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The role of animal-microbe interactions in isopod ecology and evolution*

Die Bedeutung tierlich-mikrobieller Wechselwirkungen für die Ökologie und Evolution von Asseln

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Summary: Due to their world-wide distribution in marine and terrestrial (as well as freshwater) habitats, the order Isopoda (Crustacea: Malacostraca: Peracarida) provides an excellent model for the evolutionary ecology of terrestrialization.
(1) Terrestrial isopods (Oniscidea) harbor endosymbiotic bacteria in their midgut glands (hepatopancreas) that are lacking in marine isopods of the suborders Valvifera and Sphaeromatidea, considered being (part of) a sister taxon of Oniscidea. Thus, these bacterial endosymbionts seem to be significant in the context of living in terrestrial habitats and may have been important during the course of terrestrialization. In "truly terrestrial" species (Crinocheta), two different endosymbionts have been characterized that are distantly related to known parasites and pathogens of the orders Rickettsiales and Mycoplasmatales, respectively. Both these endosymbionts form cytoplasmic appendages that are in contact with the host epithelium and may serve in the exchange of nutrients and information and or serve as holdfasts. In non-crinochete terrestrial isopods (Diplocheta, Tylida, Synocheta), hepatopancreatic bacteria belong to the genus *Pseudomonas*.
Both marine and freshwater Asellota also harbor bacteria in their midgut glands. The lack of bacteria in other marine suborders (as studied so far) may be due to antibiotic agents in these isopods. Based on the present findings, I propose a common (marine) ancestor of Asellota and Oniscidea that acquired the ability to harbor bacterial endosymbionts inside the hepatopancreas. While symbiotic relationships remained unspecific in marine Asellota, they developed towards specific primary symbioses with bacteria that aid in digesting cellulosic and phenolic compounds, and thus, facilitate the utilization of terrestrial food sources in semi-terrestrial and terrestrial Oniscidea and in freshwater Asellota. I, further, hypothesize that later during early phylogeny of Crinocheta, primary symbionts have been replaced by secondary endosymbionts that are still characteristic of recent Crinocheta.
In contrast to previous studies, suggesting a role of hepatopancreatic bacteria in nutrition, our present knowledge does not provide any evidence for crinochete symbionts to supply any digestive enzymes to their isopod host. However, *Pseudomonas* spp. are well-known to degrade both cellulosic and phenolic compounds. Thus, I hypothesize that, while primary symbionts of Oniscidea provide cellulases and/or phenol oxidase, a transfer of cellulase and/or phenol oxidase genes from symbiont to host occurred in early Crinocheta, resulting in endogenous cellulase of evolutionarily bacterial origin. Besides (a) providing enzymes for the digestion of leaf litter, further possible contributions of hepatopancreatic endosymbionts to their host's physiological constitution and fitness include (b) increasing the availability of nitrogen on a nitrogen-poor food source, (c) protecting their host from secondary (pathogenic) infection, (d) protecting their host from predatory attack, or (e) increasing fertility, mating success and fecundity of their host – these hypotheses are briefly discussed.

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(2) Terrestrial isopods interact with leaf litter-colonizing microbiota that they ingest along with their major food source. While, however, it is well-documented that isopods gain from feeding on microbially inoculated leaf litter, reasons for this dependence are not well understood. Possibly, (a) microbiota serve as supplementary high-quality food source and provide essential or otherwise limiting nutrients; (b) microbiota promote digestion of leaf litter itself, either prior to ingestion or during the gut passage; (c) microbiota simply act as indicators of easily digestible food sources of high quality. These explanations are not mutually exclusive, and the prevailing reason for preferentially consuming microbially inoculated leaf litter depends on both the species and developmental stage of the isopod and the nutritional context, i.e. the food source as such; recent results, however, indicate that cellulolytic capabilities of litter-colonizing microbiota [see (b)] may be less significant than previously thought, while a role of litter-colonizing microbiota in indicating high-quality food [see (c)] is supported. The ability to digestively utilize microbial cells as supplementary food [see (a)] depends on cell wall characteristics as indicated by gram-staining of the microbes, gram-positive bacteria being digested more effectively than gram-negative bacteria and fungi, and being preferred as food source.
Despite numerous studies, the most recent ones using modern molecular techniques, it is still debated whether or not terrestrial isopods harbor resident gut microbes in their hindgut. Most hindgut bacteria that may be candidates for hindgut residents appear to belong to gram-negative bacterial taxa, and are taxonomically related to anaerobic species. Thus, we have to assume anoxic microhabitats in cuticular wrinkles. Further, the radial center of the hindgut is anoxic, too, allowing for fermentative digestive processes, while the periphery of the hindgut lumen is largely oxic and oxidizing, thus, allowing for aerobic and oxidative digestive processes. These processes are promoted through cell compounds of ingested microbiota resulting in homeostatic maintenance of a slightly acidic pH that is optimal for the activity of involved enzymes. Potentially harmful effects of phenolic food compounds that are likely under such conditions are counteracted through hydrolytic enzymes and surfactants of microbial origin.
In conclusion, our up-to-date knowledge as summarized and discussed herein strongly confirms the assumption that (terrestrial) isopods strongly depend on microbial activity and nutrients for their capability of digestively utilizing terrestrial leaf litter; on an evolutionary scale, this dependence may indicate the role that microbiota played during the course of terrestrialization, although this aspect of isopod-microbe interactions is far from being understood.

Isopoda, terrestrialization, nutrition, digestion, endosymbiotic bacteria, symbiont-host interactions, leaf litter-colonizing microorganisms, decomposition

Zusammenfassung: Aufgrund ihrer weltweiten Verbreitung in marinen und terrestrischen (sowie limnischen) Lebensräumen eignet sich die Ordnung Isopoda (Crustacea: Malacostraca: Peracarida) hervorragend als Modell für die Evolutionsökologie des Landgangs.
(1) Landasseln (Oniscidea) beherbergen endosymbiotische Bakterien in ihren Mitteldarmdrüsen (Hepatopankreas), die ihren marinen Verwandten der Unterordnungen Valvifera und Sphaeromatidea – beide als (Teil einer) Schwestergruppe der Oniscidea betrachtet – fehlen. Demnach scheinen diese bakteriellen Endosymbionten von Bedeutung für die Besiedlung terrestrischer Habitate zu sein und könnten während der Terrestrialisierung eine wichtige Rolle übernommen haben. In "höheren Landasseln" (Crinocheta) konnten wir zwei verschiedene Endosymbionten charakterisieren, die entfernt mit bekannten Parasiten und Pathogenen der Ordnungen Rickettsiales und Mycoplasmatales verwandt sind. Beide bilden cytoplasmatische Zellfortsätze aus, die in Kontakt mit dem Wirtsepithel treten und entweder am Austausch von Nährstoffen und Information beteiligt sind oder als Verankerung dienen. In „niederen Landasseln" (Diplocheta, Tylida, Synocheta) gehören die Endosymbionten in den Mitteldarmdrüsen zur Bakteriengattung *Pseudomonas*.
Auch Asellota – sowohl marine als auch limnische – beherbergen Bakterien in ihren Mitteldarmdarmdrüsen. Das Fehlen dieser Bakterien in den bislang untersuchten anderen marinen Unterordnungen ist möglicherweise auf antibiotische Agenzien in diesen Asseln zurückzuführen. Daher schlage ich einen gemeinsamen (marinen) Vorfahren der Asellota und Oniscidea mit der Fähigkeit,

bakterielle Symbionten im Hepatopankreas zu beherbergen vor. Während die daraus resultierende Endosymbiose in marinen Asellota unspezifisch blieb, entwickelte sie sich in limnischen Asellota und semi-terrestrischen – und später terrestrischen – Oniscidea zu einer primären spezifischen Beziehung mit Bakterien, die den Abbau cellulosischer und phenolischer Verbindungen ermöglichen, und damit die Verdauung von Laubstreu erleichtern. Zudem vermute ich, dass später – während der frühen Phylogenie der Crinocheta – primäre Endosymbionten durch sekundäre Endosymbionten, die rezent in Crinocheta anzutreffen sind, ersetzt wurden.
Im Gegensatz zu früheren Untersuchungen, die eine Rolle der Bakterien im Hepatopankreas bei Verdauungsvorgängen postulierten, gibt es nach heutigem Stand keinerlei Hinweise auf entsprechende Enzyme in den Endosymbionten der Crinocheta. *Pseudomonas* spp. dagegen sind wohl bekannt für ihre Fähigkeit, cellulosische und phenolische Verbindungen abzubauen. Ich stelle also die Hypothese auf, dass primäre Endosymbionten ihrem Wirt Cellulasen und/oder Phenoloxidasen zur Verfügung stellen, vor dem evolutiven Austausch der Symbionten aber ein Gentransfer zwischen primären Endosymbionten und Wirt stattfand, so dass „höhere Landasseln" endogen über diese Enzyme verfügen. Verschiedene Beiträge der Endosymbionten zur Konstitution ihres Wirtes sind vorstellbar: (a) die Lieferung von Verdauungsenzymen, (b) eine erhöhte Stickstoffverfügbarkeit auf stickstoffarmer Nahrung, (c) Schutz vor (pathogenen) Sekundärinfektionen, (d) Schutz vor Fressfeinden, oder (e) Steigerung von Fertilität, Verpaarungserfolg und Fekundität. Diese Hypothesen werden kurz diskutiert.
(2) Landasseln interagieren mit Streu besiedelnden Mikroorganismen, die sie gemeinsam mit ihrer Hauptnahrungsquelle aufnehmen. Während aber wohl bekannt ist, dass Asseln davon profitieren, mikrobiell besiedelte Streu zu fressen, sind die Gründe hierfür nur unzureichend verstanden. Möglicherweise (a) dienen Mikroorganismen als zusätzliche hochwertige Nahrungsquelle und liefern essenzielle oder anderweitig limitierende Nährstoffe, (b) fördern Mikroorganismen die Verdauung der Laubstreu entweder vor der Konsumption oder während der Darmpassage oder (c) Mikroorganismen fungieren lediglich als Indikatoren leicht verdaulicher Nahrung hoher Qualität. Diese Erklärungen schließen sich nicht gegenseitig aus. Der Hauptgrund für eine Präferenz für mikrobiell besiedelte Laubstreu hängt sowohl von der Art und dem Stadium der Asseln, als auch von der Nahrungsquelle ab. Aktuelle Ergebnisse deuten jedoch an, dass cellulolytische Fähigkeiten Streu besiedelnder Mikroorganismen [siehe (b)] weniger bedeutend sind als bislang angenommen, während eine Rolle der Mikroorganismen als Indikatoren hochwertiger Nahrung [siehe (c)] wahrscheinlich erscheint. Die Fähigkeit der Assel, Streu besiedelnde Mikroorganismen als zusätzliche Nahrungsquelle zu nutzen [siehe (a)], hängt von deren Zellwandeigenschaften, die durch Gramfärbung angezeigt werden, ab; gram-positive Bakterien werden effizienter verdaut als gram-negative Bakterien und Pilze und zugleich als Nahrung bevorzugt.
Trotz zahlreicher Untersuchungen mit klassischen und molekularbiologischen Methoden wird bis heute kontrovers diskutiert, ob Landasseln residente mikrobielle Enddarmbewohner beherbergen. Die meisten Kandidaten scheinen zu gram-negativen Taxa zu gehören und mit Anaerobiern verwandt zu sein. Demnach müssen wir anoxische Mikrohabitate in Kutikularfalten annehmen. Außerdem ist auch das radiäre Zentrum des Enddarms anoxisch und ermöglicht fermentative Verdauungsprozesse, während die Bedingungen an der Peripherie oxisch und oxidierend sind, also aerobe und oxidative Verdauungsvorgänge ermöglichen. Derartige Prozesse werden durch pH-Homoiostasis infolge der Freisetzung mikrobieller Zellinhaltsstofe ermöglicht, die den pH-Wert in einem optimalen Bereich für die entsprechenden Enzymaktivitäten konstant halten. Potenziell schädlichen Wirkungen phenolischer Nahrungsbestandteile, die unter solchen Bedingungen wahrscheinlich wären, wirken hydrolytische Enzyme und Detergenzien mikrobiellen Ursprungs entgegen.
Zusammenfassend bestätigt unser heutiges Wissen, das in diesem Beitrag zusammengefasst und diskutiert wird, die ausgeprägte Abhängigkeit der Landasseln von mikrobiellen Nährstoffen und Enzymen für ihre Fähigkeit, sich von Laubstreu zu ernähren. In evolutivem Maßstab mag diese Abhängigkeit die bedeutende Rolle widerspiegeln, die Mikroorganismen während der Terrestrialisierung spielten, obwohl dieser Aspekt tierlich-mikrobieller Interaktionen kaum verstanden ist.

Isopoda, Asseln, Landgang, Ernährung, Verdauung, endosymbiotische Bakterien, Wirt-Symbiont Wechselwirkungen, Laubstreu besiedelnde Mikroorganismen, Dekomposition

1. Introduction

Adaptive are those characteristics of an organism that increase an individual's fitness relative to that of its conspecifics. Thus, the respective characteristics will become more and more frequent in the next generations and will eventually become a common feature of (almost) the entire population (e.g. FUTUYMA 1986).

Due to "formal constraints" (GOULD 1989; = "universal constraints" introduced by MAYNARD SMITH et al. 1985) and "historical constraints" (GOULD 1989; = "local constraints" of MAYNARD SMITH et al. 1985), however, adaptation is not necessarily complete or even optimal. On the other hand, other characteristics of organisms – having been termed "pre-adaptation" (OSCHE 1962), "exaptation" GOULD & VRBA (1982), or "pre-disposition" (see SUDHAUS & REHFELD 1992) – that are adaptive under recent conditions have been adopted from ancestors to whom they may or may not have been adaptive when they developed. Some of these pre-dispositions may have been significant for the colonization of land *via* the intertidal by animals with marine ancestors. Due to the high number of recent marine (ca 4,300), terrestrial (ca 3,500) and freshwater (ca 650) species of isopods (Crustacea: Malacostraca: Peracarida), this order (Isopoda) provides a valuable model in helping us understand the evolutionary ecology of terrestrialization.

The terrestrial environment exhibits numerous obstacles to hamper its colonization. Required adaptations comprise the structural rigidity of the body, including increased strength of extremities, the structure and function of respiratory organs, water budget and osmo- and thermoregulation, reproductive and developmental strategies, and many more. In addition, terrestrial food sources (plants and parts of them, in case of herbivores and detritivores) differ from aquatic food sources in terms of physical and chemical characteristics. Several excellent reviews have been published (e.g., EDNEY 1954, 1968; HARTENSTEIN 1968; WIESER 1968, 1984; WARBURG 1968, 1987; SCHMALFUSS 1984, 1998; CAREFOOT 1993) that describe morphological, anatomical, physiological and ethological adaptations and pre-dispositions of (terrestrial) isopods, but both reproductive (cf. ZIMMER 2001) and nutritive (cf. ZIMMER 2002a) biology of terrestrial isopods have been regarded rarely. In particular, interactions of isopods with both environmental and endosymbiotic microbiota and their potential contributions to digestive processes is far from being understood. This review aims to summarize our current knowledge extended by some unpublished data of the author and his coworkers on the significance of animal-microbe interactions in ecology and evolution of terrestrial isopods.

2. Terrestrial food sources

For most terrestrial detritivores, the carbon in plant tissue is not easily accessible, since most of it is part of recalcitrant cellulose molecules (KOZLOVSKAJA & STRIGANOVA 1977; SZEGI 1988; BREZNAK & BRUNE 1994). The degradation of native (crystalline) cellulose is thought to usually be brought about by a complex of three enzyme classes (REESE & MANDELS 1971; ERIKSSON 1978; ERIKSSON & WOOD 1985) that have been demonstrated in cellulolytic Protozoa (TRAGER 1932; YAMIN & TRAGER 1979) and fungi (LJUNGDAHL & ERIKSSON 1985). Endo-β-1,4-glucanases (endocellulases, C_x-cellulases, EC 3.2.1.4) cleave inner β-1,4-glucosidic bounds and release oligosaccharides that, in turn, are cut into cellobiose by cellobiohydrolases (exo-β-1,4-glucanases, exocellulases, C_1-cellulases, EC 3.2.1.91). Cellobiose is the substrate of β-1,4-glucosidases (cellobiases, EC 3.2.1.21) that produce two molecules of glucose. Since exocellulases could be demonstrated in only few bacteria (RAPP

& Beermann 1991), Ljungdahl & Eriksson (1985) suggest the existence of only two bacterial enzymes (corresponding to fungal endocellulases and cellobiases) that appear to be cell wall-bound (Wood & Garcia-Campayo 1990). Cellulolysis by anaerobic bacteria – the radial center of the isopod hindgut is anoxic (Zimmer & Brune, 2005) – is brought about by cellulosomes (summarized in Leschine 1995), consisting of several enzymes with endo- and exocellulase activity and additional proteins that act as structural components or serve in binding the substrate.

The degradation of cellulose is further constrained through its close association with lignins (e.g. Ljungdahl & Eriksson 1985; Breznak & Brune 1994), high-molecular phenolic polymers with a high degree of methoxylation (Swain 1979; Hagerman & Butler 1991), that can only be degraded through oxidation (Breznak & Brune 1994; Trojanowski 2001). Numerous different enzyme classes are known to be involved in oxidative degradation of phenolic compounds (Ander & Eriksson 1976; Wood 1980; Mayer 1987; Claus & Filip 1990; Summers & Felton 1994; Thurston 1994; Faure et al. 1995), all of them containing a central metal ion (Evans et al. 1991).

Abe & Higashi (1991) summarized their up-to-date knowledge by proposing that most (if not all) animals do not possess endogenous cellulases. However, Hartenstein (1964, 1982) had suggested earlier that several terrestrial isopods (Isopoda: Oniscidea) of the monophylum Crinocheta do produce such enzymes [(Hartenstein 1964: *Oniscus asellus* Linnaeus, 1758 (Oniscidae); Hartenstein 1982: *Oniscus asellus*, *Trachelipus rathkii* (Brandt, 1833) (Trachelipodidae), *Armadillidium vulgare* (Latreille, 1804) (Armadillidiidae)]. On the other hand, subsequent studies agreed with Abe & Higashi (1991) in that they suggested that woodlice depend upon cellulases produced by litter-colonizing microbiota (Hassall & Jennings 1975; Kozlovskaja & Striganova 1977), or at least utilize fungal cellulases for cellulose degradation (Kukor & Martin 1986). During their studies on the gut physiology of *Porcellio scaber* Latreille, 1804 (Porcellionidae), Zimmer & Topp (1998a) discovered contrasting data on cellulase activity and microbial counts in the hindgut: while the anterior hindgut – in accordance with findings by Hassall & Jennings (1975) in *Philoscia muscorum* (Scopoli, 1763) ("Philosciidae") – exhibited the highest cellulolytic activity, it also contained the lowest density of bacteria and fungi (Zimmer & Topp 1998a,b). Further, in contrast to Hassall & Jennings (1975), but in agreement with Hartenstein (1964a), cellulase activity was 3-30-times higher in the midgut glands (hepatopancreas) than in the leaf litter, and thus, could not be attributed to enzymes ingested along with the food (Zimmer & Topp 1998a,b) as had been suggested by Hassall & Jennings (1975). As had already been proposed on theoretical grounds (Hopkin & Martin 1982), Zimmer & Topp (1998b) concluded from results of feeding experiments with artificial diets and antibiotics that cellulases are produced by bacterial endosymbionts inhabiting the lumen of the hepatopancreas (fig. 1), or even by the isopod endogenously (cf. Hartenstein 1964a). These enzymes shall, thus, be considered "functional endogenous" (cf. Zimmer 2002a).

With respect to the origin of enzymes involved in the oxidative degradation of lignins and other phenolic compounds in the guts of invertebrates, there is little agreement either. Doubtlessly, phenol oxidases are produced by arthropods, but these enzymes are mostly required for molting (e.g., Anderson 1985) and immune response (e.g., Gillespie et al. 1997). Woodlice (*Porcellio scaber* and *Oniscus asellus*) produce endogenous enzymes that are active in degrading polycyclic aromatic hydrocarbons (PAHs) (deKnecht et al. 2001), and phe-

nolic leaf litter compounds are oxidized during the gut passage (NEUHAUSER & HARTENSTEIN 1976; ZIMMER & TOPP 1998c; ZIMMER 1999). Questing for ecophysiological reasons for isopods storing vast amounts of copper in their midgut glands (discussed in ZIMMER 2002a), ZIMMER & TOPP (1998c) performed feeding experiments with artificial diets and antibiotics to observe correlations between numbers of hepatopancreatic bacteria and phenol oxidase activity in the hindgut of *Porcellio scaber*; the copper store appears to be significant for the production of copper-containing phenol oxidases (see fig. 1).

