). It is only after several days to weeks that faeces-colonizing microbiota reach densities rendering faeces more attractive than microbially colonized leaf litter (Hassall & Rushton, 1985; Gunnarsson & Tunlid, 1986; Hassall *et al*., 1987). Coughtrey *et al*. (1980) concluded 'a stimulation of [microbial] activity after[!] passing through the gut(…)' from their results on *Oniscus asellus*. Thus, although often ignored in previous studies, the age of faeces is of considerable importance (Szlávecz & Maiorana, 1998; section V.3), since there seems to be an increase in microbial density and activity over time (Fig. 6; M. Zimmer unpublished data; but see Figs 3 and 4 in Hassall *et al*., 1987), as has been shown for diplopod faeces during the first 3–23 weeks of faecal decomposition (Tajovský *et al*., 1992).

In agreement with the pattern of microbial colonization and decomposition of isopod faeces, their C:N ratio decreases during ageing (Jambu, Juchault & Mocquard, 1988). 2–3 week old faeces, known to be preferred by *Porcellio scaber* (Hassall & Rushton, 1985), form an optimal substrate for microbial colonization – especially by coryneform bacteria, which are typically coprophilous (Ullrich *et al*., 1991). Gunnarsson & Tunlid (1986) observed a shift over time from predominantly gram-negative bacteria on the leaf litter to a microbial community increasingly dominated by gram-positive bacteria. Early and late stages of faecal decomposition differ with respect to the predominance of generalist heterotrophic and specialized oligotrophic bacteria, respectively (Tajovský *et al*., 1992).