Leaf litter, the natural food source of woodlice, is usually densely colonized by microbiota, and woodlice were frequently proven to depend upon these microbiota with respect to growth, reproduction and mortality; thus, woodlouse populations are strongly influenced by the biomass and/or activity of leaf litter-colonizing microbiota (UESBECK & TOPP 1995; ZIMMER & TOPP 1997a, 2000; KAUTZ et al. 2000). Hence, woodlice prefer feeding on densely colonized leaf litter (GUNNARSSON 1987; SOMA & SAITO 1983; STÖCKLI 1990) that is localized through olfaction (ZIMMER et al.

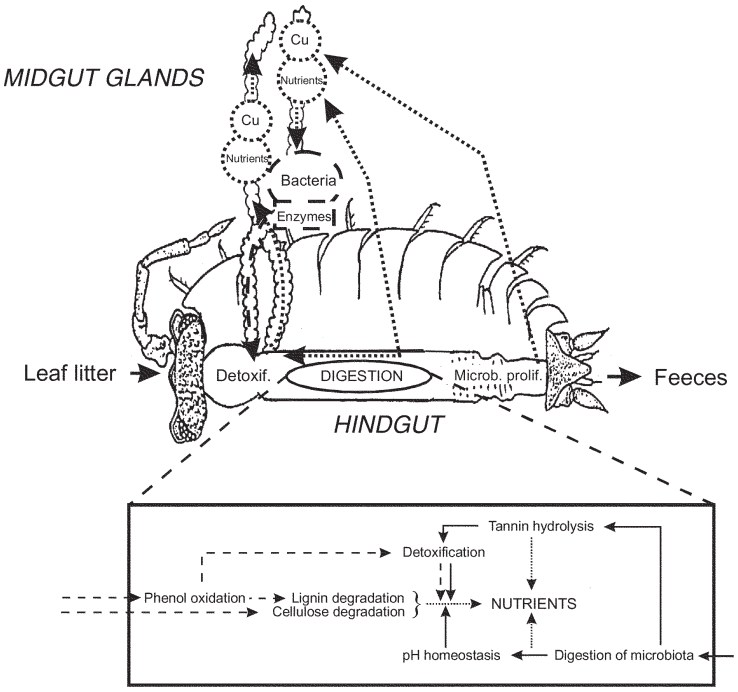

Fig. 1: Digestive processes in the hindgut of *Porcellio scaber* (Porcellionidae) (modified after ZIMMER 1998), including the ingestion of leaf litter, detoxification of ingestion phenolics (Detoxif.) in the foregut, digestion in the anterior hindgut through the activity of endogenous and bacterial enzymes, absorption of nutrients and copper, microbial proliferation (Microb. prolif.) in the posterior hindgut, and egestion of feces. See ZIMMER (2002a) for details.

Abb. 1: Verdauungsprozesse im Enddarm von *Porcellio scaber* (Porcellionidae) (verändert nach ZIMMER 1998), einschließlich der Aufnahme von Laubstreu, der Entgiftung phenolischer Inhaltsstoffe (Detoxif.) im Vorderdarm, der Verdauungsvorgänge im vorderen Enddarm durch die Aktivität endogener und mikrobieller Enzyme, der Resorption von Nährstoffen und Kupfer, der mikrobiellen Vermehrung (Microb. prolif.) im hinteren Enddarm, und der Ausscheidung von Faeces. Für weitere Details, siehe ZIMMER (2002a).

1996). Possible reasons for the significance of litter-colonizing microbiota can be subsumed as follows: (1) Microbial biomass serves as source of readily digestible (essential) nutrients (Reyes & Tiedje 1976; Martin 1984; Swift & Boddy 1984; Gunnarsson & Tunlid 1986; Carefoot 1984a,b; Ullrich et al. 1991); (2) microbial extracellular enzymes that are ingested along with the leaf litter (partly) degrade the ingested lignocellulose (Hassall & Jennings 1975; Kukor & Martin 1986); (3) microbial procession of leaf litter removes recalcitrant compounds (e.g., lignocellulose) prior to consumption by woodlice, thus facilitating digestion (Hartenstein 1964a; Rushton & Hassall 1983; Hassall et al. 1987).

Without any doubt, microbial extracellular enzymes are active in the hindgut of woodlice (fig. 1), but their role in digestive processes has been questioned (e.g., Zimmer & Topp 1998b,c). Recent results suggest that litter-colonizing microbiota mainly serve as indicators of high food quality to foraging woodlice (Zimmer et al. 2003a), but obviously, digestive processes are also somehow promoted through ingested microbiota (fig. 1). Possible reasons for this observation are (1) homeostasis of a gut pH (5.5-6.5) that is optimal for the activity of cellulases and phenol oxidases through cellular compounds of digested microbiota (Zimmer & Topp 1997b); (2) avoidance of toxic effects of phenolic litter compounds, being likely under the prevailing pH conditions (Berenbaum 1980; Martin & Martin 1983; Schultz & Lechowicz 1986) through (a) hydrolysis of hydrolyzable tannins through enzymes of microbial origin (Zimmer 1999), or (b) precipitation of phenolics through surfactants of possibly microbial origin (Zimmer 1997).

The above-mentioned aspects of isopod-microbe interactions will be discussed in detail in turn.

3. Bacterial endosymbionts

3.1 General remarks

About 25 years after the first report of bacteria in the midgut glands of terrestrial isopods (Donadey & Besse 1972), Zimmer & Topp (1998b,c) found correlations between bacterial numbers and enzymatic activities in the context of lignocellulose degradation (see fig. 1). Based on these results, they proposed that hepatopancreatic endosymbionts of isopods facilitated or even made possible the colonization of land through their contribution to the digestive utilization of terrestrial food sources (cf. Zimmer et al. 2001, 2002a). According to their original hypothesis, these endosymbionts would have been acquired once by a common ancestor of all oniscid isopods. In coincidence, bacterial endosymbionts have been found in midgut glands of numerous species of Oniscidea (tab. 1), but not in marine Valvifera [Zimmer et al. 2001: *Idotea wosnesenskii* (Brandt, 1851) (Idoteidae); Wang, Stingl, Brune & Zimmer, in review: *Idotea balthica* (Pallas, 1772) (Idoteidae)] or Sphaeromatidea [Sleeter et al. 1978: *Limnoria tripunctata* Menzies, 1951 (Limnoriidae); Zimmer et al. 2001: *Gnorimosphaeroma oregonense* (Dana, 1853) (Sphaeromatidae); Zimmer & Fraune, unpubl.: *Sphaeroma rugicauda*)]. In contrast, midgut glands of the freshwater isopod, *Asellus aquaticus* (Linnaeus, 1758) (Asellota: Asellidae), harbor bacterial endosymbionts that apparently provide cellulolytic and phenol-oxidizing enzymes (Zimmer & Bartholmé 2003). The authors conclude from their results that Oniscidea and freshwater Asellota – feeding on the same food source, terrestrial leaf litter – acquired such endosymbionts during convergent evolution. However, we recently found hepatopancreatic bacteria in marine Asellota, *Jaera albifrons* Leach, 1814 (Janiridae) and *Eurycope cornuta* Sars, 1864 (Eurycopidae) (Zimmer & Fraune, unpubl.), suggesting a

Tab. 1: Selected characteristics of hepatopancreatic bacteria in different isopod species.
Tab. 1: Ausgewählte Eigenschaften der Bakterien im Hepatopankreas verschiedenen Asselarten.

Species	Shape	Size (µm)	Density (cells per hep.)	Gram type	Affiliation	Reference
Asellus aquaticus	rod-shaped	(2.4 - 5.1) x 0.7	(0.3 - 1.7) 10^6	negative	*Rhodobacter*[a)]	1
	n.d.	n.d.	n.d.	negative	*Burkholderia*[b)]	1
	rod-shaped	1.2 x 0.8	(1.2 - 2.9) 10^6	negative	*Aeromonas*[c)]	1
	n.d.	n.d.	n.d.	negative	*Rickettsiella*[c)]	1
	n.d.	n.d.	ca 106	n.d.	n.d.	2
Eurycope cornuta	rod-shaped	n.d.	(2 - 5) x 10^5	n.d.	?	3
	coccoid	n.d.	n.d.	n.d.	?	3
Jaera albifrons	rod-shaped	n.d.	10^4 - 10^5	n.d.	?	3
Ligia oceanica	rod-shaped	n.d.	(1 - 2) 10^7	negative	*Pseudomonas*[c)]	4
Ligia pallasii	coccoid	n.d.	(2.5 - 3.5) x 10^6	n.d.	n.d.	5
	coccoid	n.d.	10^6 - 10^7	n.d.	n.d.	6
Ligidium hypnorum	rod-shaped	n.d.	(1 - 2) 10^6	negative	*Pseudomonas*[c)]	3
Tylos ponticus	rod-shaped	n.d.	(2 - 5) 10^6	negative	*Pseudomonas*[c)]	3
	coccoid	n.d.	10^6 - 10^7	n.d.	?	3
Hyloniscus riparius	rod-shaped	n.d.	(1 - 3) 10^6	negative	*Pseudomonas*[c)]	3
	ellipsoid	n.d.	n.d.	n.d.	?	3
Trichoniscus pusillus	rod-shaped	n.d.	(1 - 4) 10^6	negative	*Pseudomonas*[c)]	3
	ellipsoid	n.d.	n.d.	n.d.	?	3
Alloniscus perconvexus	rod-shaped	n.d.	(5 - 20) x 10^4	n.d.	n.d.	3
	coccoid	(0.4- 0.6) + (1.0 - 1.5)	(1 - 3) x 10^{11}	negative	Mycoplasmatales[d)]	6
Oniscus asellus	rod-shaped	n.d.	n.d.	n.d.	n.d.	7
	rod-shaped	(3.2 ± 2.2) x 0.3	n.d.	positive	n.d.	8
	rod-shaped	n.d.	n.d.	negative	Enterobacteriaceae[c)]	9
	rod-shaped	(0.7 - 1.1) x 0.5	10^5 - 10^8	negative	γ-Proteobacteria	6
	curved rods	(1.5 - 3.8) x 0.5	10^4 - 10^8	negative	Rickettsiales[a)]	4
	coccoid	0.4 - 0.6	10^4 - 10^8	negative	Mycoplasmatales[d)]	4
	coccoid	1.0 - 1.5	10^4 - 10^7	negative	Mycoplasmatales[d)]	4
	filamentous	10 - 37.5	n.d.	positive	n.d.	8
	filamentous	(4 - 18) x 0.6	10^4	n.d.	n.d.	6
Philoscia muscorum	coccoid	(0.4- 0.6) + (1.0 - 1.5)	(0.6 - 22) x 10^7	negative	Mycoplasmatales[d)]	6
Porcellio dilatatus	rod-shaped	n.d.	n.d.	n.d.	n.d.	10
Porcellio scaber	rod-shaped	(2.0 ± 1.0) x 0.3	n.d.	positive	n.d.	8
	rod-shaped	bis zu 10	n.d.	n.d.	n.d.	11
	rod-shaped	ca 2	ca 104	negative	n.d.	12
	rod-shaped	(0.7 - 1.0) x 0.5	10^5 - 10^7	negative	γ-Proteobacteria	6
	curved rods	(1.5 - 3.8) x 0.5	10^4 - 10^7	negative	Rickettsiales[a)]	13
	coccoid	0.4 - 0.6	10^4 - 10^7	negative	Mycoplasmatales[d)]	14
	coccoid	1.0 - 1.5	10^4 - 10^8	negative	Mycoplasmatales[d)]	14
	coccoid	ca 0.5	ca 104	weakly positive?	n.d.	12
	filamentous	12 µm and more	n.d.	positive	n.d.	8
	filamentous	10 - 20	ca 107	n.d.	n.d.	12
	filamentous	(4 - 18) x 0.6	10^4 - 10^6	n.d.	n.d.	6
Trachelipus rathkii	curved rods	(1.5 - 3.8) x 0.5	(1 - 2) x 10^8	negative	Rickettsiales[a)]	6
	coccoid	(0.4- 0.6) + (1.0 - 1.5)	(2 - 4) x 10^6	negative	Mycoplasmatales[d)]	6
	filamentous	n.d.	10^4	n.d.	n.d.	6
Armadillidium vulgare	coccoid	(0.4- 0.6) + (1.0 - 1.5)	(3 - 4) x 10^8	negative	Mycoplasmatales[d)]	6
	filamentous	n.d.	(0.5 - 40) x 10^5	n.d.	n.d.	6

[a)]: α-Proteobacteria; [b)]: β-Proteobacteria; [c)]: γ-Proteobacteria; [d)]: Mollicutes; n.d.: not determined; ?: determination unsuccessful; 1: WANG, BRUNE & ZIMMER, in review; 2: ZIMMER & BARTHOLMÉ 2003; 3: FRAUNE & ZIMMER, unpubl.; 4: WANG, STINGL, BRUNE & ZIMMER, in review; 5: ZIMMER et al. 2001; 6: WANG & ZIMMER unpubl.; 7: HOPKIN & MARTIN, 1982; 8: WOOD & GRIFFITHS, 1988; 9: ULLRICH et al. 1991; 10: DONADEY & BESSE 1972; 11: HAMES & HOPKIN 1989; 12: ZIMMER 1998; 13: WANG et al. 2004a; 14: WANG et al. 2004b.

common ancestor of Oniscidea and Asellota (see below).

With respect to cellulose hydrolysis and phenol oxidation in isopods, ZIMMER et al. (2002a) discuss two evolutionary scenarios: First, the ability to digest cellulose and oxidize phenolics may have been acquired simultaneously with other physiological adaptations (cf. CAREFOOT 1993) that allowed colonization of land. In this case, these adaptations would be lacking from marine isopods. Second, the ability to digest cellulose and oxidize phenolics may have been a predisposition to the colonization of land. In this case, these capabilities would be present at least in some marine species. At least

those marine isopods that feed on brown algae (Phaephycota) ingest considerale amounts of phenolics (see ZIMMER et al. 2001), while consumers of green algae (Chlorophycota) have to face relatively high cellulose contents of their food (VINOT et al. 1987; RUPEREZ & SAURA-CALIXTO 2001). Therefore, there would be a selective advantage to the ability to digest cellulose and phenolics in many marine isopods (cf. ZIMMER et al. 2001). If, however, the digestion of seaweed phenolics does not require their oxidation – in contrast to lignins (see above) – the disadvantages of potentially harmful oxidation products (AHMAD 1992; APPEL 1993) would likely constrain the evolution of phenol-oxidizing capabilities in marine isopods. Comparing the intertidal *Idotea wosnesenskii*, *Gnorimosphaeroma oregonense* and the semi-terrestrial *Ligia pallasii* Brandt, 1833 (Oniscidea), we revealed evidence for the ability to hydrolyze cellulose and oxidize phenolics in intertidal and semi-terrestrial isopods (ZIMMER et al. 2002a), and ZIMMER et al. (2002b) conclude from their comparison of semi-terrestrial and terrestrial isopods in a U.S. saltmarsh that phenolics in terrestrial leaf litter have not been an obstacle to colonizing land and utilizing this food source. However, intertidal and semi-terrestrial isopods differ in their abilitiy to both hydrolyze cellulose and oxidize phenolics, exhibiting a clear gradient of increasing digestive capabilities with terrestriality of the species' food sources – *Idotea wosnesenskii*, preferentially feeding on brown algae (*Fucus* spp.), do not oxidize phenolics, thus preventing potentially harmful effects of phenolic oxidation products.

On the other hand, as stated above, hepatopancreatic bacteria appear to be a synapomorphy of all Oniscidea (and possibly Asellota: see below). Yet no Microcheta (Mesoniscidae) have been regarded so far, and data on Tylida (Tylidae) and Synocheta are still unpublished.

3.2 Characteristics and phylogeny of bacterial endosymbionts

The up-to-date uncultured hepatopancreatic bacteria of terrestrial isopods have been studied most thoroughly in *Porcellio scaber* recently. Upon microscopic inspection, we found three morphotypes of bacteria (tab. 1); besides predominant species that could be detected frequently, there seem to be opportunistic bacteria in *Porcellio scaber* (as well as in other species). Molecular characterization (WANG et al. 2004a,b) revealed only little similarity (< 81 %) of the 16S rRNA genes of the two most frequent genotypes with any other known bacterial species. According to phylogenetic analyses, endosymbionts of *Porcellio scaber* cluster with Rickettsiales (α-Proteobacteria) and Mycoplasmatales (Mollicutes), bacterial orders mostly consisting of intracellular parasites or pathogens in plants, animals and man. For rickettsial symbionts, we propose *Candidatus* Hepatincola porcellionum (WANG et al. 2004a); for mycoplasmal symbionts, we propose *Candidatus* Hepatoplasma crinochetorum (WANG et al. 2004b).

Both *Candidatus* Hepatincola porcellionum and *Candidatus* Hepatoplasma crinochetorum live extracellularly in the hepatopancreatic lumen, but are aggregated in the periphery where they are attached to the epithelium by means of cytoplasmic appendages (henceforth "stalks") that insert into the spaces of the microvillous brush border. (WANG et al. 2004a,b). Although the function of the stalks remains unclear (see below), it is striking that two taxonomically unrelated bacteria that share the same habitat independently develop a feature that is unknown from any of their relatives. According to STEINERT et al. (2000), the ability to attach to a host is one of the prerequisites for establishing a symbiotic relationship. Since the closest known relatives of hepatopancreatic bacteria are intracellular parasites or pathogens (see

above), we hypothesize that the stalks not only serve in attaching to the host epithelium, but may represent an early evolutionary stage towards host cell invasion. *Candidatus* Hepatincola porcellionum and *Candidatus* Hepatoplasma crinochetorum would then be representatives of an early-branching phylogenetic line of Rickettsiales and Mycoplasmatales, respectively, and the low sequence similarity corroborates this assumption; *Mycoplasma penetrans*, a human pathogen that has first been isolated from AIDS patients, forms tip-like appendages that insert deeply into infected cells (e.g., LO et al. 1993; ROTTEM 2003).

Based on our limited knowledge of *Candidatus* Hepatincola and *Candidatus* Hepatoplasma, we can only speculate on functions of the stalk. In known prosthecate α-Proteobacteria (e.g., *Caulobacter* spp.; Caulobacterales: Caulobacteraceae), stalks are involved in a complex life history with stationary stages that are in close contact with the substrate in order to prevent drifting (HOLD et al. 2001); bacterial endosymbionts of *Porcellio scaber* could also utilize their stalks as holdfasts that insert in the microvillous brush border of their hosts in order to avoid being washed off their habitat. On the other hand, well-studied symbiont-host systems (cf. SAVAGE 1972) suggest an exchange of material and/or information between closely associated symbionts and host (WANG et al. 2004a,b). TOKUDA et al. (2000) concluded such an exchange from a close association of endosymbiotic bacteria (*Clostridium* spp.) and microvilli of epithelial cells in the mesenteron of their termite host (*Nasutitermes takasagoensis*; Isoptera: Termitidae).

Comparative studies of different species of Crinocheta provided evidence for *Candidatus* Hepatincola being harbored by at least three species: *Porcellio scaber* [individuals from Kiel and Cologne (Germany) and Vancouver Island (B.C., Canada)], *Oniscus asellus* [Kiel, Cologne, Poitiers (France)], and *Trachelipus rathkii* (Kiel), and *Candidatus* Hepatoplasma also being present in *Porcellio scaber*, *Oniscus asellus* and *Trachelipus rathkii*, but also in *Philoscia muscorum* (Kiel), *Armadillidium vulgare* (Kiel) and *Alloniscus perconvexus* Dana, 1856 (Alloniscidae) (Vancouver Island). Overall, however, *Candidatus* Hepatoplasma was relatively rarely found in *Alloniscus perconvexus* (n = 16; 25 %), *Philoscia muscorum* (*n* = 10; 60 %) and *Armadillidium vulgare* (n = 10; 10 %), but – if present – in high densities of 10^8-10^{11} per isopod (WANG & ZIMMER, unpubl.).