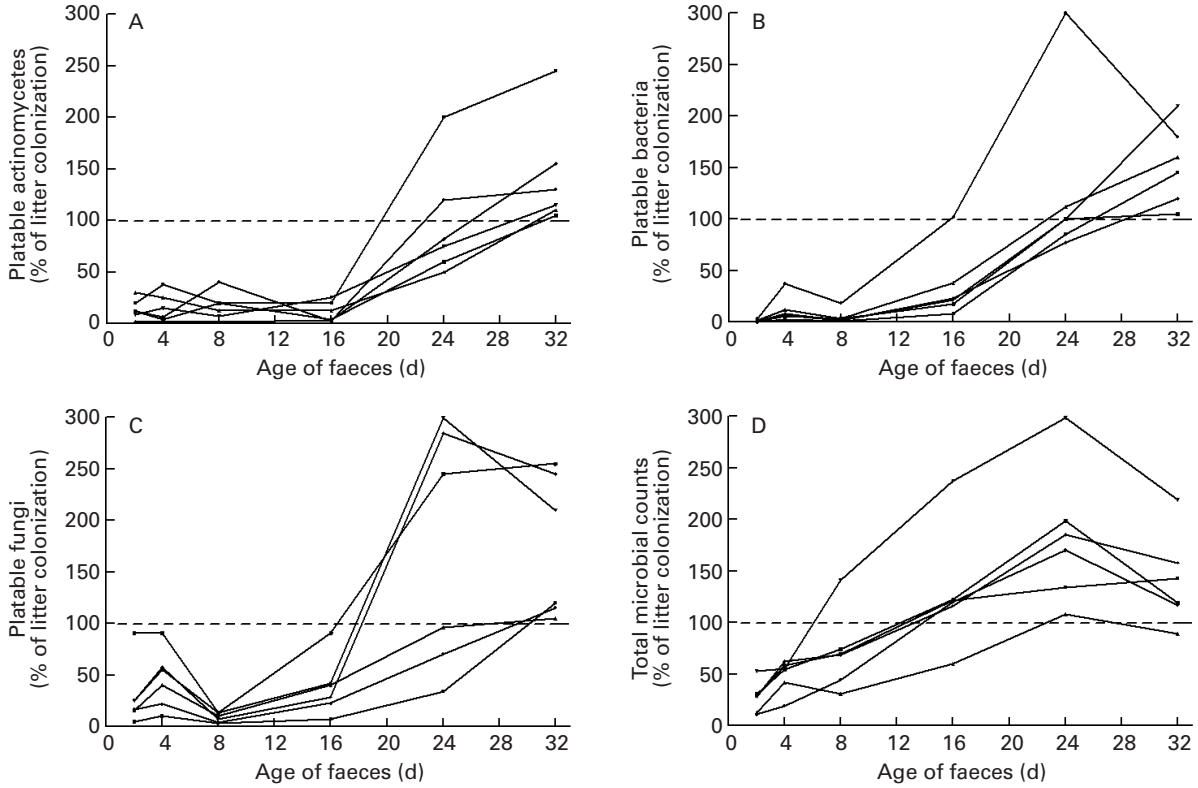

Fig. 6. Microbial succession on isopod faeces: (A) platable actinomycetes, (B) platable bacteria, (C) platable fungi, (D) total microbial counts. Data are mean values of microbial density on faeces relative to the initial density on the leaf litter, as obtained from six different litter samples. The results indicate that microbial densities similar to initial litter values are reached 16–32 days after defecation (platable microbiota), or after 6–23 days (total number of microbiota). During incubation, faeces were stored in sealed Petri dishes on moist filter paper (100% relative humidity) at 15 °C. Hassall *et al.* (1987) stored freshly deposited faeces on filter paper soaked with aqueous birch litter extract to mimic the natural deposition of faeces on leaf litter and observed highest microbial cell numbers ('viable cells') and microbial respiration 6–10 days after egestion, followed by a continuous decrease.

Faecal bacteria, some of which have not been found on decaying leaves but in the gut lumen (Reyes & Tiedje, 1976; Ullrich *et al.*, 1991; see section III.1), were identified as belonging to the Corynebacteriaceae, the Mycobacteriaceae, the Spirillaceae and the Pseudomonadaceae (Ullrich *et al.*, 1991; see section III). Some coryneform faecal bacteria produced orange or yellow pigments (Ullrich *et al.*, 1991), as do colony-forming bacteria cultivated from the hepatopancreas isolates of *Oniscus asellus* and *Porcellio scaber* (M. Zimmer, A. Kappler & A. Brune, unpublished data). If these faecal bacteria are egested hepatopancreatic bacteria (see section III.2), their presence might be one reason for coprophagy (Zimmer & Topp, 1998*c*). Repeated coprophagy led to increasing contents of bacterial cell wall compounds during each gut passage in coprophagous *Oniscus asellus* (Gunnarsson & Tunlid, 1986). However, mainly gram-negative bacteria increased in number (Gunnarsson & Tunlid, 1986); hepatopancreatic bacteria are thought to be gram-positive (see section III.2). Contamination of coprophagous isopods with faecal bacteria, e.g. streptomycetes, has been described by Márialigeti *et al.* (1984), and the need for re-inoculation with microbiota (e.g. after moulting) that are enriched on faeces may be one major reason for coprophagy. Coprophagy may also be more important for juveniles than for adults (see Kopanic *et al.*, 2001, in the cockroach *Blatella germanica*), either for the same reason (see section III.2) or because of nutritive constraints on juveniles, e.g. with respect to the structural softness of faeces (cf. Zimmer & Topp, 2000). It is obvious from present knowledge that we cannot explain convincingly why isopods are coprophagous.

(3) Feeding preference

Besides a preference for feeding on faecal material rather than on leaf litter (Szlávecz & Pobozsny, 1995; section V.2), a preference for decaying over

freshly fallen leaf litter has been described (Dunger, 1958; Biwer, 1961*a*, *b*; Hartenstein, 1964*a*; Schneider & Tschakaroff-Schuster, 1978; Rushton & Hassall, 1983*a*; Hassall & Rushton, 1984; Hassall *et al*., 1987). Yet, Beck & Brestowsky (1980) observed higher growth rates on freshly fallen than on overwintered litter in *Oniscus asellus*. Litter-colonizing and -decomposing microbiota are important for conditioning the leaf litter due to the breakdown of recalcitrant or deterrent compounds, thus, making the tissue more digestible (Martin, 1984; Swift & Boddy, 1984; Hassall & Rushton, 1984; Ullrich *et al*., 1991), although easily digestible litter may become less palatable and less nutritious through microbial activity (Rushton & Hassall, 1983*b*; Hassall & Rushton, 1984). Further, microbial litter-colonizers may assist in the digestive processes of the animals by secreting exo-enzymes (section IV.2), or may even serve as a readily available 'high-quality' food source (section III.1). The latter assumption is confirmed by the lack of nutritional requirements for vitamins, and other 'essential' substances (Beerstecher *et al*., 1954*b*; Carefoot, 1984*a*, *b*), stressing the nutritional significance of ingested microbiota (section V.1). Thus, it is not surprizing that food choice is influenced by microbial colonization of the litter (Márialigeti *et al*., 1984), and that woodlice prefer feeding on microbially colonized litter (Soma & Saito, 1983; Gunnarsson, 1987; Stöckli, 1990; Bauer & Christian, 1995; Daniel *et al*., 1997), and selectively feed upon litter-colonizing fungi (Soma & Saito, 1983; Kayang *et al*., 1996). Isopods (as well as diplopods) readily consume decomposing wood, while sound wood is not consumed in the laboratory, even after mono-species fungal decay (Neuhauser & Hartenstein, 1978).

Hassall & Rushton (1984) illustrated the dependence of preferences for, and gains from, different food sources on chemical defences and microbial conditioning of the leaves. They concluded from their results on *Armadillidium vulgare* that food selection occurs on the basis of digestibility. Thus, the differences in consumption rates of different litter types diminish with increasing digestibility of the litter with its proceeding decay (Dunger, 1958; Rushton & Hassall, 1983*a*).

Several studies revealed evidence for general preferences of saprophagous soil animals, including terrestrial isopods, for some species of leaf litter over others (e.g. Paris, 1963; Satchell & Lowe, 1967; Sakwa, 1974; Beck & Brestowsky, 1980; Rushton & Hassall, 1983*a*; Hassall & Rushton, 1984; Dudgeon *et al*., 1990). Typically litter of Betulaceae, Ulmaceae, Oleaceae, and Aceraceae is preferred over that of Fagaceae and gymnosperm trees by isopods (Dunger, 1958; Biwer, 1961*a*, *b*; White, 1968; Neuhauser & Hartenstein, 1978; Schneider & Tschakaroff-Schuster, 1978). Further, *Armadillidium vulgare* prefers litter of dicotyledonous plants over that of monocotyledonous plants (Paris, 1963; Rushton & Hassall, 1983*a*). Toughness of plant tissue, and contents of nutrients and repellents, respectively, have been suggested as reasons for the observed feedings preferences (Dunger, 1958; Biwer, 1961*a*, *b*; Rushton & Hassall, 1983*a*; Hassall & Rushton, 1984), but experimental confirmation is scarce. Several authors pointed out that no single food source may be sufficient, but that switching between different food sources is preferred, when given a choice (Hassall & Rushton, 1984; Wieser, 1984; Szlávecz, 1993; cf. Dudgeon *et al*., 1990; Ma *et al*., 1991).

Phenolics are generally thought to reduce consumption by terrestrial isopods (Cameron & LaPoint, 1978: condensed tannins; Poinsot-Balaguer *et al*., 1993; Zimmer, 1999: hydrolyzable tannins). Consequently, high phenol contents of litter slow down decomposition processes (Harrison, 1971; Savoie & Gourbière, 1989). Apparently, phenolics exhibit low palatability for isopods (Neuhauser & Hartenstein, 1978), and are toxic inasmuch as condensed tannins, even at low concentrations, cause increased mortality and decreased reproduction (Zimmer & Topp, 1997*a*, in *Porcellio scaber*). Cameron and LaPoint (1978) observed decreased mortality after leaching of phenolics, in *Armadillidium vulgare*. Under the pH conditions prevalent in the isopod hindgut (section II.2), phenolics would be expected to exert deleterious effects, due to protein precipitation or the genesis of hazardous oxidation products (for discussion see Zimmer, 1999).