Considering the existence and identity of hepatopancreatic endosymbionts a valuable taxonomic feature (cf. HENNIG 1966; E1966; Brooks 1985), we propose a (preliminary) phylogenetic tree of the mentioned species (fig. 2a) that is in good agreement with trees based on morphological (SCHMIDT & WÄGELE 2001: fig. 2b) and molecular data (MICHEL-SALZAT & BOUCHON 2000: fig. 2b; MATTERN & SCHLEGEL 2001: fig. 2c); it is only the relation of *Armadillidium* (Armadillidiidae in SCHMIDT & WÄGELE 2001) to the other Crinocheta that distinguishes our tree from that of SCHMIDT & WÄGELE (2001) and of MICHEL-SALZAT & BOUCHON (2000) in that their tree would require a secondary loss of *Candidatus* Hepatincola in *Armadillidium* if we considered the identity of hepatopancreatic symbionts we found in this species. In addition, our tree deviates from that by MATTERN & SCHLEGEL (2001) in that their tree would require a secondary loss of *Candidatus* Hepatincola in *Philoscia*, too. Thus, our phylogenetic tree of crinochete isopods as based on microbiological characteristics provides the simplest solution to the interspecific distribution of endosymbiotic bacteria. However, in contrast to morphology-based trees, the current proposition does not consider numerous complex characteristics but, alike most molecular trees, only a single feature, namely the identity of hepatopancreatic endosymbionts. Furthermore, we cannot exclude that

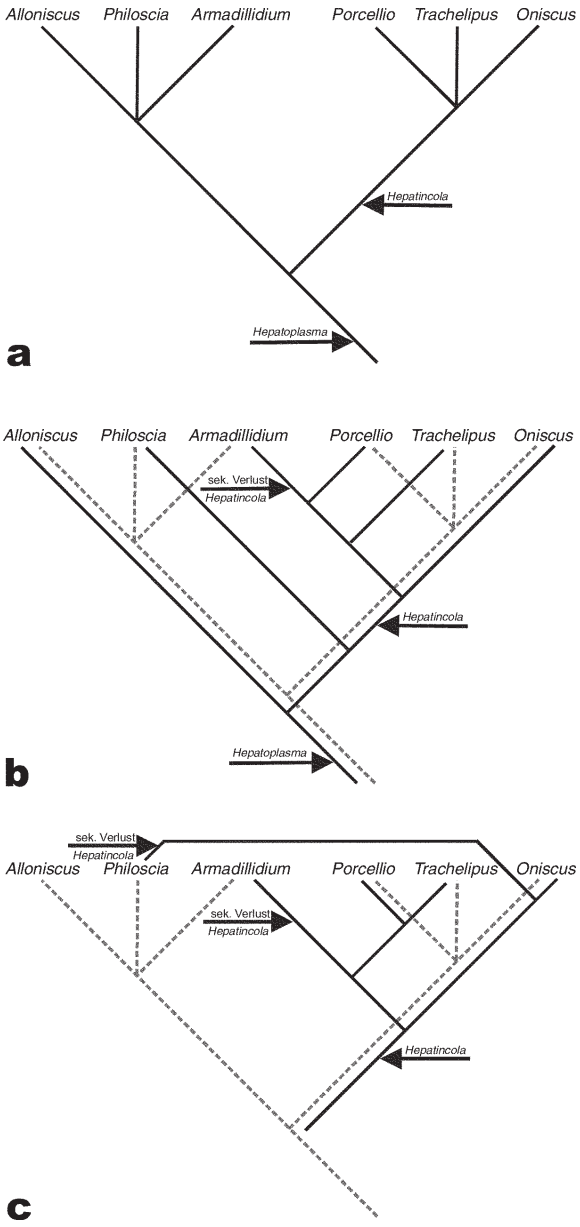

Fig. 2: Phylogenetic tree of some families of Crinocheta; (a) as based on the identity of hepatopancreatic bacteria; (b) in comparison with a tree as proposed by MICHEL-SALZAT & BOUCHON (2000) and SCHMIDT & WÄGELE (2001); (c) in comparison with a tree as proposed by MATTERN & SCHLEGEL (2001).
Abb. 2: Stammbaum einiger Familien der Crinocheta, (a) auf der Basis der Identität der Bakterien im Hepatopankreas, (b) im Vergleich mit einem Stammbaum nach MICHEL-SALZAT & BOUCHON (2000) und SCHMIDT & WÄGELE (2001), und (c) im Vergleich mit einem Stammbaum nach MATTERN & SCHLEGEL (2001).

Candidatus Hepatincola does exist in *Armadillidium* and/or *Philoscia*, but we were thus far unable to detect this endosymbiont. Detailed studies are needed and in progress in our laboratory.

Candidatus Hepatincola and *Candidatus* Hepatoplasma never occurred together in a single specimen; the former was less frequent than the latter both in *Porcellio scaber* (20:80) and in *Oniscus asellus* (40:60). About 30 % of all screened individuals of *Oniscus asellus* (n = 171) but only ca 10 % of all investigated *Porcellio scaber* (n = 265) did not harbor any bacteria in their hepatopancreas (tab. 2; WANG & ZIMMER, unpubl.; cf. WOOD & GRIFFITHS 1988). Preliminary results of

Tab. 2: Percent of aposymbiotic individuals of different species of crinochete isopods (after WANG & ZIMMER, in prep.).
Tab. 2: Anteil aposymbiotischer Individuen verschiedener Crinocheta (nach WANG & ZIMMER, in Vorb.).

Host	Location	Percent aposymbiotic Isopods	*N*
Alloniscus perconvexus	Canada	75 %	16
Philoscia muscorum	Germany	50 %	10
Oniscus asellus	Germany	10 %	161
	France	30 %	10
Porcellio scaber	Germany	10 %	265
	Canada	70 %	31
Armadillidium vulgare	Germany	90 %	10
Trachelipus rathkii	Germany	0 %	4

long-term studies in the laboratory (WANG & ZIMMER, unpubl.) suggest that both loss and re-acquisition of hepatopancreatic bacteria are possible and occur frequently in *Porcellio scaber*. However, seasonal changes in frequency or density of these endosymbionts could be detected neither in *Porcellio scaber* nor in *Oniscus asellus* in the field (WANG & ZIMMER, in prep.). In addition to our observation of symbiont loss without any obvious harm, the relatively high number of aposymbiotic isopod specimens (tab. 2) casts doubt on the nutritive significance of hepatopancreatic bacteria (as will be discussed below) that had been proposed repeatedly (ZIMMER & TOPP 1998b,c; ZIMMER 1999; ZIMMER et al. 2001, 2002a; ZIMMER & BARTHOLMÉ 2003). On the other hand, the proportion of aposymbiotic *Porcellio scaber* in a given population appears at least in part to be controlled by food quality. When feeding on high-quality food (leaf litter of the raspberry, *Rubus* cf. *fruticosus*; Rosaceae), the number of symbiotic isopods decreases (WANG & ZIMMER, unpubl.). Possibly, the degradation of lignocellulose or an additional source of nitrogenous nutrients is not necessary on this food source. According to HASSALL (pers. comm.) three nutritional strategies of isopods are possible: (1) on high-quality food with high moisture, woodlice simply squeeze out water-soluble nutrients off the food and draw the nutritious fluid into the hepatopancreas for resorption of nutrients, while the remaining food compounds pass through the hindgut essentially without any further nutritive utilization; (2) food of intermediate quality is enriched with digestive enzymes derived from the hepatopancreas at the transition of proventricle and hindgut and is digested as efficiently as possible during a slowed-down gut passage; (3) since digestive utilization of low-quality food is hardly possible, this kind of food source is egested virtually undigested, and after microbial incubation and processing of feces they are utilized as food source with increased quality (for a recent discussion of coprophagy, see KAUTZ et al. 2002).

Under favorable nutritional conditions (high-quality food; see above), the gain from harboring bacterial endosymbionts might be lower than costs (e.g., by contributing little to digestion but utilizing food-derived nutrients); according to a model by JOHNSTONE & BSHARY (2002), a host would be expected to get rid of symbionts under such conditions, particularly, if re-acquisition of symbionts is possible when conditions change. On the opposite, one can deduce that digestively mutualistic symbionts are promoted by their host when only low-quality food is available, as had been assumed for cockroaches (Blattopteroidea: Blattodea: Blattariae) and their intracellular endosymbionts (BROOKS 1970) and could later be proven experimentally (GIJZEN et al. 1994) for *Periplaneta americana* and their symbiotic ciliates, *Nyctotherus ovalis* (Protista: Ciliophora), that presumably provide cellulases. This hypothesis would also explain why not all

woodlice harbor hepatopancreatic bacteria (see above). GOMULKIEWICZ et al. (2003) developed a model to demonstrate that interactions of two potential mutualists need not necessarily be mutualistic at any given time, at any given place; reciprocal adaptations (co-evolution) exhibit geographical variation (cf. THOMPSON & CUNNINGHAM 2002). Although our data show that both *Candidatus* Hepatoplasma and *Candidatus* Hepatincola are abundant in *Porcellio scaber* and *Oniscus asellus* from Germany, France and Canada (WANG & ZIMMER, unpubl.: tab. 2), we do not know anything about geographical variation in symbiont-host interactions or local adaptation of isopods and their symbionts (cf. LIVELY 1999).

To test the hypothesis of the common ancestor of all Oniscidea already harboring the hepatopancreatic endosymbionts we found in crinochete species as an early adaptation to a new habitat, we investigated representatives of the prototypal (SCHMALFUSS 1978, 1989; CAREFOOT & TAYLOR 1995) genus *Ligia* (Diplocheta: Ligiidae). Although we found *Pseudomonas* n. sp. (γ-Proteobacteria: Pseudomonadales) in midgut glands of *Ligia oceanica* (Linnaeus, 1767) (WANG et al., in review), we were unable to demonstrate the existence of *Candidatus* Hepatincola or *Candidatus* Hepatoplasma. On the other hand, some individuals of both *Porcellio scaber* and *Oniscus asellus* (and *Alloniscus perconvexus*: ZIMMER & FRAUNE, unpubl.) also contain rod-shaped bacteria (HOPKIN & MARTIN 1982; WOOD & GRIFFITHS 1988; ULLRICH et al. 1991; ZIMMER 1998; tab. 1) that resemble *Pseudomonas* spp. and were classified as γ-Proteobacteria (WANG et al., unpubl.). Rod-shaped bacteria in *Ligidium hypnorum* (Cuvier, 1792) (Diplocheta: Ligiidae), in *Tylos ponticus* Grebnitzsky, 1874 (Tylida: Tylidae) and in *Trichoniscus pusillus* Brandt, 1833 and *Hyloniscus riparius* (Koch, 1838) (Synocheta: Trichoniscidae) were also identified as representatives of the genus *Pseudomonas* by hybridization of their 16S rRNA genes with specific oligonucleotide probes (ZIMMER & FRAUNE, unpubl.). By contrast, coccoid cells in *Ligia pallasii* (ZIMMER et al. 2001; WANG & ZIMMER, unpubl.), in *T. ponticus* and in *T. pusillus* and *H. riparius* (ZIMMER & FRAUNE, unpubl.) as well as rod-shaped symbionts in the marine Asellota *Jaera albifrons* and *Eurycope cornuta* could thus far not be determined (tab. 1). The coincidence between different phylogenetic lineages of Oniscidea (see fig. 3) with respect to the existence of *Pseudomonas* corroborates our hypothesis concerning a single initial acquisition event of bacterial symbionts in an early evolutionary stage of terrestrialization. Possibly, the common ancestors of the Diplocheta (here: *Ligia* and *Ligidium*) and all other Oniscidea or even a common marine ancestor of Oniscidea and Asellota somehow developed the ability to harbor bacteria in its midgut glands that get there by chance, and implemented an unspecific endosymbiosis. In evolutionary early stages of Oniscidea, bacteria of the genus *Pseudomonas* then established as specific symbionts of terrestrial isopods that are still present in Diplocheta, Tylida and Synocheta (and in some Crinocheta?) and may be capable of degrading cellulose and/or phenolics. Based on a comparison of 16S rRNA gene sequences, we conclude that endosymbionts on *Ligia oceanica* derived from marine pseudomonads. Thus, the acquisition of the primary symbionts of Oniscidea probably took place before the colonization of terrestrial habitats, at least, however, no later than in the intertidal (WANG et al., in review). By contrast, marine Asellota appear to exhibit unspecific endosymbioses with different bacterial species (WANG et al., in review; cf. tab. 1). In *Asellus aquaticus* evolution may – in convergence to Oniscidea – have led to specific symbioses that enable the host to feed on leaf litter.

Hepatopancreatic bacteria have been demonstrated in several aquatic crustaceans (MUSGROVE 1988; HARRIS et al. 1991; ZIM-

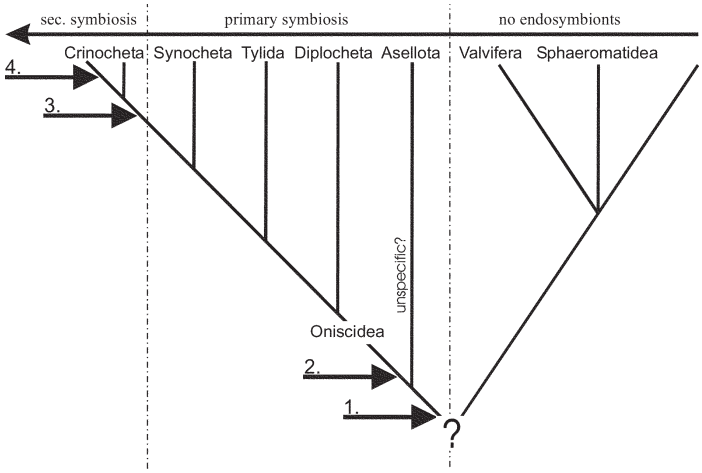

Fig. 3: Phylogenetic tree of some suborders of Isopoda as based on the existence and identity of endosymbiotic bacteria, with four evolutionary steps of symbiotic establishment; 1.: loss of antibiotic agent and (passive) acquisition of hepatopancreatic bacteria in an unspecific endosymbiosis; 2.: specific acquisition of *Pseudomonas* n. sp. in a common ancestor of all Oniscidea; 3.: acquisition of *Candidatus* Hepatoplasma sp. in a common ancestor of all Crinocheta; 4.: acquisition of *Candidatus* Hepatincola sp. (see also Figure 2).

Abb. 3: Stammbaum einiger Unterordnungen der Isopoda, auf der Basis von Existenz und Identität endosymbiotischer Bakterien, mit vier evolutiven Schritten: 1. Verlust antibiotischer Agentien und (passive) Akquirierung bakterieller Mitteldarmsymbionten, 2. spezifische Akquirierung von *Pseudomonas* n. sp. in einem gemeinsamen Vorfahren aller Oniscidea, 3. Akquirierung von *Candidatus* Hepatoplasma sp. in einem gemeinsamen Vorfahren aller Crinocheta, 4. Akquirierung von *Candidatus* Hepatincola sp. (s. Abbildung 2).

MER & BARTHOLMÉ 2003; WANG et al., in review; ZIMMER & FRAUNE, unpubl.); the symbionts of the freshwater crayfish, *Paranephrops zealandicus* (Decapoda: Parastacidae), for instance, belong to the γ-proteobacterial genera *Aeromonas* (Aeromonadales), *Citrobacter* and *Hafnia* (Enterobacteriales), and seem to provide cellulases for the digestion of leaf litter (MUSGROVE 1988). Freshwater isopods of the species *Asellus aquaticus* also harbor endosymbiotic bacteria (see tab. 1) of the genera *Rhodobacter* (α-Proteobacteria: Rhodobacteriales), *Burkholderia* (β-Proteobacteria: Burkholderiales), *Aeromonas*, and *Rickettsiella* (γ-Proetobacteria: Legionellales) in their midgut glands (WANG et al., in review). Both the high intraspecific diversity of bacterial endosymbionts and their taxonomic identity apparently contradicts a common evolutionary origin of endosymbioses in Asellota and Oniscidea and suggests convergent adaptations to terrestrial food sources (leaf litter) in *Asellus aquaticus* and terrestrial isopods, unless we accept the idea of an intially unspecific symbiotic relationship in marine ancestors of Asellota and Oniscidea that is still unspecific in marine Asellota and evolved towards the functional endosymbiosis in freshwater Asellota. Feeding experiments actually provided evidence that (some of) the bacteria in *A. aquaticus* produce cellulases as well as phenol oxidases that are utilized for the digestion of leaf litter (ZIMMER & BARTHOLMÉ 2003). As discussed by ZIMMER (2002a) and ZIMMER & BARTHOLMÉ (2003), we can, however, not exclude the possibility of endogenous cellulases in the tested isopods. The conclusion by ZIMMER & TOPP (1998b,c) and ZIMMER & BARTHOLMÉ (2003) are based on

correlations between bacterial numbers and enymatic activities. According to HARTENSTEIN (1964a), suggesting endogenous cellulases in crinochete isopods (see above), and to RAY & JULIAN (1952), providing evidence for endogenous cellulases in the wood-boring *Limnoria lignorum* (Rathke, 1799) (Sphaeromatidea: Limnoriidae), it is well possible that the experimental treatment simultaneously but independently reduced both the number of hepatopancreatic bacteria and the release of endogenous cellulases into the gut lumen (for further discussion, see below).

The endosymbionts of Crinocheta make us conclude that primary symbionts (*Pseudomonas*) of Oniscidea were replaced (or supplemented) by secondary symbionts (*Candidatus* Hepatoplasma and *Candidatus* Hepatincola) soon after the branching of Crinocheta (see fig. 3). Such an evolutionary takeover has recently been demonstrated experimentally in aphids (Hemiptera: Sternorrhyncha: Aphidomorpha: Aphidina), replacing their primary symbionts, *Buchnera aphidicola*, by secondary symbionts (unknown γ-Proteobacteria), and has been discussed in the context of establishing symbiotic relationships (KOGA et al. 2003). Even in natural systems, aphids harbor at least three different secondary symbionts, belonging to the genus *Spiroplasma* (Mollicutes: Mycoplasmatales) (FUKATSU et al. 2001), the γ-3 subdivision of the Proteobacteria and to the genus *Rickettsia* (α-Proteobacteria: Rickettsiales) (MONTLLOR et al. 2002). Similarly, tsetse flies (*Glossina* spp.; Diptera: Glossinidae) may lodge a commensal, *Sodalis glossinidius* (γ-Proteobacteria: Enterobacteriaceae) as secondary symbiont that belongs to the same family as the primary symbiont, *Wigglesworthia glossinidia* (DALE & MAUDLIN 1999). In dryophtherid beetles (Coleoptera: Curculionoidea) even three lineages of Enterobactericeae exist that colonized their host in independent evolutionary steps (cf. NARDON et al. 2003).

Applying a model by DOEBELI & DIECKMANN (2000), I conclude that either the initial acquisiton of *Pseudomonas* sp. or the subsequent symbiotic takeover, possibly, led to the branching and later speciation of Oniscidea or Crinocheta, respectively, as has been discussed by BUCKLING & RAINEY (2002) in a broader context. LEONARDO & MUIRU (2003) recently presented evidence for nutritional specialization being determined by the identity of facultative bacterial symbionts in aphids.

In contrast to Asellota, marine Valvifera and Sphaeromatidea do not harbor hepatopancreatic bacteria, although these animals live in a microbe-rich environment and not being infected by bacterial endosymbionts seems unlikely. SLEETER et al. (1978) proposed the production of antibiotics in the gut of the wood-boring *Limnoria tripunctata* (although ZACHARY & COLWELL (1979) found gut microbiota in this species). Thus, I extend the above hypothesis in that antibiotics of endogenous or external origin in marine isopods (except Asellota; see below) prevent the colonization of the midgut glands by bacteria (see fig. 3). HELLIO et al. (2000) found antibiotic agents in 9 out of 16 species of marine macroalgae that might still be active in the guts of consumers (e.g., isopods or amphipods) and may prevent bacteria from conquering the hepatopancreas. The initially unspecific(?) acquisition of hepatopancreatic endosymbionts as a result of the loss of antibiotic agents would then simply be a consequence of an evolutionary change in feeding habits from consuming fresh algae to preferring detritus.