Tannins tend to affect adversely species that do not come into contact with large amounts of phenolics in their natural diet (Bernays, 1981). Hydrolyzable tannins are typically found in many deciduous trees (Bernays, 1981), the litter of which serves as food for terrestrial isopods (but see Szlávecz, 1993), although tannins as well as many other phenolics are readily removed from the litter through leaching (Kuiters & Sarink, 1986; Racon *et al*., 1988; Poinsot-Balaguer *et al*., 1993; Schofield, Hagerman & Harold, 1998; Zimmer, 2002). Thus, woodlice are usually not confronted with high levels of phenolics, and may, consequently, be expected not to have evolved specific mechanisms to counteract their potentially harmful effects (Zimmer, 1999).

Tannic acid, when ingested with an artificial diet, significantly reduced the density of hindgut microbiota and hepatopancreatic bacteria (Zimmer, 1999), both being important for digestive process (section III). However, surfactants in the hindgut fluids counteract the potential hazardous effects of ingested phenolics (Zimmer, 1997), and thus allow the slightly acidic pH levels required for the optimal activity of digestive enzymes (Zimmer & Topp, 1997*b*) but also increase the potential toxicity of ingested tannins (cf. Appel, 1993). Hydrolyzable tannins are detoxified in the anterior hindgut through the activity of ingested microbiota (Zimmer, 1999). By contrast, the oxidation of phenolics, as has been described by Neuhauser & Hartenstein (1978), Zimmer & Topp (1998*c*) and Zimmer (1999), might initiate deleterious effects of phenolics (Appel, 1993). However, phenol oxidation is a prerequisite for the enzymatic degradation of lignocellulose (Ander & Eriksson, 1976; Sinsabaugh & Linkins, 1987; Breznak & Brune, 1994). The hindgut cuticle (section II.3) may prevent damage to the epithelium brought about by digestively activated phenolics (Appel, 1993), by serving as an ultrafilter (Zimmer, 1999). In summary, although phenolics in the litter may reduce its palatability, digestion of phenolic compounds (Neuhauser & Hartenstein, 1976; Zimmer & Topp, 1998*c*; Zimmer, 1999) result in a decrease in phenol content by up to 50 % in several isopod species (Neuhauser & Hartenstein, 1978), and experimentally added tannic acid does not affect assimilation efficiencies in isopods when fed on their natural diet (Zimmer, 1999). Due to hydrolyzable tannins being degraded to gallic acid and glucose, both promoting hepatopancreatic bacterial growth, during gut passage in *Porcellio scaber* (Zimmer, 1999), we might actually expect a preference for these phenolics; Zimmer & Topp (2000) observed a positive effect of hydrolyzable tannins on the performance of adult *Porcellio scaber* and *Oniscus asellus*. However, the preferred overwintered and decaying litter (Dunger, 1958; Biwer, 1961*a*, *b*; Hartenstein, 1964*a*; Schneider & Tschakaroff-Schuster, 1978; Rushton & Hassall, 1983*a*; Hassall & Rushton, 1984; Hassall *et al*., 1987) is low in phenolics (Kuiters & Sarink, 1986; Racon *et al*., 1988; Poinsot-Balaguer *et al*., 1993; Zimmer, 2002).

Tylos punctatus Holmes & Gay 1909 (Tylidae), foraging in the intertidal zone during low tide, prefers wrack seaweed (*Macrocystis pyrifera*) over zooplankton (Hayes, 1974). In food-choice tests, the congeneric *Tylos granulatus* preferred dead fish over several algal species (genera *Ulva*, *Laminaria*, *Gigartina*, *Macrocystis*) (Kensley, 1974). In the laboratory, *Ligia pallasii* prefers feeding upon food sources (seaweeds of the genera *Ulva* and *Nereocystis*) that are not easily accessible in the field, while natural food sources (mainly diatoms) were not accepted in the laboratory (Carefoot, 1973). Further, litter of terrestrial plants were not ingested by these isopods – hence, considering this species terrestrial *sensu strictu* may be questioned. Feeding preference was not related to the energy content of the food (Carefoot, 1973). In a recent study, Pennings *et al*. (2000) found evidence for pH and phenolics possibly being significant for food choice in *Ligia pallasii*, while toughness and the content of salts and nitrogen did not affect the preference for stranded seaweed over fresh seaweed. In agreement with Carefoot's (1973) findings, Neuhauser & Hartenstein (1978) did not find any correlation between food choice of several isopod (and diplopod) species and the content of phenolics or water-soluble compounds in the food sources, although Biwer (1961*a*, *b*) did observe a correlation between the nitrogen content of the food and feeding preference in *Porcellio scaber* and *Armadillidium vulgare*. However, she admits that nitrogen and proteins are less important for digestive processes than carbonic compounds of the food (Biwer, 1961*a*, *b*; but see Zimmer & Topp, 2000; Zimmer *et al*., 2001; section V.1).

(4) Foraging

Relatively little is known about foraging and the underlying mechanisms of food choice and food preference. This is, in part, due to the lack in our knowledge regarding the chemoreceptory capabilities of terrestrial isopods. Terrestrial isopods are capable of both contact-perception of solubilized chemicals and distance-perception of air-borne chemicals.

Receptors for contact chemoreception are probably located on the flagellum of the antennae (Henke, 1960; Gupta, 1962; Mead, Gabouriaut & Corbière-Tichané, 1976; Seelinger, 1977; Hoese & Schneider, 1990, as discussed by Zimmer *et al*., 1996) and on the mouthparts (Ábrahám & Wolsky, 1930*b*). Contact chemoreceptors respond to several saccharides, a few amino acids, particular minerals (chloride salts), and to haemolymph and ectocuticular substances of conspecific isopods (Seelinger, 1977, 1983). While foraging, parallel and antiparallel movements of the left and right antennae enable the tips to be dragged along the ground to obtain tactile and chemical information (Hoese &

Schneider, 1990: 'surface probing'), the tip of the antenna being moistened to allow contact chemoreception (Seelinger, 1977; Hoese, 1989; Hoese & Schneider, 1990).

Isopods that are experimentally hindered from contacting potential food sources are capable of orientating towards these food sources (Schneider & Glass, 1993; Zimmer *et al*., 1996). Kensley (1974) suggested isopods of the genus *Tylos* (Tylidae) to be attracted to their food sources by olfactory stimulation. Receptors for distance chemoreception (olfaction) were suspected to be located on the tip of the antennae (Ábrahám & Wolsky, 1929; Fischbach, 1954; Seelinger, 1977; Hoese, 1989), on its terminal segment (Henke, 1960; Schneider & Tschakaroff-Schuster, 1978; Schneider & Glass, 1993), on the antennulae (Ábrahám & Wolsky, 1930*a*; Risler, 1977, 1978; Schneider & Glass, 1993), or on the mouthparts (Schneider & Glass, 1993). Distance chemoreceptors were successfully stimulated with carbonic (fatty) acids, aldehydes, amines, and with grass extracts (Seelinger, 1977, 1983). On a behavioural basis, Zimmer *et al*. (1996) provided evidence for an olfactory response to air-borne microbial metabolites. Based on these results, M. Zimmer & K. Lunau (unpublished data) experimentally tested the contact-chemotactic responses of woodlice to aqueous leaf litter extracts: *Porcellio scaber* and *Oniscus asellus* respond positively to extracts of microbially inoculated litter, but not to extracts of sterilized litter (see Zimmer, in press). Preliminary results even hint on perception of copper (M. Weißenburg, M. Zimmer & K. Lunau, unpublished data), as was also implied by Dallinger's (1977) results showing a preference for copper-rich diet in copper-deficient isopods (section V.1).

Compared to marine Crustacea, antennular chemoreceptors of terrestrial isopods appear to be shorter (Schneider, 1973; Mead *et al*., 1976). This observation is in accordance with an evolutionary reduction in size of the antennula (Risler, 1978; Schmalfuss, 1998), but an increase in the numbers of chemoreceptors (Risler, 1978), so that orientation through the antennulae is still possible after the antennae are attacked by predators (Schmalfuss, 1998). The increasing significance of the antennae for orientation is accompanied by general morphological adaptations, e.g. a reduction in the number of flagellular segments (Hoese, 1989; Schmalfuss, 1998). Increased olfactory capabilities have been postulated to parallel an evolutionary reduction in visual performance (Ábrahám & Wolsky, 1930*a*).