In this context, PLANTE et al. (1990) discuss the significance of the habitat in determining an invertebrate's role as host to microbial endosymbionts. In case of marine invertebrates, the gut lumen and the environment exhibit virtually identical conditions in terms of ionic and osmotic levels, while this is not true for freshwater invertebrates. The gut of terrestrial invertebrates

provides a valuable aquatic habitat in a terrestrial environment. Thus, the significance of microbial gut symbionts can be explained from different points of view: (1) For marine microbiota, it is not advantageous to colonize the gut of an invertebrate instead of living in sea water, while the gut of a terrestrial invertebrate grants a more favorable environment than soil or leaf litter; (2) for terrestrial invertebrates, in turn, gut symbionts in a stable environment are more reliable than soil or litter-colonizing microbes in a variable milieu, while this difference is supposed to be insignificant for marine invertebrates (HARRIS 1993). Gut anatomy – in particular, the existence of midgut glands in shape of blind-ending tubes – can be interpreted as pre-disposition (cf. HARRIS 1993).

Our current knowledge of endosymbiotic bacteria in isopods makes the proposal of a (preliminary) phylogenetic tree of some suborders of Isopoda possible (fig. 3); this tree contradicts most of the currently discussed trees (WÄGELE 1989; BRUSCA & WILSON 1991; TABACARU & DANIELOPOL 1999) in that Asellota and Oniscidea are considered sister taxa here, forming a monophylum that propose to be named Hepatoconvivata (if the hosts provide nutrients) or Hepatohospita (if the hosts provide a habitat rather than food). For the verification or rejection of this hypothesis and thus a decision upon the validity of this taxon, we urgently need additional data from aquatic isopod suborders.

3.3 Symbiont-host interactions

Symbioses are generally accepted to act as evolutionary motor (MARGULIS & FESTER 1991; DOUGLAS 1992a; MAYNARD SMITH & SZATHMÁRY 1995; WATSON & POLLACK 2003). Further, it is frequently assumed that mutualistic symbioses derive from parasitic ones (BOUCHER et al. 1982; VANDERMEER 1983; PRICE 1991; YAMAMURA 1993; but see NUISMER et al. 2003, for a different opinion), since the aim of a (vertically transmitted) parasite to be transferred to its host's offspring conflicts the host's interest of keeping its offspring free of parasites, and results in an evolutionary arms race. The symbiont increases its transmission rate by reducing its virulence until both partners gain from its transmission to the next generation. If this is the case, the symbiotic relationship will be mutualistic (cf. THOMPSON 1982). In addition, the exploitation of the host by the symbiont should not reduce the host's longevity and fitness, because this would simultaneously reduce the fitness of a vertically transmitted symbiont (ROUGHGARDEN 1975). Even though – in spite of initial assumptions by ZIMMER & TOPP (1998b,c) and ZIMMER et al. (2001, 2002a) – we could not yet unambiguously clarify what kind of relation exists between isopods and their hepatopancreatic symbionts, their phylogenetic affiliation with predominantly parasitic and pathogenic bacteria is in agreement with this model.

Both aphids and their intracellular bacterial endosymbionts, *Buchnera aphidicola*, evolved towards obligatory dependence on each other (CHARLES & ISHIKAWA 1999; SHIGENOBU et al. 2000). *Buchnera* symbionts are hosted in specialized cells, bacteriocytes, and provide essential amino acids to their host that feeds on nitrogen poor food sources (see above) (WILKINSON & DOUGLAS 1996; WILKINSON & ISHIKAWA 2000; DOUGLAS et al. 2001; BERNAYS & KLEIN 2002). As briefly discussed above, the transmission of symbionts is critical in mutualistic symbioses, both for obligatory endosymbionts and for their host. It is only through vertical transmission that a host can ensure that none of his progeny will stay aposymbiotic. Further, given that competition between different symbionts may exert negative effects on the host (discussed in KOGA et al. 2003), it seems advantageous to the host to keep the diversity of symbionts low, and

the best way to achieve this aim is controlled vertical transmission (KORB & AANEN 2003). Symbiotic bacteria of the nudibranch, *Dendrodoris nigra* (Gastropoda: Ophistobranchia), are directly transferred from the vestibular gland, where they intrude between the epithelial microvilli, to the egg masses prior to spawning (KLUSSMANN-KOLB & BRODIE 1999). The transmission of yeast-like intracellular endosymbionts (*Symbiotraphina* spp.) in the ceca of *Stegobium paniceum* and *Lasioderma serricorne* (Coleoptera: Anobiidae) that provide vitamin B and sterols (PANT & FRAENKEL 1954) and detoxify harmful food compounds (DOWD 1989; SHEN & DOWD 1991) is brought about by smearing the eggs during oviposition (NODA & KODAMA 1996).

Yet, many mutualists rely on horizontal transmission (discussed in WILKINSON & SHERRATT 2001), and horizontal transfer of symbionts is the rule in sexually reproducing animals with symbionts that are not harbored inside the reproductive tract (DOUGLAS 1995; but see YAMAMURA 1993). Larvae of pony fish (*Leiognathus nuchalis*; Perciformes: Leiognathidae) hatch aposymbiotic and get infected by luminescent bacteria at an age of at least 45 days (WADA et al. 1999). Similarly, aposymbiotic juveniles of lucinid mussels (Mollusca: Bivalvia) acquire sulfide-oxidizing intracellular gill symbionts (γ-Proteobacteria) horizontally. The flatworm, *Convoluta roscoffensis* (Plathelminthes: Turbellaria), harbors endosymbiotic algae of the genus *Tetraselmis* (Chlorophyta), but host individuals differ in what species of *Tetraselmis* they accommodate. Aposymbiotic juveniles take up algae while feeding and reject all but one species (DOUGLAS 1980). A similar transmission mechanism, with bacteria being ingested along with the food, have been proposed for the sponge, *Halichondria panicae* (Porifera: Demospongiae), and its symbionts of the genus *Rhodobacter* (α-Proteobacteria) (ALTHOFF et al. 1998; discussed in STACKEBRANDT & PUKALL 1999; MÜLLER 1999).

Both *Candidatus* Hepatoplasma and *Candidatus* Hepatincola, too, appear to be transmitted horizontally or even through abiotic vectors in the environment: under sterile conditions in the laboratory, neither embryos nor 1d-old mancae I or 1wk-old mancae II of *Porcellio scaber* harbored hepatopancreatic bacteria (WANG et al., in review). If kept non-sterile, however, both embryos and mancae I are void of bacteria, too, while bacteria can be found in the midgut glands at the age of one week. Thus, either marsupial fluids are free of bacteria – contrasting preliminary results by STEVENS & ZIMMER, unpubl. (in ZIMMER 2002a) and electron-microscopic studies by STEVENS & GREVEN (pers. comm.) – or embryos and marsupial mancae are unable to take up bacteria into their digestive tract. One possible obstacle to bacterial colonization of the midgut glands could be the filter system between proventricle and hepatopancreas that is common in Isopoda, Amphipoda and most Malacostraca, preventing the influx of particles into the glands (MARTIN 1964; SCHELOSKE 1976; OSHEL & STEELE 1988; WÄGELE 1989). According to WOOD & GRIFFITHS (1988) particles larger than 1.17 μm in diameter are excluded, but HAMES & HOPKIN (1989) observed a mesh size of just 40-50 nm. However, it is questionable how the pressure should be built up that would be needed to push fluids through a filter of such small mesh size into the hepatopancreas. STORCH (1987) discussed the possibility of actively changing the mesh size of the proventricular filter. Yet, in this case, contamation of the midgut glands with litter-colonizing microbiota would be likely. On the other hand, there must be some way for hepatopancreatic endosymbionts to pass the filter and enter the glands; this problem could thus far not be solved (cf. ZIMMER 2002a).

In the Spider Crab, *Chionoectes opilio* (Decapoda: Brachyura: Majidae), males transfer antibiotic agents with their sperm (BENHALIMA

& MORIYASU 2001), and comparable findings have been reported for the fruitfly, *Drosophila melanogaster* (LUNG et al. 2001). In isopods, too, such substances could be drawn into the marsupium to help prevent microbial contamination of marsupial embryos (but see above).

Horizontal transfer of symbionts *via* feces or litter, as suggested by our findings in *Porcellio scaber* (see above), seems to be inefficient, since it cannot be ensured that all offspring get access to (the correct) symbionts (see above). On the other hand, even vertical transmission of (bacterial) symbionts is a bottleneck with respect to the number of transferred symbionts (MIRA & MORAN 2002), and the risk of enriching harmful mutations in symbionts is higher than in symbiont-host systems with horizontal transmission (RISPE & MORAN 2000). In this context, a comparison of *Candidatus* Hepatincola with other Rickettsiales is interesting: while *Wolbachia* (see BOUCHON et al. 2005, in this issue) is usually transmitted vertically, horizontal transmission is typical for *Rickettsia* and *Ehrlichia* (ANDERSON & KARR 2001; SCHULENBURG et al. 2001); but *Wolbachia* can be transferred horizontally, too (CORDEAUX et al. 2001).

Despite the risk inherent to horizontal transmitting, *Candidatus* Hepatincola or *Candidatus* Hepatoplasma are present in 60-100 % (depending on the population and the season; see above) (WANG & ZIMMER, unpubl.). Thus, woodlice successfully detect and find bacteria in their environment (see also ZIMMER et al. 1996), or the probability of encountering and taking up these bacteria (or their propagules) is increased by the wide distribution in the isopods' environment (see YAMAMURA 1993). Since bacteria inside the hepatopancreatic lumen actively proliferate (WANG et al., unpubl. TEM studies), we expect surplus bacteria to be drawn to the hindgut and egested in feces (discussed in ZIMMER 2002a). Extracellular luminescent endosymbionts of deep sea fish (Beryciformes: flashlight fishes, Anomalopidae; pinecone fishes, Monocentridae) (NEALSON et al. 1984) and of cuttlefish (*Euprymna scolopes*; Cephalopoda: Sepiidae) (LEE & RUBY 1994) are excreted at rates of 10^6-10^8 per day. Such a transfer mechanism could explain the presence of *Candidatus* Hepatincola and *Candidatus* Hepatoplasma in most crinochete species tested thus far, if we assume that isopods but not their bacterial endosymbionts exhibit high specificity with respect to their symbiotic partner (cf. FEINSINGER 1983). Up to now, however, we were unable to detect either *Candidatus* Hepatincola or *Candidatus* Hepatoplasma using specific fluorescence-labeled probes in the hindgut, or the feces of isopods or in leaf litter or soil (WANG & ZIMMER, unpubl.). Possibly, the symbionts are present as propagules that cannot be detected with this technique. We currently try to detect them through PCR-amplification of their 16S rDNA using sequence-specific primers.

Neither in *Porcellio scaber* nor in *Onicus asellus* we ever found *Candidatus* Hepatincola and *Candidatus* Hepatoplasma occurring together (WANG & ZIMMER, unpubl.). Given that symbionts are transmitted horizontally (see above), an infection of an isopod with one of its potential endosymbionts seems to preclude a secondary infection with the other one. Such interactions have been explained in terms of competition between symbionts for their habitat (see KOGA et al. 2003), but could also be due to induced defense of the host (cf. KURTZ & FRANZ 2003).

Based on our current knowledge we are to suppose that the initial inoculation of juveniles (as well as re-inoculation of aposymbiotic adults; see above) depends on the uptake of potential endosymbionts with the food, the most likely and reliable source of symbionts are probably feces of conspecifics. Beside its nutritional role (cf. KAUTZ et al. 2002), coprophagy, thus, seems to be adaptive in the context of acquiring hepatopancreatic endosymbionts.

Symbiotic relationships between microbiota and blood- or sapsuckers or detritivores (cf. BUCHNER 1965) have frequently been described to include the transfer of nutrients or a nutritive exploitation of symbionts by the host (e.g., BAUMANN & MORAN 1997; CAZEMIER et al. 1997; STEINERT et al. 2000). Aphids (see above) and termites (Blattopteroidea: Blattodea: Isoptera) are among the best-studied symbiotic arthropods. Although both face the problem of nitrogen-poor food source, termites – in contrast to the sap-sucking aphids – are in addition confronted with remarkable amounts of lignocellulose and other recalcitrant and deterrent compounds of their natural food sources (see BREZNAK & BRUNE 1994). However, only some termite species rely on gut symbionts for the production of cellulases (cf. DOUGLAS 1992): lower termites (Mastotermitidae, Kalotermitidae, Hodotermitidae and Rhinotermitidae) harbor cellulolytic flagellates (Protista: Sarcomastigophora: Mastigophora) in their gut that provide short-chained fatty acids to the nutrition of their host; cellulases of symbiotic origin are supplemented by endogenous cellulases (MARTIN 1984; TOKUDA et al. 2002; OHKUMA 2003). Higher termites (Termitidae) hydrolyze cellulose by endogenous cellulases that are produced in their midgut, but do not harbor cellulolytic protists (cf. OHKUMA 2003). Macrotermitinae, on the other hand, garden fungi (genus *Termitomyces*) in their colonies and feed on cellulase-rich nodules of the fruit bodies; cellulases maintain their activity during the gut passage and contribute to cellulose digestion (MARTIN 1984). However, the nutritive significance of these enzymes for digestive processes is unclear (cf. VEIVERS et al. 1991) as has also been stated with respect to cellulases in midguts of wood-feeding beetles (Coleoptera; e.g., Cerambycidae, Anobiidae, Bupestridae) or wood wasps (Hymenoptera: Symphyta: Siricoidea: Siricidae) (MARTIN 1991) and detritivorous stoneflies (*Pteronarcys proteus*; Plecoptera) or caddisflies (*Pycnopsyche luculenta*; Trichoptera) (SINSABAUGH et al. 1985).

Although ABE & HIGASHI (1991) stated, that "most animals [...] lack the ability to produce the enzymes necessary for decomposing cellulose" (p. 127), evidence for endogenous cellulases have been presented for the marine isopod *Limnoria lignorum* (RAY & JULIAN 1952) and the freshwater amphipod *Gammarus pulex* (MONK 1977; ZIMMER & BARTHOLMÉ 2003; but see BÄRLOCHER 1982, and BÄRLOCHER & PORTER 1986) as well as in the silverfish *Thermobia domestica* (Zygentoma: Lepismatidae) (TREVES & MARTIN 1994) and the applesnail *Ampullaria crossean* (Mollusca: Gastropoda) (WANG et al. 2003). Further, parts of an active cellulase complex, namely β-glucosidases, have been demonstrated in numerous invertebrates: *Locusta migratoria* (Orthopteroidea: Caelifera: Acrididae) (MORGAN 1975), *Rhynchosciara americana* (Diptera: Nematocera: Sciaridae) (FERREIRA & TERRA 1983), *Erinnyis ello* (Lepidoptera: Sphingidae) (SANTOS & TERRA 1985), *Sitophilus oryzae* (Coleoptera: Curculionidae) (BAKER & WOO 1992), *Abracris flavolineata* (Orthopteroidea: Caelifera: Acrididae) (MARANA et al. 1995), *Spodoptera frugiperda* (Lepidoptera: Noctuidae) (MARANA et al. 2000). "Incomplete" (see above) cellulase complexes, consisting of endo-β-1,4-glucanases and β-glucosidases but lacking exocellulases and being capable of degrading soluble but not native crystalline cellulose (see SKAMBRACKS & ZIMMER 1998), have also been described: *Trachelipus rathkii* (KUKOR & MARTIN 1986), *Gammarus lacustris* (Amphipoda: Gammaridea) (MCGRATH & MATTHEWS 2000), *Macrotermes mülleri* (Isoptera: Termitidae) (ROULAND et al. 1988), *Panesthia cribrata* (Blattopteroidea: Blattodea: Blattariae) (SCRIVENER & SLAYTOR 1994a). Although the degradative capacity of such enzymes is lower than that of microbial cellulases (SLAYTOR 1992; SCRIVENER & SLAYTOR 1994b), it is obviously sufficient to hy-

drolyze cellulose without microbial assistance (SLAYTOR 1992); the low efficacy is compensated through high rates of production (SCRIVENER & SLAYTOR 1994b). Possibly, the supplementary uptake of fungal cellulases that provide critical components of cellulase complexes is significant for these animals (MARTIN 1984). Neither ZIMMER & TOPP (1998b,c) nor ZIMMER & BARTHOLMÉ (2003) distinguished between different components of the cellulase complex in their analyses of cellulase activity.

At least the fungal symbionts (genus *Termitomyces*) of some termites (*Macrotermes* spp.) degrade lignins, thus facilitating cellulose digestion by the hosts (HYODO et al. 2000, 2003); JOHJIMA et al. (2003) isolated and characterized a peroxidase from *Termitomyces albuminosus*. Leaf-cutting ants (Hymenoptera: Apocrita: Formicoidea: Myrmicidae) and their gardened fungi show only little overlap in their enzymes (D'ETTORE et al. 2002), suggesting a stable dependence of the hosts on their symbionts. No matter whether or not cellulolytic or pectinolytic enyzmes are provided by the fungi (cf. ABRIL & BUCHER 2002), the fungal activity seems to facilitate the ants' access to the nutritious cell contents of plant tissues. Jobsharing is also common in the marine abalone, *Haliotis midae* (Mollusca: Gastropoda: Prosobranchia), with resident gut bacteria degrading cellulose (ERASMUS et al. 1997). In this same context, we are to interpret the suggestion that cellulases and phenol oxidases in terrestrial isopods – and, as a result of convergent evolution to feeding on terrestrial leaf litter, also in the freshwater isopod, *Asellus aquaticus* (ZIMMER & BARTHOLMÉ 2003) – are provided by hepatopancreatic bacteria (ZIMMER & TOPP 1998b,c; ZIMMER 1999; ZIMMER et al. 2001, 2002a).

Whether or not bacterial endosymbionts of isopods contribute cellulases and/or phenol oxidases can only be clarified by means of genetic detection of the respective genes. Relatives of *Candidatus* Hepatoplasma and *Candidatus* Hepatincola within the Mollicutes and Rickettsiales, respectively, are not known to produce any cellulolytic or phenol-oxidizing enyzmes which contradicts the proposed function of these symbionts. However, even the closest relatives are so distantly related that we cannot convincingly deduce any physiological characteristics of *Candidatus* Hepatoplasma or *Candidatus* Hepatincola from what we know about mycoplasmas or rickettsias. ESHAM et al. (2000) were unable to predict the ability to degrade lignins based on the phylogenetic affiliation of several α- and γ-Proteobacteria and gram-positive bacteria.

On the other hand, close relatives of endosymbionts in non-crinochete isopods (see above), e.g. *Pseudomonas fluorescens*, are capable of degrading both cellulose and hemicellulose and polycyclic aromatic hydrocarbons (see also *Pseudomonas putida*: PLAGGENBORG et al. 2003). Similarly, relatives of hepatopancreatic symbionts in *Asellus aquaticus*, *Aeromonas* spp. and *Burkholderia* spp. are well-known as xylanase and phenol oxidase postive; these symbionts, thus, could well be involved in litter degradation in *Asellus aquaticus* (cf. ZIMMER & BARTHOLMÉ 2003). Based on these, I hypothesize that the primary symbiosis with *Pseudomonas* n. sp. provided digestive enzymes for the degradation of terrestrial food source to early semi-terrestrial isopods. Afterwards, prior to the evolutionary loss of *Pseudomonas* and the takeover by *Candidatus* Hepatoplasma (and later *Candidatus* Hepatincola), a gene transfer took place between symbiont and host, resulting in endogenous production of cellulase and/or phenol oxidase by the host (alternatively, the respective genes could have been transferred from the primary to the secondary symbiont). Horizontal gene transfer beyond the species level is well-known from both bacteria (e.g., JAENECKE et al. 1996; KELLY & KADO 2002; HILL & WEIGHTMAN 2003) and between prokaryotes and

eukaryotes (e.g., NESTER 2000; BIRD et al. 2003; DOUGLAS & RAVEN 2003), and are considered significant for the evolution of symbiosis-specific capabilities of symbionts (FARRANT et al. 1997; TSUDA et al. 1999; NESTER 2000; DOUGLAS & RAVEN 2003; HILL & WEIGHTMAN 2003; PARKER 2003; VAN ELSAS et al. 2003). YAN et al. (1998) assume that endogenous cellulases in plant-parasitic nematodes are evolutionarily of bacterial origin. In some cases, close relatives of the proposed primary symbionts of Oniscidea, *Pseudomonas putida* (JAENECKE et al. 1996) and *P. fluorescens* (LILLEY et al. 2003), are involved in such events; especially under nutrient-rich conditions, as prevail in the lumen of the midgut glands, the probability of interspecific gene transfer is high (DROGE et al. 1998) and could play an important role during the establishment of pathogens and parasites in their prospective host (WILSON & SALYERS 2003).