VI. FOOD QUALITY

Food quality can strictly only be defined in terms of consumer fitness (Leather, 1984). The fitness of an individual is, *per definitionem*, determined by individual longevity and reproductive success. Thus, 'food quality' describes physical or chemical food characteristics that positively or negatively affect reproductive success of the consumer.

Since fecundity of female isopods is closely related to their size (Merriam, 1971; Standen, 1973; Sutton *et al*., 1984), growth rates have been used to assess the 'quality' of different food sources. One of the first to point out that growth in terrestrial isopods is not constant, but depends on environmental factors, was Merriam (1971). Growth is greatly affected by the available food source (Merriam, 1971; Sunderland, Hassall & Sutton, 1976; Kheirallah & El-Sharkawy, 1981; Rushton & Hassall, 1983*b*; Kautz *et al*., 2000), and so is mortality (Rushton & Hassall, 1983*b*; Zimmer & Topp, 1997*a*, 2000; Kautz *et al*., 2000). In a few studies, reproductive success was observed directly in terms of the number of released mancae (Rushton & Hassall, 1983*b*; Zimmer & Topp, 1997*a*; Kautz *et al*., 2000). According to these studies and some authors who observed entire populations and the gravidity of single females (Stachurski, 1968, 1972; Merriam, 1971; Zimmer & Topp, 2000), changes in population size also depend on the available food source. Characteristics that affect individual and population development, and thus, determine 'food quality', are closely associated with the microbial colonization of the food (Zimmer & Topp, 1997*a*, 2000; Kautz *et al*., 2000). However, species-specific differences between sympatric species have been found, indicating that *Porcellio scaber* depends only weakly on the tree species the litter originates from (Zimmer & Topp, 1997*a*), and responds more strongly to microbial activity and biomass than does *Oniscus asellus* that, in turn, is affected more strongly by physico-chemical litter characteristics (Zimmer & Topp, 2000). The nitrogen content of the food was described to partially determine the 'food quality' for *Armadillidium vulgare* (Rushton & Hassall, 1983*b*; cf. Biwer, 1961*a*, *b*).

Feeding studies have suggested that no single food source is sufficient from a nutritive point of view, if eaten alone (Rushton & Hassall, 1983*a*), but a mixture of several 'high-quality' food sources will provide optimal nutritional conditions (Rushton & Hassall, 1983*b*; Hassall & Rushton, 1984; Wieser, 1984; Szlávecz, 1993; Dudgeon *et al*., 1990; Ma *et al*., 1991). From this, we can expect self-selection of

optimal food sources to occur, as has been shown for many terrestrial (e.g. Waldbauer & Friedman, 1991, and references therein) and aquatic (e.g. Pennings, Nadeau & Paul, 1993, and references therein) animals. Possible reasons include an imbalance of nutrients in single food sources, as well as unfavourable concentrations of particular deterrents or toxicants.

VII. ECOSYSTEM IMPACTS

The digestive capabilities and characteristics of terrestrial isopods, as discussed above, lead us to conclude that they make both direct and indirect contributions to decomposition processes (Gere, 1956; Biwer, 1961*a*, *b*; White, 1968; Striganova, 1971; Neuhauser & Hartenstein, 1976, 1978; Hassall, 1977*a*; Kozlovskaja & Striganova, 1977; Standen, 1978; Hartenstein, 1982; Gunnarsson & Tunlid, 1986; Hassall *et al*., 1987; Szlávecz, 1993; Kayang *et al*., 1994, 1996; Zimmer & Topp, 1998*b*, *c*; Zimmer, 1999; Kautz & Topp, 2000). Due to their utilization (but see section V.3) of weakly decomposed litter and their digestive capabilities, Biwer (1961*a*, *b*) even stressed the significance of terrestrial isopods in decomposition processes as compared to other soil animals. Although only approximately 5% of the annual litter is consumed by *Philoscia muscorum* in British grassland (Hassall, 1977*a*), the isopods' contribution to ecosystem processes may be significant. Due to cellulose digestion during gut passage (Hartenstein, 1964*a*, 1982; Hassall & Jennings, 1975; Kozlovskaja & Striganova, 1977; Kukor & Martin, 1986; Zimmer & Topp, 1998*b*), the content of recalcitrant compounds is lower in isopod faeces than in leaf litter. Through phenol degradation brought about by isopods or their intestinal microbiota (Zimmer & Topp, 1998*a*; Zimmer, 1999), isopods play a significant role in soil development (Neuhauser & Hartenstein, 1976). In arid regions, burrowing activity of *Hemilepistus* appears to be an important factor in soil formation (Kozlovskaja & Striganova, 1977).

Most investigations have stressed the significance of interactions between soil animals and microbial decomposers (e.g. Biwer, 1961*a*, *b*; Reyes & Tiedje, 1973; Hassall *et al*., 1987; Zimmer & Topp, 1999). By voiding faecal pellets that contain fungal spores and bacterial propagules, isopods contribute to the dispersal of microbiota participating in decomposition processes (Hassall *et al*., 1987; Kayang *et al*., 1994, 1996) and enhance microbial activity (Teuben & Roelofsma, 1990: *Philoscia muscorum*; Kautz & Topp, 2000: *Porcellio scaber*), not only due to comminution and surface area increase (Hassall *et al*., 1987), but also by grazing. Uesbeck & Topp (1995) even suggested a selective promotion of cellulolytic microbiota by *Oniscus asellus*.

Isopods probably compete with other members of the guild of saprophagous soil animals for 'high-quality' food (section VI). It has recently been discussed whether some of the digestive capabilities of terrestrial isopods (sections IV.2 and IV.3) may render them competitively superior to other soil animals (Zimmer, in press). Further, interspecific competition among sympatric isopods may be reduced by species-specific nutritional requirements and digestive capabilities (Zimmer, in press). The resulting intra-guild coexistence through species-specificity appears to be important for ecosystem processes by providing biodiversity without functional redundancy.

VIII. OUTLOOK

The morphology of the mouthparts as well as the anatomy and physiology of the alimentary system represent adaptations of isopods to the terrestrial habitat and their respective food sources. Principal adaptations to terrestrial food sources concern digestive processes, including endogenous enzymes and the utilization of acquired microbial enzymes, and the maintenace of favourable pH conditions for digestion and microbial proliferation. Further prerequisites for the nutritional utilization of terrestrial food sources include the ability to detect food sources by both olfaction and gustation, the development of strong chewing mouthparts, the excretion of volatile ammonia as the nitrogenous waste product, and the shift from the gills to the hindgut for osmoregulation and water budgeting, with particular emphasis on the formation of a typhlosolis. The ability to store copper in the hepatopancreas, and the reduction of the number of hepatopancreatic caeca also seem to have been involved in terrestrialization.

Yet, still many questions remain open. Are the enzymes involved in lignocellulose degradation ingested along with the food, or are they of endogenous origin? If hepatopancreatic endosymbionts are involved in these digestive processes, have symbiotic bacteria been acquired prior to or during the colonization of land? What is the role of phenolic compounds of the leaf litter in isopod nutrition?

What do terrestrial isopods gain from coprophagy? Why do woodlice store copper in hepatopancreatic tissue? These and many other questions warrant further comparative studies on the evolutionary shift from water to land in isopods that might help us to understand general patterns in this important evolutionary step.

IX. CONCLUSIONS

(1) Studying the nutritional biology of terrestrial isopods, particularly in comparison with their marine relatives, provides numerous examples for physiological and ecological adaptations to the food sources available in terrestrial habitats. Many nutritional aspects of terrestrialization, however, remain open to debate, and contrary hypotheses are to be tested.