In contrast to termites, ingesting remarkable amounts of lignocellulose and its derivates as well as other recalcitrant compounds (e.g., BREZNAK & BRUNE 1994), aphids, being sapsuckers, do not have to face many recalcitrant or deterrent food compounds. Both, however, have in common that their food sources are extremely nitrogen-limited so that they are in need of additional sources of nitrogen. In the gut of *Tetraponera* ants, VAN BORM et al. (2002) recently demonstrated nitrogen-fixing *Pseudomonas* that share >97 % sequence similarity with the endosymbionts of *Ligia oceanica*. The closely related *Ligia pallasii* mostly feeds on stranded macroalgae (CAREFOOT 1973; PENNINGS et al. 2000) containing significantly less than 1 % N, and we assume a similar nutritive behavior of *Ligia oceanica*. Thus, the nutritive significance of bacterial symbionts could also be related to their capability of making nitrogen available to their N-limited host (discussed by NARDI et al. 2002), as has been demonstrated repeatedly for the intracellular endosymbionts of aphids (*Buchnera aphidicola*) and yeast-like symbionts in the grasshopper *Nilparvata lugens* (Hemiptera: Auchenorrhyncha: Delphacidae) (cf. DOUGLAS et al. 2001; WILKINSON & ISHIKAWA 2001; BERNAYS & KLEIN 2002). In addition, vitamins and essential amino acids are produced and released by endosymbiotic microbiota and can be utilized by their hosts (DOUGLAS 1989, 1992). However, bacteria in the midgut glands of *Ligia pallasii* are apparently not closely related to those in *L. oceanica* (WANG & ZIMMER, unpubl.; tab. 1), questioning the evolutionary significance of a potential nitrogen source by means of endosymbiotic bacteria.

Overall, our up-to-date knowledge as summarized herein (phylogenetic affiliation of symbionts, high proportion of aposymbiotic isopods without any obvious harm) does provide only weak arguments in favor of a nutritional significance of hepatopancreatic bacteria. Further, the ability to hydrolyze cellulose and oxidize phenolics is present (as a pre-disposition for the terrestrial habitat) in (some) Sphaeromatidea and Valvifera (ZIMMER et al. 2002a). On the other hand, despite their phylogenetic affiliation, nothing hints on a parasitic or pathogenic life style of bacterial symbionts in Oniscidea. Thus far, we can only speculate on the nature of the symbiotic relationship and the role symbionts play in the life of their host. I will discuss some hypotheses in turn.

- Hepatopancreatic symbionts protect their host from secondary infections by (microbial) pathogens or parasites.

Although woodlice are confronted with high densities of (potentially pathogenic) microbiota in their natural environment, the microbial diversity in their midgut glands is remarkably low (see above). While the cuticular intima of the fore- and hindgut protects from pathogens intruding the body cavity, there is no such protection for the midgut epithelium; solely the proventricular

filters might act in this respect (see below). Most insects and crustaceans counteract pathogens through phenol oxidase activity (cf. GILLESPIE et al. 1997; see above). Although we proved phenol oxidation in the gut lumen of *Porcellio scaber* (ZIMMER & TOPP 1998c), alike *Glyptonotus antarcticus* Eights 1852 (Valvifera) (SMITH & SÖDERHÄLL 1991) and presumably *Asellus aquaticus* (DEZFULI 2000), woodlice apparently do not possess phenol oxidases in their hemolymph (IRMAK et al. 2005). Presumably, hemocyanine is involved here (for review, see DECKER & TUCZEK 2000) that also exerts antibacterial activity (BOUCHON, pers. comm.; HERBINIÈRE, unpubl.). On the other hand, hepatopancreatic bacteria may prevent the establishment of (microbial) parasites and pathogens in the hepatopancreatic lumen before they can enter the body cavity, either as well-adapted, and thus superior, competitors, or through antibiotic agents; obviously, both *Candidatus* Hepatoplasma and *Candidatus* Hepatincola are capable of excluding the other potential symbiont from its habitat (see above). Comparable interactions between potential symbionts have recently been described in the pea aphid, *Acyrthosiphon pisum* (KOGA et al. 2003). Besides producing a endo-β-(1-4)-glucanase (PASTOR et al. 2001), *Paenibacillus* sp. (Bacillales) exhibits a endo-β-(1-3)-glucanase that exerts fungicidal effects through degrading the fungal cell wall (HONG & MENG 2003). Several unidentified *Pseudomonas* strains produce both chitinases and cellulases as well as additional enzymes that act fungicidal (SINDHU & DADARWAL 2001), and some fluorescing soil pseudomonads bring about a derivate of the phenolic phloroglucinol that also acts as fungicide (RAMETTE et al. 2003). *Pseudonocardia*-like (Actinomycetes) symbionts in leaf-cutting ants provide antibiotics that prevents parasitic fungi from intruding nutritionally significant fungal colonies (CURRIE et al. 1999). However, thus far we were unable to detect any antibiotic activity in the hepatopancreas of *Porcellio scaber* (WANG & ZIMMER, unpubl.).

- Metabolites of hepatopancreatic symbionts protect their hosts from predators.

A close relative of *Pseudomonas aeruginosa* and the symbionts in *Ligia oceanica*, *Ligidium hypnorum*, *Tylos ponticus*, *Hyloniscus riparius* and *Trichoniscus pusillus* gives rise to the defensive compound pederine in the rove beetle, *Paederus sabaeus* (Coleoptera: Staphylinidae) (KELLNER 2001, 2002). Woodlice, too, exert chemical defense against predatory attack. Lobed glands in their uropods and the margins of their epimera secret fluids upon stimulation that deter at least some invertebrate predators (GORVETT 1952). Epimeral glands contain fluorescing compounds that exhibit similar characteristics as those in Zenker cells of the freshwater isopod, *Asellus aquaticus* (LORENZEN & ZIMMER, in prep.). Since lobed glands of terrestrial isopods are assumed homologous to the Zenker cells of Asellidae (TER-POGHOSSIAN 1909), and bacterial symbionts in the gut of *Asellus aquaticus* may bring forth the fluorescence of the Zenker cells (ZIMMER et al. 2002c), we hypothesize a correlation between bacterial symbionts and the defensive function of the lobed glands. However, experimental evidence is lacking thus far.

- Hepatopancreatic bacteria increase fertility (production of oocytes or sperm) and reproductive success (mate choice) of their host.

If bacterial endosymbionts are (evolutionarily) advantageous to their host, we will expect a positive effect on their host's fitness. Aphids, for instance grow more slowly if kept void of *Buchnera* (ADAMS et al. 1996). Experimental tests of selective advantages to isopods from harboring hepatopancreatic bacteria in terms of higher growth rates, higher fecundity, or higher mating success thus far failed to demonstrate any gain to *P. scaber* (WANG & ZIMMER, unpubl.).

4. Leaf litter-colonizing microbiota

Interactions of woodlice and litter-colonizing microbiota can be classified either as predator-prey interactions, i.e., ingested microbiota are digested and utilized as food (e.g., Reyes & Tiedje 1976; Kozlovskaja & Striganova 1977; Coughtrey et al. 1980; Beck & Friebe 1981; Márialigeti et al. 1984; Gunnarsson & Tunlid 1986; Hassall et al. 1987; Zimmer & Topp 1998b), or as synergism or even mutualism with promotion of microbial biomass and/or activity and distribution of microbial propagules (Dunger 1958; Striganova 1967; Hassall 1977; Soma & Saito 1983; Hassall et al. 1987; Teuben & Roelofsma 1990; Teuben 1991; Lussenhop 1992; Szlávecz 1993; Van Wemsen et al. 1993; Kautz & Topp 2000; Zimmer & Topp 1999; Zimmer et al. 2002b) on one hand, and microbial processing of leaf litter prior to feeding by woodlice (Hartenstein 1964a; Rushton & Hassall 1983; Hassall et al. 1987) and/or during the gut passage (Hassall & Jennings 1975; Kukor & Martin 1986) on the other hand. With respect to the latter, it has been shown repeatedly that consumption of densely colonized leaf litter is advantageous both on individual (Uesbeck & Topp 1995; Zimmer & Topp 1997a) and on population level (Kautz et al. 2000; Zimmer & Topp 1997a, 2000). Despite this general agreement, the nutritive significance of litter-colonizing microbiota is not well understood in detail (Zimmer et al. 2003); the debated results and hypotheses can be summarized as follows:

(1) Digestion and utilization of microbial cells increase the nutritive value of leaf litter to consumers, since ingested microbiota – upon digestion – serve as source of easily accessible (essential?) nutrients, such as nitrogen (Carefoot 1984a,b; Ullrich et al. 1991). However, other strategies than utilizing microbiota as food source to cope with nitrogen limitation are known, too: shrimp, *Litopenaeus setiferus* (Decapoda: Penaeidae), respond to protein deficiency with increased production of proteolytic enzymes (Brito et al. 2000), and, similarly, aquatic detritivorous cranefly larvae (Diptera: Nematocera: Tipulidae) counteract the low nitrogen availability in their food with extremely efficient protein degradation in their midgut with a correspondingly high pH level of 11.5 (Martin et al. 1980) for optimal proteolytic activity and, at the same time, minimal harm through phenolic compounds (cf. Graça & Bärlocher 1998); in addition, β-1,4- and β-1,3-glucanases make the digestion of ingested fungi, and access to valuable, possibly even essential, nutrients, possible. Woodlice (*Trachelipus rathkii*) also exhibit these enzyme activities in their hindgut, and thus, are capable of digesting fungal cells (see above; Kukor & Martin 1986). Wood-boring isopods, *Limnoria* spp., although presumably producing endogenous cellulases (Ray & Julian 1952), are in need of wood-colonizing fungi as a supplemental source of high-quality food (Ray 1959).

According to the literature (e.g., Reyes & Tiedje 1976; Kozlovskaja & Striganova 1977; Coughtrey et al. 1980; Beck & Friebe 1981; Márialigeti et al. 1984; Gunnarsson & Tunlid 1986; Hassall et al. 1987), we know that ingested microbiota are digested in the anterior hindgut (Zimmer & Topp 1998b), and surviving cells are egested in feces (Coughtrey et al. 1980; Hanlon & Anderson 1980; Ineson & Anderson 1985; Hassall et al. 1987; Ullrich et al. 1991) after extensive proliferation (Gunnarsson & Tunlid 1986; Hassall et al. 1987) in the posterior hindgut (Zimmer & Topp 1998b). Thus, microbial density of feces equals or surpasses that of the ingested leaf litter (discussed in Zimmer 2002a). Due to the prevailing pH conditions in different gut sections (Zimmer & Topp 1997b; Zimmer & Brune 2005), however, this predominantly applies to bacteria but not to fungi (Zimmer & Topp 1998b).

Yeasts (*Saccharomyces cerevisiae*), accelerate growth and increase fecundity of the millipede, *Polydesmus angustus* (Myriapoda: Diplopoda), when experimentally supplemented to the diet (DAVID & CÉLÉRIER 1997); yeast cells are digested in the midgut of millipedes (BYZOV et al. 1993), but their energetic contribution to the consumers' nutrition is low, and DAVID & CÉLÉRIER (1997) assume them to be sources of nitrogen (see above). In earthworms (*Lumbricus terrestris*; Annelida: Oligochaeta), microbial cells are cleaved before they reach the foregut (SCHÖNHOLZER et al. 2002). During the subsequent gut passage, mostly Proteobacteria (gram-negative) of the α-, β- and γ-division are reduced in their number (SCHÖNHOLZER et al. 2002), but overall there is an increase in bacterial numbers from fore- to hindgut (SCHÖNHOLZER et al. 1999). By contrast, it is chiefly δ-Proteobacteria that proliferate on feces (SCHÖNHOLZER et al. 2002). The mayfly, *Ephemera danica* (Ephemeroptera), digests unselectively ingested bacterial species with different efficacies (AUSTIN & BAKER 1988): while gram-negative α-Proteobacteria – *Aeromonas hydrophila* (Aeromonadales) and *Citrobacter freundii* (Enterobacteriales) – are digested effectively, *Flavobacterium* spp. (Bacteroidetes = *Flavobacterium-Flexibacter-Bacteroides-Cytophaga* group: KIRCHMANN 2002; gram-negative) attach to the hindgut wall. In *Porcellio scaber*, too, we found specific digestibilities of different microbial taxa (IHNEN & ZIMMER, in prep.). Thus, digestibility of actinomycetes [gram-positive: *Streptomyces celluloflavus* (Streptomycetaceae) and *Pseudonocardia autotrophica* (Pseudonocardiaceae)] is significantly higher that that of gram-negative bacteria [*Pseudomonas fluorescens* (α-Proteobacteria: Pseudomonaceae) and *Myxococcus xanthus* (δ-Proteobacteria: Myxococcaceae)] and fungi [*Chaetomium globosum* (Ascomycetes: Pyrenomycetaceae) and *Fusarium ventricosum* (Deuteromycetes)], possibly due to cell wall characteristics. Digestive specificity is, in addition, reflected by feeding preferences (IHNEN & ZIMMER, in prep.). In preference tests, *P. scaber* consumed artificial diets in higher rates when inoculated with actinomycetes than any other offered food, no matter whether cellulolytic or non-cellulolytic microbiota were offered. Overall, microbial inoculation increased consumption rates only in case of low-quality food (cellulose), while consumption of diets of high quality (cf. ZIMMER & TOPP 1998b) was not altered by microbial inoculation. These results are in agreement with findings by KAUTZ et al. (2002), indicating a decreasing nutritional significance of feces-colonizing microbiota with increasing quality of the initial leaf litter material, but, on the other hand, contradict ZIMMER et al. (2003), concluding an increasing positive effect of litter-colonizing microbiota on digestion and utilization of food with increasing food quality. In any case, our recent results (IHNEN & ZIMMER, in prep.; see above) indicate (i) that microbiota obviously increase the attractiveness of low-quality food, but (ii) that microbial cellulases do not appear to be significant in this context (see also ZIMMER et al. 2003), since the increased consumption rates due to microbial inoculation did not depend on the cellulolytic capability of actinomycetes. Actinomycetes also increased consumption by *Oniscus asellus*, but the same was true for different microbiota and high-quality food (IHNEN & ZIMMER, in prep.). As already suggested by ZIMMER & TOPP (2000), *Porcellio scaber* and *Oniscus asellus* obviously differ from each other with respect to nutritional requirements.

In addition to the above potential direct nutritive gain, indirect ways of how ingested microbiota positively influence digestive processes have been described, too. In terrestrial isopods (*Porcellio scaber*), litter-colonizing microbiota appear to be involved in hindgut pH homeostasis (ZIMMER & TOPP 1997b) and in detoxification of phenolic compounds through providing surfactants

(ZIMMER 1997) and/or hydrolytic enzymes (ZIMMER 1999), releasing simple, harmless phenolics and glucose. However, the release of glucose is not always advantageous, since most microbial β-glucosidases are inhibited by their product glucose (cf. DECKER et al. 2001).

Similarly, bacterial proliferation in the hindgut need not have positive effects on a consumer, since the gut lumen may simply act as an incubator, providing appropriate environmental conditions, without any gain from microbial activity to the consumer, particularly if microbial proliferation occurs in the posterior hindgut where no resorption of nutrients takes place (as in terrestrial isopods: ZIMMER & TOPP 1998b). Woodlice appear to gain from bacterial proliferation in the posterior hindgut through being coprophagous (discussed in ZIMMER 2002a). The advantages of coprophagy to isopods have, however, been discussed controversially during the last couple of decades (summarized in ZIMMER 2002a; see also KAUTZ et al. 2002). While WIESER (1966) stressed the essential importance of coprophagy to survival of *Porcellio scaber*, others (WHITE 1968; COUGHTREY et al. 1980; HASSALL & RUSHTON 1982, 1985; HOPKIN & MARTIN 1984) maintained isopod populations in the laboratory without access to feces; SZLÁVECZ & MAIORANA (1998: *Porcellio scaber*) did not find any evidence for a nutritional advantage of being coprophagous, and this behavior may be insignificant in the field (HASSALL & RUSHTON 1982; HOPKIN & MARTIN 1984; but see above). In the laboratory, the gain from feeding on feces is generally low, but depends upon the quality of the initial leaf litter, increasing with decreasing litter quality (KAUTZ et al. 2002). It is only in case of low-quality food (e.g., wide C:N ratio) that microbial activity or biomass adds to the nutritive value of the feces, while high-quality litter is of higher value than feces. These findings are in good agreement of HASSALL's (pers. comm., see above) suggestion of different nutritive strategies in terrestrial isopods.

(2) Activity of microbial cells promotes digestion of leaf litter by consumers, since extracellular microbial enzymes are utilized for digestive processes (HASSALL & JENNINGS 1975; KUKOR & MARTIN 1986), and microbial processing of the leaf litter prior to consumption may be even more important. Woodlice prefer feeding on decomposing rather than fresh leaf litter (HARTENSTEIN 1964a; HASSALL et al. 1987; RUSHTON & HASSALL 1983), the former being reduced in toughness (RUSHTON & HASSALL 1983) and in phenolics and other repellents (KUITERS & SARINK 1986; POINSOT-BALAGUER et al. 1993; ZIMMER 2002b). BROOKS & BELL (2001) state that fungal processing of the substrate plays a significant role in habitat choice by the wood-boring *Sphaeroma terebrans* Bate, 1866 (Sphaeromatidea: Sphaeromatidae).

Wood wasps, *Sirex cyaneus* (Hymenoptera: Symphyta: Siricoidea: Siricidae), digest wood with assistance of enzymes derived from their fungal symbiont *Amylostereum chailletii* (Basidiomycetes) (KUKOR & MARTIN 1983). Unknown bacteria provide cellulases to desert millipedes (Myriapoda: Diplopoda: *Orthoporus ornatus* und *Comanchelus* sp.) (TAYLOR 1982). In marine blood-sucking isopods of the genus *Gnathia* (Gnathiidea: Gnathiidae) bacteria have been isolated from the hindgut that belong to the genera *Pseudomonas* (Pseudomonadales), *Bacillus* (Bacillales) und *Streptococcus* (Streptococcales) and presumably are involved in digesting fish blood (JUILF & WÄGELE 1987; DAVIES 1995). In natural microbial soil communities, *Pseudomonas fluorescens* is one of the most effective degraders of humic acids (FILIP & BIELEK 2002), but complex bacterial communities are much better in degrading such substances than any tested isolate (ESHAM et al. 2000). By contrast, it is mostly fungi that are responsible for the degradation of aromatic compounds in wood and leaf litter (cf. RABINOVICH et al. 2004).

Enzymes of microbial origin may also play a role in the digestion of ingested microbiota. The degradation of chitin in the gut of fungus-feeding springtails, *Folsomia candida* (Collembola: Isotomidae), is brought about by *Xanthomonas maltophilia* (γ-Proteobacteria: Pseudomonaceae) and *Curtobacterium* sp. (Actinomycetales: Corynebacteriaceae) (BORKOTT & INSAM 1990). In consequence, leaf litter that is inoculated with these bacteria is preferred as food, but mechanisms of how springtails find and choose this food source remain unclear. In *Porcellio scaber*, volatile microbial metabolites are detected by olfaction and serve in finding food by foraging isopods (ZIMMER et al. 1996).

(3) In both of the above cases, we would expect increased digestibility by, as well as higher growth rates of, consumers. Alternatively, litter-colonizing microbiota may serve as indicators of nutrient-rich, easily digestible food source that are used as cues while foraging. Actually, *Porcellio scaber* responds positively to volatile metabolites of litter-colonizing microbiota (ZIMMER et al. 1996). If so, we expect increased consumption of densely colonized litter, while digestion and growth may be affected only marginally. Recent results by ZIMMER et al. (2003) are in favor of the latter hypothesis: microbial inoculation of experimental food increased consumption and slightly enhanced growth rates, but did not affect digestibility.

The millipede, *Polydesmus angustus*, by contrast, did not show any effect of microbial colonization (yeasts) of experimental food on mortality, but both growth and fecundity were promoted significantly (DAVID & CÉLÉRIER 1997). These authors conclude that the microbial contribution to nutrition is qualitative rather than quantitative (see above). In contrast to our recent results (ZIMMER et al. 2003), previous studies revealed a positive effect of litter-colonizing microbiota on female fecundity and juvenile mortality (ZIMMER & TOPP 1997a). Thus, the nutritional significance of litter-colonizing microbiota is not only species-specific, but also depends on the context. Both extracellular microbial enzymes and essential nutrients may promote some physiological processes that are related to growth and reproduction. In addition, the litter itself appears to be of predominantly quantitative importance. Such nutritional differences have been demonstrated in a comparison of aquatic detritivores, *Asellus aquaticus* and *Gammarus pulex*; while isopods preferentially graze fungal biomass off the leaf surface and thus directly depends on fungal biomass, amphipods consume fungally inoculated and processed leaf litter. As we demonstrated for terrestrial isopods (see above; IHNEN & ZIMMER, in prep.), the fungal species is of crucial significance for the nutritive value of the fungal biomass (BÄRLOCHER & KENDRICK 1973a,b).