(2) Consumption and nutritive utilization of terrestrial food sources required evolutionary responses with respect to mouth part morphology and gut anatomy. Species-specific differences in mouth part morphology reflect an evolutionary trend towards more terrestrial food sources. The alimentary tract did not only change in response to terrestrial food sources (e.g. masticatory apparatus, reduction of midgut, typhlosole channels) but also adopted functions in osmoregulation and water balance.

(3) Digestion of terrestrial leaf litter is facilitated by both ingested leaf-litter-colonizing microbiota in the hindgut and hepatopancreatic bacterial endosymbionts. Ingested microbiota are digested in the hindgut and act as nutrient source and in pH maintenance of optimal conditions for enzymatic activity; prior to their digestion, they provide extracellular enzymes that are, in addition to those derived from hepatopancreatic endosymbionts, involved in degradation of leaf litter compounds. Hepatopancreatic bacteria may have been of particular evolutionary significance in facilitating the colonization of terrestrial habitats, since they appear to provide cellulases and phenoloxidases to digest lignocellulose in terrestrial leaf litter. The debate on whether the necessary enzymes for leaf litter degradation are provided by gut microbiota or are endogenously produced remains, however, unsolved. Marine and intertidal ancestors of terrestrial isopods may have had the ability to digest both cellulose and phenolic compounds of the respective food sources, but they probably did not contain hepatopancreatic symbionts; in any way, in terrestrial isopods endogenous enzymes are supplemented by microbial enzymes that may be considered 'functionally endogenous'.

(4) Besides its function in osmoregulation (see above), the hindgut epithelium may be involved in nutrient absorption. The hindgut cuticle is permeable in the anterior section, but less so in the posterior section. Digestively released nutrients may be passed to the hepatopancreas through the hindgut epithelium, or the typhlosole channels and/or an ectocuticular space between hindgut epithelium and cuticle may assist in transporting nutrient-loaded digestive fluids towards the hepatopancreas against the prevailing movement of the food bolus. Nitrogenous waste products are excreted as volatile ammonia, since free water to wash away ammonia is not available in terrestrial habitats. The evolutionary retention of ammonotelism may have facilitated terrestrialization due to low energetic costs.

(5) Little is known about nutritional requirements of terrestrial isopods. The digestion of ingested microbiota may provide essential nutrients. Copper appears to be important with respect to the degradation of phenolics through microbial phenoloxidases; the ability to extract copper from sea water and/or food *via* the hindgut epithelium may have been a pre-adaptation of marine ancestors. The storage of vast amounts of copper in hepatopancreatic tissue is presumably a trade-off between nutritional requirements and the avoidance of copper intoxification. Coprophagy is discussed in the context of low digestibility of terrestrial leaf litter, but its nutritive significance is controversial. In any way, the digestibility of leaf litter mediates feeding preferences of terrestrial isopods, as do leaf-litter-colonizing microbiota. Chemical and microbial leaf litter characteristics are probed through chemoreception; in adaptation to their habitat, terrestrial isopods are capable of both distance (olfaction) and contact (gustation) chemoreception, and antennae and antennulae have evolved accordingly.

(6) The dependence of growth, repdroduction and mortality on leaf-litter-colonizing microbiota stresses their nutritive significance. Probably, the evolutionary adaptations of terretrial isopods to terrestrial food sources include the nutritive utilization of microbiota as source of digestive enzymes and of essential nutrients.

(7) Due to their feeding activity and their digestive capabilities, terrestrial isopods contribute to decomposition processes by degrading leaf litter and by promoting microbial activity. Microbial population dynamics during the gut passage result in densely colonized faeces; probably one reason for

coprophagous behaviour in evolutionary response to food sources of low digestibility.

(8) After more than a hundred years of research in nutritional biology of isopods, the evolutionary ecological approach of explaining ecological and physiological traits in the context of adaptations to environmental constraints and trade-offs between conflicting interests proved to be valuable in answering so far unanswered questions. Understanding the nutritional biology of terrestrial isopods may help us to understand underlying mechanisms of the colonization of terrestrial habitats by aquatic organisms.

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