5. Gut microbiota and their environment

Until now is unclear, and still controversially debated, whether (species-specific?) resident gut microbes exist in terrestrial isopods, or whether the community of gut microbiota is a random assemblage that depends on the ingested food with microbes simply being passive gut passengers. The abundance of *Chryseobacterium* sp. (Bacteroidetes) in the hindgut of the cockroach, *Periplaneta americana* (Blatteroptoidea: Blattodea: Blattariae), alters with changing food sources (DUGAS et al. 2001), and the abundance of *Mycoplasma* sp. in the gut of the Atlantic Salmon, *Salmo salar* (Salmonidae), differs between populations fed on different food sources (HOLBEN et al. 2002). By contrast, the microbial community in the hindgut of *Neotrypeaea* (*Callianassa*) *californiensis* (Decapoda: Thalassinidae) seems to be independent of nutritional conditions. Predominantly α-Proteobacteria, Bacteroidetes and gram-positive bacteria make up the resident gut microbiota (LAU et al. 2002).

HASSALL & JENNINGS (1975) doubted the existence of microbial residents in the isopod hindgut, while other authors disagreed (summarized in ZIMMER 2002a). In starving crinochete isopods (REYES & TIEDJE 1976; BECK & FRIEBE 1981; INESON & ANDERSON 1985), and during feeding on sterile artificial diet (ZIMMER & TOPP 1998b; ZIMMER 1999), the number of gut microbes is drastically reduced. Both observations argue against resident gut microbes. CAREFOOT (1984a), however, did not notice any changes in the microbial community of *Ligia pallasii* after five weeks of starving; two out of 21 platable bacteria were only found in the hindgut but not on stranded macroalgae, the natural food source of this species (SPENCE, unpubl.; cited in CAREFOOT 1984b).

GUNNARSSON & TUNLID (1986) assumed gram-positive bacteria to prevail in the hindgut of *O. asellus*, and ULLRICH et al. (1991) characterized predominantly coryneformous Micrococcaceae (Firmicutes). Most other investigators, however, mainly found gram-negative bacteria. BEERSTECHER et al. (1954) isolated nitrogen-fixing *Azotobacter* sp. (γ-Proteobacteria: Azotobacteriaceae) in the hindgut of cf. *Armadillidium vulgare*. REYES & TIEDJE (1976) were unable to find some of the (gram-negative) bacteria that colonized feces of *Trachelipus rathkii* in the litter layer, while hindgut and feces were similar in species composition, and HASSALL et al. (1987) isolated (cellulolytic?) *Cytophaga* spp. (Bacteroidetes) from feces of *O. asellus* that could not be detected in the leaf litter, either. As early as 1985, GRIFFITHS & WOOD (1985) found irregularly distributed rod-shaped bacteria in close association with the (posterior) hindgut cuticle of *Oniscus asellus* that they affiliated to the genera *Pseudomonas* (see also REYES & TIEDJE 1976: *Trachelipus rathkii*), *Plesiomonas* (Vibrionaceae) and *Enterobacter* (along with other Enterobacteriaceae) of the gram-negative γ-Proteobacteria – at least some representative of these genera are (facultatively) anaerobic (see below). GRIFFITHS & WOOD (1985) did not notice actinomycetes, and MÁRIALIGETI et al. (1984) proposed that these gram-positive bacteria do not belong to any kind of gut community but are passive gut passengers. DROBNE et al. (1996) described by means of SEM filamentous and rod-shaped bacteria attached to the hindgut wall in *Porcellio scaber*, but did not provide any information on whether or not these bacteria were also detectable in feces and/or litter. Later, KOSTANJIŠEK et al. (2002) found high bacterial diversity in the hindgut of this species and concluded from results of molecular studies that about half of the present species are not only unknown, but share less than 80 % sequence similarity with any known bacteria. About 70 % of these bacteria are, however, distantly related to typical (anaerobic) intestinal bacteria, namely Streptococci and Enterococci (Streptococcales; gram-positive) and *Bacteroides* group (Bacteroidetes; gram-negative), while the remaining species are related to soil bacteria such as *Bacillus* and *Pseudomonas*. From these data, and from that some bacteria are specifically attached to cuticular spines of the hindgut, KOSTANJIŠEK et al. (2002) concluded that *Porcellio scaber* do harbor resident gut microbiota. Similarly, DROBNE (1995) described numerous bacteria in association with the hindgut cuticle of *Porcellio scaber* – some of them having been characterized by KOSTANJIŠEK et al. (2002) – and *Ligidium hypnorum* (Diplocheta: Ligiidae), but not in *Hyloniscus riparius* (Synocheta: Trichoniscidae). On the other hand, freshly molted *Porcellio scaber* and *Ligidium hypnorum* do not contain cuticle-attached bacteria in their hindgut (DROBNE 1995); she discusses this observation as active protective mechanism by the isopod against microbial infection during a sensitive phase with a unsklerotized gut cuticle, and thus, proposes re-acquisition of specific bacteria from the environment (see above).

Despite the assumption of a relatively short gut passage of several hours (HARTENSTEIN 1964a, in *Oniscus asellus*; ALIKHAN 1969, in *Porcellio laevis*; ZIMMER 1998, in *Porcellio scaber*; GRÜNWALD 1987, in different species), fluorescent markers of the size of bacterial cells could be detected as long as 16 days after ingestion by *Porcellio scaber* (CLEGG et al. 1996). Bacteria can be expected to be retained in and on cuticular structures (wrinkles and spines) and to remain in the gut for some time as transient resident (KOSTANJŠEK et al. 2002). Since some of the mentioned bacteria are taxonomically related to obligate anaerobic species, we have to consider that the radial center of the hindgut, but not the periphery is anoxic (ZIMMER & BRUNE 2005); thus, anoxic microhabitats in cuticular wrinkles are to be postulated.

As early as 1976, REYES & TIEDJE (1976) suggested hypoxic conditions to prevail in the hindgut of *Trachelipus rathkii* due to oxygen consumption and limited gas diffusion, and MÁRIALIGETI et al. (1984) proposed facultatively anaerobic microbiota (mostly actinomycetes) to be the most stable gut passengers. The assumption of aerobic activity and oxygen consumption is confirmed by *in situ* and *in vivo* measurements with microelectrodes, demonstrating an oxic hindgut periphery but an anoxic hindgut center (ZIMMER & BRUNE 2005). Thus, the periphery allows for aerobic and oxidative digestive processes, while the radial center may be a site of fermentative degradation. However, thus far, we could not detect any fermentation products.

Optimal pH conditions for digestive processes (cellulose digestion and phenol oxidation) in the anterior, and for bacterial proliferation in the posterior, hindgut as well as coinciding redox potentials were also demonstrated by utilizing microelectrodes *in situ* (ZIMMER & BRUNE 2005). Both cellulases and most known phenol oxidases exhibit maximal activity under these pH conditions (HARTENSTEIN 1964a; MAYER & HAREL 1979; WOOD 1980; ZIMMER & TOPP 1997b), and actually, pH gradients are reflected by gradients of enzymatic activities (HARTENSTEIN 1964b; SALEEM & ALIKHAN 1974; HASSALL & JENNINGS 1975; ZIMMER & TOPP 1998a,b; ZIMMER 1999). Exceptionally high redoxpotentials of > +600 mV in the hindgut and the midgut glands facilitate the aerobic and oxidative degradation of leaf litter compounds. Despite potentially harmful or toxic effects of phenolic litter compounds at acidic pH conditions (BERENBAUM 1980; MARTIN & MARTIN 1983; SCHULTZ & LECHOWICZ 1986) and under oxidizing conditions (APPEL 1993), a slightly acidic gut pH of 5.0-6.0 in the anterior hindgut (Crinocheta: ZIMMER & TOPP 1997b; ZIMMER & BRUNE 2005), thus, appears to be adaptive to the need of digesting the most common leaf litter compounds. Further, surfactants (ZIMMER 1997) and tannin hydrolysis (ZIMMER 1999) in the hindgut lumen counteract potentially damage caused by phenolics. Proliferation of surviving bacteria in the posterior hindgut takes place under optimal pH conditions of 5.5-7.0 (ZIMMER & TOPP 1998b). A rise in pH, thus, seems to be adaptive with respect to coprophagy (see above), since favorable conditions for microbial processing of undigested litter compounds are provided in freshly dropped feces. Homeostasis of gut pH in the hindgut lumen have been attributed to cell compounds of ingested and digested microbiota (ZIMMER & TOPP 1997b). ZIMMER & BRUNE (2005), by contrast, discuss pH reduction as a consequence of fermentative digestive processes in the anoxic hindgut center; the rise of pH in the posterior hindgut would then be brought about by active influx of K^+ ions as has been described for caterpillars (DOW 1992).

While NICHOLLS (1931) in *Ligia oceanica* also found a pH gradient of 6.0 to 7.2, the pH level in the anterior hindgut of *Tylos granulatus* Krauss, 1843 (Tylida: Tylidae) changes from 6.9 to 7.4 to drop to 6.8 again

in the posterior hindgut (KENSLEY 1974). In the hindgut of *Trichoniscus pusillus* it is solely the most anterior section that exhibits a higher pH (6.8) than the remaining regions with pH 6.3-6.5 (ZIMMER & BRUNE 2005). Overall, the pH gradients are rather insignificant in the latter species as compared with *Ligia oceanica* and some studied Crinocheta; furthermore, the gut pH is significantly higher in *Ligia oceanica*, *Tylos granulatus* and *Trichoniscus pusillus* than in any of the studied Crinocheta. No pattern in hepatopancreatic pH can be brought in congruence with isopod phylogeny (ZIMMER & BRUNE 2005): values range from 6.1 in *Oniscus asellus* and *Porcellio scaber* to 6.3 in *Tylos granulatus* (KENSLEY 1974) and 6.5 in *Trichoniscus pusillus* and *Trachelipus rathkii*. In homogenates of the midgut glands WOOD & GRIFFITHS (1988) used colored indicators to determine data of pH 4.7-5.4 and pH 5.4-6.1 in *Oniscus asellus* and *Porcellio scaber*. Thus, the nutritive and/or evolutionary significance of these differences between phylogenetic lineages of Oniscidea remains unclear.

6. Conclusions

Although we do not yet fully understand isopod-microbe interactions in detail, it is obvious that microbiota are significant to the ecology of terrestrial isopods, and may have been important evolutionarily in the course of terrestrialization. Possibly, the acquisition of hepatopancreatic symbionts rendered woodlice less dependent on litter-colonizing microbiota. Although the nutritional utilization of terrestrial leaf litter is promoted by litter-colonizing microbiota through their activity and their role as a supplementary nutrient source, and this may have facilitated the evolutionary colonization of land, woodlice appear to be able to feed upon litter of low quality – low microbial density, wide C:N ratio, high structural toughness – during early stages of decomposition. This difference to other detritivores, brought about by endosymbiotic bacteria, may explain the evolutionary success of terrestrial isopods as detritivores ages after occupation of this niche by insects, millipedes and eartworms, but the function(s) of hepatopancreatic bacteria as well as how they interact with their host are only beginning to be understood.

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References

ABE, T., HIGASHI, M., 1991: Cellulose centered perspective on terrestrial community structure. – Oikos **60**, 127-133.

ABRIL, B.A., BUCHER, E.H., 2002: Evidence that the fungus cultured by leaf-cutting ants does not metabolize cellulose. – Ecology Letters **5**, 325-328.

ADAMS, D., WILKINSON, T.L., DOUGLAS, A.E., 1996: The aphid-bacterial symbiosis: a comparison between pea aphids and black bean aphids. – Entomologia Experimentalis at Applicata **80**, 275-278.

AHMAD, S., 1992: Biochemical defense of pro-oxidant plant allelochemicals by herbivorous insects. – Biochemical Systematics and Ecology **20**, 269-296.

ALIKHAN, M.A., 1969: The physiology of the woodlouse, *Porcellio laevis* (Porcellionidae: Peracarida) – I: Studies on the gut epithelium cytology and its relation to maltase se-

cretion. – Canadian Journal of Zoology **47**, 65-75.

ALTHOFF, K., SCHÜTT, C., STEFFEN, R., BATEL, R., MÜLLER, W.E.G., 1998: Evidence for a symbiosis between bacteria of the genus *Rhodobacter* and the marine sponge *Halichondria panicea*: harbor also for putatively toxic bacteria? – Marine Biology **130**, 529-536.

ANDER, P., ERIKSSON, K.-E., 1976: The importance of phenol oxidase activity in lignin degradation by the white-rot fungus *Sporotrichum pulverulentum*. – Archives of Microbiology **109**, 1-8.

ANDERSON, S.O., 1985: Sclerotization and tanning of the cuticle, pp. 59-75. In: Comprehensive insect physiology, biochemistry and pharmacology (Kerkut, G.A., Gilbert, L.I., eds). – Pergamon Press, Oxford.

ANDERSON, C.L., KARR, T.L., 2001: *Wolbachia*: evolutionary novelty in a rickettsial bacteria. – BMC Evolutionary Biology **1**, 10.

APPEL, H.M., 1993: Phenolics in ecological interactions: the importance of oxidation. – Journal of Chemical Ecology **19**, 1521-1552.

AUSTIN, D.A., BAKER, J.H., 1988: Fate of bacteria ingested by larvae of the freshwater mayfly, *Ephemera danica*. – Microbial Ecology **15**, 323-332.

BÄRLOCHER, F. 1982: The contribution of fungal enzymes to the digestion of leaves by *Gammarus fossarum* Koch (Amphipoda). – Oecologia **52**, 1-4.

BÄRLOCHER, F., KENDRICK, B., 1973a: Fungi in the diet of *Gammarus pseudolimnaeus* (Amphipoda). – Oikos **24**, 295-300.

BÄRLOCHER, F., KENDRICK, B., 1973b: Fungi and food preferences of *Gammarus pseudolimnaeus*. – Archiv für Hydrobiologie **72**, 501-516.

BÄRLOCHER, F., PORTER, C.W., 1986: Digestive enzymes and feeding strategies of three stream invertebrates. – Journal of the North American Benthological Society **5**, 58-66.

BAKER, J.E., WOO, S.M., 1992: α-glucosidases in the rice weevil, *Sitophilus oryzae*: purification, properties, and activity levels in wheat- and legume-feeding strains. – Insect Biochemistry and Molecular Biology **22**, 495-504.

BAUMANN, P., MORAN, N.A., 1997: Non-cultivable microorganisms from symbiotic associations with insects and other hosts. – Antonie van Leeuwenhoek **72**, 39-48.

BECK, L., FRIEBE, B., 1981: Verwertung von Kohlenhydraten bei *Onsicus asellus* (Isopoda) und *Polydesmus angustus* (Diplopoda). – Pedobiologia **21**, 19-29.

BEERSTECHER, E., CORNYN, J., VOLKMANN, C., CARDO, L., HARPER, R., 1954: Invertebrate nutrition I: a preliminary survey of the nutritional requirements of an isopod: *Oniscus asellus*. – Texas Reports on Biology and Medicine **12**, 207-210.

BENHALIMA, K., MORIYASU, M., 2001: Prevalence of bacteria in the spermathecae of female snow crab, *Chinoectes opilio* (Brachyura: Majidae). – Hydrobiologia **449**, 261-266.

BERENBAUM, M., 1980: Adaptive significance of midgut pH in larval Lepidoptera. – The American Naturalist **115**, 138-146.

BERNAYS, E.A., KLEIN, B.A., 2002: Quantifying the symbiont contribution to esssential amino acids in aphids: the importance of tryptophan for *Uroleucon ambrosiae*. – Physiological Entomology **27**, 275-284.

BIRD, D.M., OPPERMAN, C.H., DAVIES, K.G., 2003: Interactions between bacteria and plant-parasitic nematodes: now and then. – International Journal of Parasitology **33**, 1269-1276.

BORKOTT, H., INSAM, H., 1990: Symbiosis with bacteria enhances the use of chitin by the springtail, *Folsomia candida* (Collembola). – Biology and Fertility of Soils **9**, 126-129.

BOUCHER, D.H., JAMES, S., KEELER, K.H., 1982: The ecology of mutualisms. – Annual Review of Ecology and Systematics **13**, 315-347.

BREZNAK, J.A., BRUNE, A., 1994: Role of microorganisms in the digestion of lignocellulose by termites. – Annual Review of Entomology **39**, 453-487.

BRITO, R., CHIMAL, M.E., GAXIOLA, G., ROSAS, C., 2000: Growth, metabolic rate, and digestive enzyme activity in the white shrimp *Litopenaeus setiferus* early postlarvae fed different diets. – Journal of Experimental Marine Biology and Ecology **255**, 21-36.

BROOKS, D.R., 1985: Historical ecology: a new approach to studying the evolution of ecological associations. – Annals of the Missouri Botanical Garden **72**, 660-680.

BROOKS, M.A., 1970: Comments on the classification of intracellular symbiotes of cockroaches and a description of the species. – Journal of Invertebrate Pathology **16**, 249-258.

BROOKS, R.A., BELL, S.S., 2001: Colonization of a dynamic substrate: factors influencing recruitment of the wood-boring isopod, *Sphaeroma*

terebrans, onto red mangrove (*Rhizophora mangle*) prop roots. – Oecologia **127**, 522-532.

Brusca, R.C., Wilson, G.D.F., 1991: A phylogenetic analysis of the Isopoda with some classificatory recommendations. – Memoirs of the Queensland Museum **31,** 143-204.

Buchner, P., 1965: Endosymbiosis of animals with plant microorganisms. – Interscience, New York.

Buckling, A., Rainey, P.B., 2002: The role of parasites in sympatric and allopatric host diversification. – Nature **420**, 496-499.

Byzov, B.A., Nguyen Thanh, V., Babjeva, I.P., 1993: Interrelationships between yeasts and soil diplopods. – Soil Biology and Biochemsitry **25**, 1119-1126.

Carefoot, T.H., 1984: Studies on the nutrition of the supralitoral isopod *Ligia pallasii* using chemically defined artificial diets: assessment of vitamin, carbohydrate, fatty acid, cholesterol and mineral requirements. – Comparative Biochemistry and Physiology A **79**, 655-665.

Carefoot, T.H., 1984: Nutrition and growth of *Ligia pallasii*. – Symposia of the Zoological Society of London **53**, 455-467.

Carefoot, T.H., 1993: Physiology of terrestrial isopods. – Comparative Biochemistry and Physiology A **106**, 413-429.

Carefoot, T.H., Taylor, B.E., 1995: *Ligia*: a prototypal terrestrial isopod, pp. 47-60. In: Terrestrial isopod biology (Alikhan MA, ed). – Balkema, Rotterdam.

Cazemier, A.E., Hackstein, J.H.P., Op den Camp, H.J.M., Rosenberg, J., van der Drift C., 1997: Bacteria in the intestinal tract of different species of arthropods. – Microbial Ecology **33**, 189-197.

Charles, H., Ishikawa, H., 1999: Physical and genetic map of the genome of *Buchnera*, the primary symbiont of the pea aphid *Acyrthosiphon pisum*. – Journal of Molecular Evolution **48**, 142-150.

Claus, H., Filip, Z., 1990: Effects of clays and other solids on the activity of phenoloxidases produced by some fungi and actinomycetes. – Soil Biology and Biochemistry **22**, 483-488.

Clegg, C.D., Anderson, J.M., Lappin-Scott, H.M., 1996: Biophysical processes affecting the transit of a genetically-modied *Pseudomonas fluorescens* through the gut of the woodlouse *Porcellio scaber*. – Soil Biology and Biochemistry **28**, 997-1004

Cordaux, R., Michel-Salzat, A., Bouchon, D., 2001: *Wolbachia* infection in crustaceans: novel hosts and potential routes for horizontal transmission. – Journal of Evolutionary Biology **14**, 237-243.

Coughtrey, P.J., Martin, M.H., Chard, J., Shales, S.W., 1980: Micro-organisms and metal retention in the woodlouse *Oniscus asellus*. – Soil Biology and Biochemistry **12**, 23-27.

Currie, C.R., Scott, J.A., Summerbell, R.C., Malloch, D., 1999: Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. – Nature **398**, 701-704.

Dale, C., Maudlin, I., 1999: *Sodalis* gen. nov. and *Sodalis glossinidius* sp. nov., a microaerophilic secondary endosymbiont of the tsetse fly *Glossina morsitans morsitans*. – International Journal of Systematic Bacteriology **49**,267-275.

David, J.-F., Célérier, M.-L., 1997: Effects of yeast on the growth and the reproduction of the saprophagous millipede *Polydesmus angustus* (Diplopoda, Polydesmidae). – Biology and Fertility of Soils **24**, 66-69

Davies, A.J., 1995: Studies on the gut flora of the haematophagous fish parasite *Gnathia maxillaris* Montagu. – Bulletin of the European Association of Fish Pathology **15**, 32-35.

Decker, C.H., Visser, J., Schreier, P., 2001: β-Glucosidase multiplicity from *Aspergillus tubingensis* CBS 643.92: purification and characterization of four β-glucosidases and their differentiation with respect to substrate specificity, glucose inhibition and acid tolerance. – Applied Microbiology and Biotechnology **55**, 157-163.

Decker, H., Tuczek, F., 2000: Tyrosinase/catecholoxidase activity in hemocyanins: structural basis and molecular mechanism. – Trends in Biochemical Sciences 25, 392-397.

de Knecht, J.A., Stroomberg, G.J., Tump, C., Helms, M., Verweij, R.A., Commandeur, J., van Gestel, C.A., van Straalen, N.M., 2001: Characterization of enzymes involved in biotransformation of polycyclic hydrocarbons in terrestrial isopods. – Environmental Toxicology and Chemistry **20**, 1475-1464.

D'Ettore, P., Mora, P., Dibangou, V., Rouland, C., Errard, C., 2002: The role of the symbiotic fungus in the digestive metabolism of two species of fungus-growing ants. – Journal of Comparative Physiology B **172**, 169-176.

DEZFULI, B.S., 2000: Host-parasite interfaces between *Asellus aquaticus* (Isopoda) and larvae of *Acanthocephalus anguillae* (Acanthocephala). – Folia Parasitologica 47, 154-156.

DOBZHANSKY, T., 1973: Nothing in biology makes sense except in the light of evolution. – American Biology Teacher **35**, 125-129.

DOEBELI, M., DIECKMANN, U., 2000: Evolutionary branching and sympatric speciation caused by different types of ecological interactions. – The American Naturalist **156**, S77-S101.

DONADEY, C., BESSE, G., 1972: Étude histologique ultrastructurale et expérimentale des caecums digestifs de *Porcellio dilatatus* et Ligia oceanica (Crustacea, Isopoda). – Téthys **4,** 145-162.

DOUGLAS, A.E., 1980: Establishment of the symbiosis in *Convoluta roscoffensis*. – Journal of the Marine Biological Association UK **63**, 419-434.

DOUGLAS, A.E., 1989: Mycetocyte symbiosis in insects. – Biological Reviews **64**, 409-434.

DOUGLAS, A.E., 1992a: Symbiosis in evolution. – Oxford Surveys in Environmental Biology **8**, 347-382.

DOUGLAS, A.E., 1992b: Microbial brokers of insect-plant interactions, pp. 329-336. In: Proceedings of the 8th International Symposium on Insect-plant relationships (Menken, S.B.J., Visser, J.H., Harrewijn, P., eds). – Kluwer Academic Publishers: Dordrecht.

DOUGLAS, A.E., 1995: The ecology of symbiotic micro-organisms. – Advances in Ecological Research **26**, 69-103.

DOUGLAS, A.E., MINTO, L.B., WILKINSON, T.L., 2001: Quantifying nutrient production by the microbial symbionts in an aphid. – Journal of Experimental Biology **204**, 349-358.

DOUGLAS, A.E., RAVEN, J.A., 2003: Genomes at the interface between bacteria and organelles. – Philosophical Transactions of the Royal Society of London: Biological Sciences **358**, 5-18.

DOW, J.A.T., 1992: pH gradients in lepidopteran midgut. – Journal of Experimental Biology **172**, 355-375.

DOWD, P.F., 1989: In situ production of hydrolytic detoxifying enzymes by symbiotic yeasts in the cigarette beetle (Coleoptera: Anobiidae). – Journal of Economical Entomology **82**, 396-400.

DROBNE, D., 1995: Bacteria adherent to the hindgut of terrestrial isopods. – Acta Microbiologica et Immunologica Hungarica **42**, 45-52.

DROBNE, D., PRIMOZ, Z., ŠTRUS, J., 1996: SEM Analysis of midgut glands in isopod *Porcellio scaber* (Isopod, Crustacea) fed with metal contaminated food. – Journal of Computer-Assisted Microscopy **8**, 249-250.

DROGE, M., PUHLER, A., SELBITSCHKA, W., 1998: Horizontal gene transfer as a biosafety issue: a natural phenomenon of public concern. – Journal of Biotechnology **64**, 75-90.

DUGAS, J.E., ZUREK, L., PASTER, B.J., KEDDIE, B.A., LEADBETTER, E.R., 2001: Isolation and characterization of a *Chryseobacterium* strain from the gut of the American cockroach, *Periplaneta americana*. – Achives of Microbiology **175**, 259-262.

DUNGER, W., 1958: Über die Zersetzung der Laubstreu durch die Boden-Makrofauna im Auenwald. – Zoologisches Jahrbuch Systematik und Ökologie **86**, 139-180.

EDNEY, E.B., 1954: Woodlice and the land habitat. – Biological Reviews **29**, 185-220.

EDNEY, E.B., 1968: Transition from water to land in isopod crustaceans. – American Zoologist **8**, 309-326.

ERASMUS, J.H., COOK, P.A., COYNE, V.E., 1997: The role of bacteria in the digestion of seaweed by the abalone *Haliotis midae*. – Aquaculture **155**, 377-386.

ERIKSSON, K.-E., 1978: Enzyme mechanisms involved in cellulose hydrolysis by the rot fungus *Sporotrichum pulveruletum*. – Biotechnology and Bioengineering **20**, 317-332.

ERIKSSON, K.-E., WOOD, T.M., 1985: Biogeradation of cellulose, pp. 469-504. In: Biosynthesis and biodegradation of wood components (Higuchi, T., ed.). – Academic Press: London.

ESHAM, E.C., YE, W., MORAN, M.A., 2000: Identification and characterization of humic substances-degrading bacterial isolates from an estuarine environment. – FEMS Microbiology Ecology **34**, 103-111.

EVANS, C.S., GALLAGHER, I.M., ATKEY, P.T., WOOD, D.A., 1991: Localisation of degradative enzymes in white-rot decay of lignocellulose. – Biodegradation **2**, 93-106.

FARRANT, J.L., SANSONE, A., CANVIN, J.R., PALLEN, M.J., LANGFORD, P.R., WALLIS, T.S., DOUGAN,. G., KROLL, J.S., 1997: Bacterial copper- and zinc-cofactored superoxide dismutase contributes to the pathogenesis of systemic salmonellosis. – Molecular Microbiology **25**, 785-796.

FAURE, D., BOUILLANT, M.-L., BALLY, R., 1995: Comparative study of substrates and inhibitors of *Azospirillum lipoferum* and *Pyricularia oryzae* laccases. – Applied and Environmental Microbiology **61**, 1144-1146.

FEINSINGER, P., 1983: Coevolution and pollination, pp. 282-310. In: Coevolution (Futuyma, D.J., Slatkin, M., eds). – Sinauer Associates, Sunderland (MA).

FERREIRA, C., TERRA, W.R., 1983: Physical and kinetic properties of a plasma-membrane-bound α-D-glucosidase (cellobiase) from midgut cells of an insect (*Rhynchosciara americana* larva). – Biochemistry Journal **213**, 43-51.

FILIP, Z., BIELEK, P., 2002: Susceptibility of humic acids from soils with various contents of metals to microbial utilization and transformation. – Biology and Fertility of Soils **36**, 426-433.

FUKATSU, T., TSUCHIDA, T., NIKOH, N., KOGA, R., 2001: *Spiroplasma* symbiont of the pea aphid, *Acyrthosiphon pisum* (Insecta: Homoptera). – Applied and Environmental Microbiology 67, 1284-1291.

FUTUYMA, D.J., 1986: Evolutionary Biology. – Sinauer Associates, Sunderland (MA), USA.

GIJZEN, H.J., VAN DER DRIFT, C., BARUGAHARE, M., OP DEN CAMP, H.J.M., 1994: Effect of host diet and hindgut microbial composition on cellulolytic activity in the hindgut of the American Cockroach, *Periplaneta americana*. – Applied and Environmental Microbiology **60**, 1822-1826.

GILLESPIE, J.P., KANOST, M.R., TRENCZEK, T., 1997: Biological mediators of insect immunity. – Annual Review of Entomology **42**, 611-643.

GOMULKIEWICZ, R., NUISMER, S.L., THOMPSON, J.N., 2003: Coevolution in variable mutualisms. – The American Naturalist **162**, S80-S93.

GORVETT, H., 1952: The tegumental glands in the land Isopoda C – the lobed glands: the properties of their secretion and their mode of action. – Quarterly Journal of Microscopic Sciences **93**, 17-29.

GOULD, S.J., 1989: A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. – Evolution **43**, 516-539.

GOULD, S.J., VRBA, E.S., 1982: Exaptation – a missing term in the science of form. – Paleobiology **8**, 4-15.

GRAÇA, M.A.S., BÄRLOCHER, F., 1998: Proteolytic gut enzymes in *Tipula caloptera* – interaction with phenolics. – Aquatic Insects **21**, 11-18.

GRIFFITHS, B.S., WOOD, S., 1985: Microorganisms associated with the hindgut of *Oniscus asellus* (Crustacea, Isopoda). – Pedobiologia **28**, 377-381.

GRÜNWALD, M., 1987: Adaption und Dekompositionsleistung von Landasseln (Isopoda, Oniscidea) an Standorten der Großen Brennessel (*Urtica dioica* L). – Hochschulsammlung Naturwissenschaften – Biologie 20. Dissertation, Universität Bayreuth.

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

GUNNARSSON, T., TUNLID, A., 1986: Recycling of fecal pellets in isopods: microorganisms and nitrogen compounds as potential food for *Oniscus asellus*. – Soil Biology and Biochemistry **18**, 595-600.

HAGERMAN, A.E., BUTLER, L.G., 1991: Tannins and lignins, pp. 355-388. In: Herbivores: Their interactions with secondary plant metabolites I: The chemical participants (Rosenthal, G.A., Berenbaum, M.R., eds). – Academic Press, New York.

HANLON, R.D.G., ANDERSON, J.M., 1980: Influence of macroarthropod feeding activities on microflora in the decomposing oak leaves. – Soil Biology and Biochemistry **12,** 255-261.

HARRIS, J.M., 1993: The presence, nature, and role of gut microflora in aquatic invertebrates: a synthesis. – Microbial Ecology **25**, 195-231.

HARRIS, J.M., SEIDERER, L.J., LUCAS, M.I., 1991: Gut microflora of two saltmarsh detritivore Thalassinid prawns, *Ubogebia africana* and *Callianassa kraussi*. – Microbial Ecology **21**, 63-82.

HARTENSTEIN, R., 1964a: Feeding, digestion, glycogen and the environmental conditions of the digestive system in *Oniscus asellus*. – Journal of Insect Physiology **10**, 611-621.

HARTENSTEIN, R., 1964b: Histochemical and spectrophotometrical studies on several dehydrogenases of carbohydrate metabolism in *Oniscus asellus*. – Journal of Insect Physiology **10**, 623-631.

HARTENSTEIN, R., 1968: Nitrogen metabolism in the terrestrial isopod, *Oniscus asellus*. – American Zoologist **8**, 507-519.

HASSALL, M., 1977: Consumption of leaf litter by the terrestrial isopod *Philoscia muscorum* in relation to food availability in a dune grassland ecosystem. – Ecological Bulletin **45**, 550-553.

HASSALL, M., JENNINGS, J.B., 1975: Adaptive features of gut structure and digestive physiology in the terrestrial isopod *Philoscia muscorum* (Scopoli) 1763. – Biological Bulletin **149**, 348-364.

HASSALL, M., RUSHTON, S.P., 1982: The role of coprophagy in the feeding strategies of terrestrial isopods. – Oecologia **53**, 374-381.

HASSALL, M., RUSHTON, S.P., 1985: The adaptive significance of coprophagous behaviour in the terrestrial isopod *Porcellio scaber*. – Pedobiologia **28**, 169-175.

HASSALL, M., TURNER, J.G., RANDS, M.R.W., 1987: Effects of terrestrial isopods on the decomposition of woodland leaf litter. – Oecologia **72**, 597-604.

HELLIO, C., BREMER, G., PONS, A.M., LE GAL, Y., BOURGOUGNON, N., 2000: Inhibition of the development of microorganisms (bacteria and fungi) by extracts of marine algae from Brittany, France. – Applied Microbiology and Biotechnology **54**, 543-549.

HENNIG, W., 1966: Phylogenetic systematics. – University of Illinois Press, Urbana.

HILL, K.E., WEIGHTMAN, A.J., 2003: Horizontal trnasfer of dehalogenase genes on IncP1â plasmids during bacterial adaptation to degrade α-halocarboxylic acids. – FEMS Microbiology Ecology **45**, 273-282.

HOLBEN, W.E., WILLIAMS, P., SAARINEN, M., SÄRKILAHTI, L.K., APAJALAHTI, J.H.A., 2001: Phylogenetic analysis of intestinal microflora indicates a novel *Mycoplasma* phylotype in farmed and wild salmon. – Microbial Ecology **44**, 175-185.

HOLD, G.L., SMITH, E.A., RAPPÉ, M.S., MAAS, E.W., MOORE, E.R.B., STROEMPL, C., STEPHEN, J.R., PROSSER, J.I., BIRKBECK, H., GALLACHER, S., 2001: Characterisation of bacterial communities associated with toxic and non-toxic dinoflagellates: *Alexandrium* spp. and *Scrippsiella trochoidea*. – FEMS Microbiology Ecology **37**, 161-173.

HONG, T.-Y., MENG, M., 2003: Biochemical characterization and antifungal activity of an endo-1,3-b-glucanase of *Paenibacillus* sp. isolated from garden soil. – Applied Microbiology and Biotechnology **61**, 472–478

HOPKIN, S.P., MARTIN, M.H., 1982: The distribution of zinc, cadmium, lead and copper within the woodlouse *Oniscus asellus* (Crustacea, Isopoda). – Oecologia **54**, 227-232.

HOPKIN, S.P., MARTIN, M.H., 1984: Heavy metals in woodlice. Symposia of the Zoological Society of London **53**, 143-166.

HYODO, F., INOUE, T., AZUMA, J.-I., TAYASU, I., ABE, T., 2000: Role of mutualistic fungus in lignin degradation in the fungus-growing termite *Macrotermes gilvus* (Isoptera; Macrotermitinae). – Soil Biology and Biochemistry **32**, 653-658

HYODO, F., TAYASU, I., INOUE, T., AZUMA, J.-I., KUDO, T., ABE, T., 2003: Differential role of symbiotic fungi in lignin degradation and food provision for fungus-growing termites (Macrotermitinae: Isoptera). – Functional Ecology **17**, 186-193.

INESON, P., ANDERSON, J.M., 1985: Aerobically isolated bacteria associated with the gut and feces of the litter feeding macroarthropods *Oniscus asellus* and *Glomeris marginata*. – Soil Biology and Biochemistry **17,** 843-849.

JAENECKE, S., DE LORENZO, V., TIMMIS, K.N., DIAZ, E., 1996: A stringently controlled expression system for analysing lateral gene transfer between bacteria. – Molecular Microbiology **21**, 293-300.

JOHJIMA, T., OHKUMA, M., KUDO, T., 2003: Isolation and cDNA cloning of novel hydrogen peroxide-dependent phenol oxidase from the basidiomycete *Termitomyces albuminosus*. – Applied Microbiology and Biotechnology **61**, 220-225

JOHNSTONE, R.A., BSHARY, R., 2002: From parasitism to mutualism: partner control in asymmetric interactions. – Ecology Letters **5**, 634-639.

JUILFS, H.B., WÄGELE, J.W., 1987: Symbiotic bacteria in the gut of the blood-sucking antarctic fish parasite *Gnathia calva* (Crustacea: Isopoda). – Marine Biology **95**, 493-499.

KAUTZ, G., ZIMMER, M., TOPP, W., 2000: Responses of the parthenogenetic isopod, *Trichoniscus pusillus*, to changes in food quality. – Pedobiologia **44**, 75-85.

KAUTZ, G., ZIMMER, M., TOPP, W., 2002: Does *Porcellio scaber* (Isopoda: Oniscidea) gain from coprophagy? – Soil Biology and Biochemistry **34**, 1253–1259.

KAUTZ, G., TOPP, W., 2000: Acquisition of microbial communities and enhanced availability of soil nutrients by the isopod *Porcellio scaber*

(Latr.) (Isopoda: Oniscidea). – Biology and Fertility of Soils **31**, 102-107.

KELLNER, R.L.L., 2001: Suppression of pederin biosynthesis through antibiotic elimination of endosymbionts in *Paederus sabaeus*. – Journal of Insect Physiology **47**, 475-483.

KELLNER, R.L.L., 2002: Molecular identification of an endosymbiotic bacterium associated with pederin biosynthesis in *Paederus sabaeus* (Coleoptera: Staphylinidae). – Insect Biochemistry and Molecular Biology **32**, 289-295.

KELLY, B.A., KADO, C.I., 2002: Agrobacterium-mediated T-DNA transfer and integration into the chromosome of *Streptomyces lividans*. – Molecular Plant Pathology **3**, 125-134.

KENSLEY, B., 1974: Aspects of the biology and ecology of the genus *Tylos* Latreille. – Annals of the South African Museum **65,** 401-471.

KIRCHMAN, D.L., 2002: The ecology of *Cytophaga-Flavobacteria* in aquatic environments. – FEMS Microbiology Ecology **39**, 91-100.

KLUSSMANN-KOLB, A., BRODIE, G.D., 1999: Internal storage and production of symbiotic bacteria in the reproductive system of a tropical marine gastropod. – Marine Biology **133**, 443-447.

KOGA, R., TSUCHIDA, T., FUKATSU, T., 2003: Changing partners in an obligate symbiosis: a facultative endosymbiont can compensate for loss of the essential endosymbiont *Buchnera* in an aphid. – Proceedings of the Royal Society of London B **270**, 2543-2550.

KORB, J., AANEN, D.K., 2003: The evolution of uniparental transmission of fungal symbionts in fungus-growing termites (Macrotermitinae). – Behavioral Ecology Sociobiology **53**, 65-71.

KOSTANJŠEK, R., ŠTRUS, J., AVGUŠTIN, G., 2002: Genetic diversity of bacteria associated with the hindgut of the terrestrial crustacean *Porcellio scaber* (Crustacea: Isopoda). – FEMS Microbiology Ecology **40**, 171-179.

KOZLOVSKAJA, L.S., STRIGANOVA, B.R., 1977: Food, digestion and assimilation in desert woodlice and their relations to the soil microflora. – Ecological Bulletin **25**, 240-245.

KUITERS, A.T., SARINK, H.M., 1986: Leaching of phenolic compounds from leaf and needle litter of several deciduous and coniferous trees. – Soil Biology and Biochemistry **18**, 475-480.

KUKOR, J.J., MARTIN, M.M., 1983: Acquisition of digestive enzymes by siricid woodwasps from their fungal symbionts. – Science **220**, 1161-1163.

KUKOR, J.J., MARTIN, M.M., 1986: The effect of acquired microbial enzymes on assimilation efficiency in the common woodlouse, *Tracheoniscus rathkei*. – Oecologia **69**, 360-366.

KURTZ, J., FRANZ, K., 2003: Evidence for memory in invertebrate immunity. – Nature **425**, 37-38.

LAU, W.W.Y., JUMARS, P.A., ARMBRUST, E.V., 2002: Genetic diversity of attached bacteria in the hindgut of the deposit-feeding shrimp *Neotrypaea* (formerly *Callianassa*) *californiensis* (Decapoda: Thalassinidae). – Microbial Ecology **43**, 455-466.

LEE, K.-H., RUBY, E.G., 1994: Effects of the squid host on the abundance and distribution of symbiotic *Vibrio fischeri* in nature. – Applied and Environmental Microbiology **60**, 1565-1571..

LEONARDO, T.E., MUIRU, G.T., 2003: Facultative symbionts are associated with host plant specialization in pea aphid populations. – Proceedings of the Royal Society of London B **270**, S209-S212

LESCHINE, S.B., 1995: Cellulose degradation in anaerobic environments. – Annual Review of Microbiology **49**, 399-426.

LILLEY, A.K., BAILEY, M.J., BARR, M., KILSHAW, K., TIMMS-WILSON, T.M., DAY, M.J., NORRIS, S.J., JONES, T.H., GODFRAY, H.C.J., 2003: Population dynamics and gene transfer in genetically modified bacteria in a model microcosm. – Molecular Ecology **12**, 3097-3107.

LIVELY, C.M., 1999: Migration, virulence, and the geographic mosaic of adaptation by parasites. – The American Naturalist **153**, S34-S47.

LJUNGDAHL, L.G., ERIKSSON, K.-E., 1985: Ecology of microbial cellulose degradation. – Advances in Microbial Ecology **8**, 237-299.

LO, S.C., HAYES, M.M., KOTANI, H., PIERCE, P.F., WEAR, D.J., NEWTON, P.B., TULLY, J.G., SHIH, J.W., 1993: Adhesion to and invasion into mammalian cells by *Mycoplasma penetrans*: a newly isolated mycoplasma from patients with AIDS. – Modern Pathology **6**, 276-280.

LUNG, O., KUO, L., WOLFNER, M.F., 2001: *Drosophila* males transfer antibacterial proteins from their accessory gland and ejaculatory duct to their mates. – Journal of Insect Physiology **47**, 617-622.

LUSSENHOP, J., 1992: Mechanisms of microarthropod-microbial interactions in soil. – Advances in Ecological Research **23**, 1-33.

MANTER, H.W., 1966: Parasites of fishes as biological indicators of recent and ancient conditions. In: Host-parasite relationships (McCauley, J.E., ed). – Oregon State University Press, Corvallis.

MARANA, S.R., TERRA, W.R., FERREIRA, C., 1995: Midgut β-D-Glucosidases from *Abracris flavolineata* (Orthoptera: Acrididae): physical properties, substrate specificities and function. – Insect Biochemistry and Molecular Biology **25**, 835-843.

MARANA, S.R., TERRA, W.R., FERREIRA, C., 2000: Purification and properties of a β-glycosidase purified from midgut cells of *Spodoptera frugiperda* (Lepidoptera) larvae. – Insect Biochemistry and Molecular Biology **30**, 1139-1146.

MARGULIS, L., FESTER, R. (eds), 1991: Symbioses as a source of evolutionary innovation. – MIT Press, Cambridge (MA, USA).

MÁRIALIGETI, K., JÁGER, K., SZABÓ, I.M., POBOZSNY, M., DZINGOV, A., 1984: The faecal actinomycete flora of *Protracheoniscus amoenus* (Woodlice; Isopoda). – Acta Microbiologica Hungarica **31**, 339-344.

MARTIN, A.L., 1964: The alimentary canal of *Marinogammarus obtusatus* (Crustacea, Amphipoda). – Proceedings of the Zoological Society of London **143,** 525-544.

MARTIN, J.S., MARTIN, M.M., 1983: Tannin assays in ecological studies: precipitation of Ribulose-1, 5-Bisphosphate Carboxylase/Oxygenase by tannic acid, quebracho, and oak foliage extracts. – Journal of Chemical Ecology **9**, 285-294.

MARTIN, M.M., 1984: The role of ingested enzymes in the digestive processes of insects, pp. 155-172. In: Invertebrate-microbial interactions (Anderson, J.M., Rayner, A.D.M., Walton, D.W.H., eds). – Cambridge University Press, Cambridge.

MARTIN, M.M., 1991: The evolution of cellulose digestion in insects. – Philosophical Transactions of the Royal Society of London B **333**, 281-288.

MARTIN, M.M., MARTIN, J.S., KUKOR, J.J., MERRITT, R.W., 1980: The digestion of protein and carbohydrate by the stream detritivore, *Tipula abdominalis* (Diptera, Tipulidae). – Oecologia **46**, 360-364.

MATTERN, D., SCHLEGEL, M., 2001: Molecular evolution of the small subunit ribosomal DNA in woodlice (Crustacea, Isopoda, Oniscidea) and implications for Oniscidean phylogeny. – Molecular Phylogenetics and Evolution, **18**, 54-65.

MAYER, A.M., 1987: Polyphenol oxidases in plants – recent progress. – Phytochemistry **26**, 11-20.

MAYER, A.M., HAREL, E., 1979: Polyphenol oxidases in plants. – Phytochemistry **18**, 193-215.

MAYNARD SMITH, J., SZATHMÁRY, E., 1995: The major transitions in evolution. – Freeman, San Francisco.

MAYNARD SMITH, J., BURIAN, R., KAUFFMAN, S., ALBERCH, P., CAMPBELL, J., GOODWIN, B., LANDE, R., RAUP, D., WOLPERT, L., 1985: Developmental constraints and evolution. – Quarterly Review of Biology **60**, 265-287.

MCGRATH, C.C., MATTHEWS, R.A., 2000: Cellulase activity in the freshwater amphipod *Gammarus lacustris*. – Journal of the North American Benthological Society **19**, 298-307.

MICHEL-SALZAT, A., BOUCHON, D., 2000: Phylogenetic analysis of mitochondrial LSU rRNA in oniscids. – Comptes Rendus de l'Academie des Sciences de Paris **323**, 827-837

MIRA, A., MORAN, N.A., 2002: Estimating population size and transmission bottlenecks in maternally transmitted endosymbiotic bacteria. – Microbial Ecology **44**, 137-143.

MONK, D.C., 1977: The digestion of cellulose and other dietary components, and pH of the gut in the amphipod *Gammarus pulex* (L.). – Freshwater Biololgy **7**, 431-440.

MONTLLOR, C.B., MAXMEN, A., PURCELL, A.H., 2002: Facultative bacterial endosymbionts benefit pea aphids *Acyrthosiphon pisum* under heat stress. – Ecological Entomology **27**, 189-195.

MORGAN, M.R.J., 1975: Relationship between gut cellobiase, lactase, ary-β-glucosidase, and aryl-β-galactosidase activities of *Locusta migratoria*. – Insect Biomchemistry **5**, 609-617.

MÜLLER, W.E.G., 1999: 16S rRNA sequences as diagnostic tools to elucidate potential symbiotic relationships between bacteria and the marine sponge *Halichondria panicea*: reply to Stackebrandt and Pukall (Mar Biol 133: 159-161). – Marine Biology **134**, 213-215.

MUSGROVE, R.J., 1988: Digestive ability of the freshwater crayfish *Paranephrops zealandicus* (Parastacidae) and the role of microbial enzymes. – Freshwater Biology **19**, 305-314.

NARDI, J.B., MACKIE, R.I., DAWSON, J.O., 2002: Could microbial symbionts of arthropod guts contribute significantly to nitrogen fixation in terrestrial ecosystems? – Journal of Insect Physiology **48**, 751-763.

NARDON, P., CHARLES, H., DELOBEL, B., LEFEVRE, C., HEDDI, A., 2003: Symbiosis in the Dryophthoridae weevils (Coleoptera, Cuculionoidea): morphological variability of symbiotic intracellular bacteria. – Symbiosis **34**, 231-251.

NEALSON, K.H., HAYGOOD, M.G., TEBO, B.M., ROMAN, M., MILLER, E., MCCOSKER, J.E., 1984: Contribution by symbiotically luminous fishes to the occurrence and bioluminescence of luminous bacteria in sea water. – Microbial Ecology **10**, 69-77.

NESTER, E.W., 2000: DNA and protein transfer from bacteria to eukaryotes – the *Agrobacterium* story. – Molecular Plant Pathology **1**, 87-90.

NEUHAUSER, E., HARTENSTEIN, R., 1976: Degradation of phenol, cinnamic acid and quinic acid in the terrestrial crustacea, *Oniscus asellus*. – Soil Biology and Biochemistry **8**, 95-98.

NICHOLLS, A.G., 1931: Studies on *Ligia oceanica* – II: The processes of feeding, digestion and absorption, with a description of the structure of the foregut. – Journal of the Marine Biological Association of the UK **17,** 675-705.

NODA, H., KODAMA, K., 1996: Phylogenetic position of yeastlike endosymbionts of anobiid beetles. – Applied and Environmental Microbiology **62**, 162-167.

NUISMER, S.L., GOMULKIEWICZ, R., MORGAN, M.T., 2003: Coevolution in Temporally Variable Environments. – The American Naturalist **162**, 195-204

OHKUMA, M., 2003: Termite symbiotic systems: efficient bio-recycling of lignocellulose. – Applied Microbiology and Biotechnology **61**, 1-9.

OSHEL, P.E., STEELE, D.H., 1988: SEM morphology of the foreguts of gammaridean amphipods compared to *Anaspides tasmaniae* (Anaspidacea: Anaspididae), *Gnathophausia ingens* (Mysidacea: Lophogastridae), and *Idotea balthica* (Isopoda: Idoteidae). – Crustaceana Supplement **13,** 209-219.

PANT, N.C., FRAENKEL, G., 1954: Studies on the symbiotic yeasts of two insect species *Lasioderma serricorne* F. and *Stegobium paniceum* L. – Biological Bulletin **107**, 420-432.

PARKER, M.A., 2003: Genetic markers for analysing symbiotic relationships and lateral gene transfer in neotropical bradyrhizobia. – Molecular Ecology **12**, 2447-2455.

PASTOR, F.I.J., PUJOL, X., BLANCO, A., VIDAL, T., TORRES, A.L., DÍAZ, P., 2001: Molecular cloning and characterization of a mulitdomain endoglucanase from *Paenibacillus* sp. BP-23: evaluation of its performance in pulp refining. – Applied Microbiology and Biotechnology **55**, 61-68.

PENNINGS, S.C., CAREFOOT, T.H., ZIMMER, M., DANKO, J.P., ZIEGLER, A., 2000: Feeding preferences of supralittoral isopods and amphipods. – Canadian Journal of Zoology **78**, 1918-1929.

PLANTE, C.J., JUMARS, P.A., BAROSS, J.A., 1990: Digestive associations between marine invertebrates and bacteria. – Annual Review in Ecology and Systematics **21**, 93-127.

POINSOT-BALAGUER, N., RACON, L., SADAKA, N., LE PETIT, J., 1993: Effects of tannin compounds on two species of Collembola. – European Journal of Soil Biology **29**, 13-16.

PRICE, P.W., 1991: The web of life: development over 3.8 billion years of trophic relationships, pp. 262-272. In: Symbiosis as a source of evolutionary innovation – speciation and morphogenesis (Margulis, L., Fester, R., eds). – Cambridge MIT Press, Cambridge.

RABINOVICH, M.L., BOLOBOVA, A.V., VASIL'CHENKO, L.G., 2004: Fungal decomposition of natural aromatic structures and xenobiotics: A review. – Applied Biochemistry and Microbiology **40**, 1-17.

RAMETTE, A., MOËNNE-LOCCOZ, Y., DÉFAGO, G., 2003: Prevalence of fluorecent pseudomonads producing antifungal phloroglucinols and/or hydrogen cynide in soils naturally suppressive or conducive to tobacco black root rot. – FEMS Microbiology Ecology **44**, 35-43.

RAPP, P., BEERMANN, A., 1991: Bacterial cellulases, pp. 269-276. In: Biosynthesis and biodegradation of cellulose (Haigler, C.H., Weimer, P.J., eds). – Marcel Dekker, New York.

RAY, D.L., 1959: Marine fungi and wood borer attack. – Proceedings of the American Wood Preservation Association **54**, 1-7.

RAY, D.L., JULIAN, J.R., 1952: Occurrence of cellulase in *Limnoria*. – Nature **169**, 32-33.

REESE, E.T., MANDELS, M., 1971: Degradation of cellulose and its derivates – enzymic degra-

dation, pp. 1079-1094. In: High polymers 5 (Bikales, N.M., Segal, L., eds). – Wiley-Interscience: New York.

REYES, V.G., TIEDJE, J.M., 1976: Ecology of the gut microbiota of *Tracheoniscus rathkei* (Crustacea, Isopoda). – Pedobiologia **16**, 67-74.

RISPE, C., MORAN, N.A., 2000: Accumulation of deleterious mutations in endosymbionts: Muller's ratchet with two levels of selection. – The American Naturalist **156**, 425-441.

ROTTEM, S., 2003: Interaction of Mycoplasmas with host cells. – Physiological Review **83**, 417-432.

ROUGHGARDEN, J., 1975: Evolution of marine symbioses – a simple cost-benefit model. – Ecology **56**, 1201-1208.

RUPEREZ, P., SAURA-CALIXTO, F., 2001: Dietary and physicochemical properties of edible Spanish seaweeds. – Zeitschrift für Lebensmittel Untersuchung und Forschung A **212**, 349-354.

RUSHTON, S.P., HASSALL, M., 1983a: Food and feeding rates of the terrestrial isopod *Armadillidium vulgare* (Latreille). – Oecologia **57,** 415-419.

SALEEM, M., ALIKHAN, M.A., 1974: The distribution of phosphomonoesterases in the digestive gut of *Porcellio laevis* Latreille (Porcellionidae, Isopoda). – Comparative Biochemistry and Physiology **48A,** 375-385.

SANTOS, C.D., TERRA, W.R., 1985: Physical properties, substrate specificities and a probable mechanism for a α-D-glucosidase (cellobiase) from midgut cells of the cassava hornworm (*Erinnyis ello*). – Biochimica et Biophysica Acta **831**, 179-185.

SAVAGE, D.C., 1972: Survival on mucosal epithelia, epithelial penetration and growth in tissues of pathogenic bacteria, pp. 25-57. In: Microbiol pathogenicity of man and animals (Smith, H., Pearce, J.H., eds). – Cambridge University Press, Cambridge

SCHELOSKE, H.W., 1976: Ist die Unterteilung des Magens der Malacostraca in "Cardia" und "Pylorus" berechtigt? – Zeitschrift für Zoologie: Systematik und Evolutionsforschung **14,** 253-280.

SCHMALFUSS, H., 1978: *Ligia simoni*: a model for the evolution of terrestrial isopods. – Stuttgarter Beiträge zur Naturkunde **317**, 1-5.

SCHMALFUSS, H., 1984: Eco-morphological strategies in terrestrial isopods. – Symposia of the Zoological Society of London **53**, 49-63.

SCHMALFUSS, H., 1998: Evolutionary strategies of the antennae in terrestrial isopods. – Journal of Crustacean Biology **18**, 10-24.

SCHMIDT, C., WÄGELE, J.W., 2001: Morphology and evolution of respiratory structures in the pleopod exopodites of terrestrial Isopoda (Crustacea, Isopoda, Oniscidea). – Acta Zoologica **82**, 315-330.

SCHÖNHOLZER, F., HAHN, D., ZARDA, B., ZEYER, J., 2002: Automated image analysis and in situ hybridization as tools to study bacterial populations in food resources, gut and cast of *Lumbricus terrestris* L. – Journal of Microbiological Methods **48**, 53-68.

SCHÖNHOLZER, F., HAHN, D., ZEYER, J., 1999: Origins and fate of fungi and bacteria in the gut of *Lumbricus terrestris* L. studied by image analysis. – FEMS Microbiology Ecology **28**, 235-248.

SCHULENBURG, GRAF VON DER J.H., HABIG, M., SLOGGETT, J.J., WEBBERLEY, K.M., BERTRAND, D., HURST, G.D.D., MAJERUS, M.E.N., 2001: Incidence of male-killing *Rickettsia* spp. (α-Proteobacteria) in the Ten-Spot Ladybird Beetle *Adalia decempunctata* L. (Coleoptera: Coccinellidae). – Applied and Environmental Microbiology **67**, 270-277.

SCHULTZ, J.C., LECHOWICZ, M.J., 1986: Host plant, larval age and feeding behavior influence midgut pH in the Gypsy Moth (*Lymantria dispar* L.). – Oecologia **71**, 133-137.

SCRIVENER, A.M., SLAYTOR, M., 1994a: Cellulose digestion in *Panesthia cribrata* Saussure: does fungal cellulase play a role? – Comparative Biochemistry and Physiology **107B**, 309-315.

SCRIVENER, A.M., SLAYTOR, M., 1994b: Properties of the endogenous cellulase from *Panesthia cribrata* Saussure and purification of major endo-β-1,4-glucanase components. – Insect Biochemistry and Molecular Biology **24**, 223-231.

SHEN, S.K., DOWD, P.F., 1991: Detoxification spectrum of the cigarette beetle symbiont *Symbiotaphrina kochii* in culture. – Entomologia Experimentalis et Applicata **60**, 51-59.

SHIGENOBU, S., WATANABE, H., HATTORI, M., SAKAKI, Y., ISHIKAWA, H., 2000: Genosequence of the endocellular bacterial symbiont of aphids *Buchnera* sp. APS. – Nature **407**, 81-86.

SINDHU, S.S., DADARWAL, K.R., 2001: Chitinolytic and cellulolytic *Pseudomonas* sp. antagonistic to fungal pathogens enhances nodulation by *Mesorhizobium* sp. cicer in chickpea. – Microbiological Research **156**, 353-358.

SINSABAUGH, R.L., LINKINS, A.E., BENFIELD, E.F., 1985: Cellulose digestion and assimilation by three leaf-shredding aquatic insects. – Ecology **66**, 1464-1471.

SKAMBRACKS, D., ZIMMER, M., 1998: Combined methods for the determination of microbial activity in leaf litter. – European Journal of Soil Biology **34**, 105-110.

SLAYTOR, M., 1992: Cellulose digestion in termites and cockroaches: what role do symbionts play? – Comparative Biochemistry and Physiology A **103**, 775-784.

SLEETER, T.D., BOYLE, P.J., CUNDELL, A.M., MITCHELL, R., 1978: Relationships between marine microorganisms and the wood-boring isopod *Limnoria tripunctata*. – Marine Biology **45**, 329-336.

SMITH, V.J., SÖDERHÄLL, K., 1991: A comparison of phenoloxidase activity in the blood of marine invertebrates. – Developmental and Comparative Immunology **15**, 251-261.

SOMA, K., SAITO, T., 1983: Ecological studies of soil organisms with references to the decomposition of pine needles – II. Litter feeding and breakdown by the woodlouse, *Porcellio scaber*. – Plant and Soil **75**, 139-151.

STACKEBRANDT, E., PUKALL, R., 1999: Deriving taxonomic decisions from 16S rDNA: a case study: Response to Althoff et al. (Mar Biol 130: 529-536). – Marine Biology **130**, 529-536.

STEINERT, M., HENTSCHEL, U., HACKER, J., 2000: Symbiosis and parthogenesis: evolution of the microbe-host interaction. – Naturwissenschaften **87**, 1-11.

STÖCKLI, H., 1990: Das Unterscheidungsvermögen von *Porcellio scaber* (Crustacea, Isopoda) zwischen Blättern einer Baumart, unter Berücksichtigung der makroskopisch sichtbaren Verpilzung. – Pedobiologia **34**, 191-205.

STORCH, V., 1987: Microscopic anatomy and ultrastructure of the stomach of *Porcellio scaber* (Crustacea, Isopoda). – Zoomorphology **106**, 301-311.

SUDHAUS, W., REHFELD, K., 1992: Einführung in die Phylogenetik und Systematik. – Gustav Fischer, Stuttgart.

SUMMERS, C.B., FELTON, G.W., 1994: Prooxidant effects of phenolic acids on the generalist herbivore *Helicoverpa zea* (Lepidoptera: Noctuidae): Potential mode of action for phenolic compounds in plant anti-herbivore chemistry. – Insect Biochemistry and Molecular Biology **24**, 943-953.

STRIGANOVA, B.R., 1967: Über die Zersetzung von überwinterter Laubstreu durch Tausendfüßler und Landasseln. – Pedobiologia **7**, 125-134.

SWAIN, T., 1979: Tannins and lignins, pp. 657-718. In: Herbivores their interactions with secondary plant metabolites. I: The chemical participants (Rosenthal, G.A., Janzen, D.H., eds). – Academic Press, San Diego.

SWIFT, M.J., BODDY, L., 1984: Animal-microbial interactions in wood decomposition, pp. 89-131. In: Invertebrate-microbial interactions (Anderson, J.M., Rayner, A.D.M., Walton D.W.H., eds). – Cambridge University Press, Cambridge.

SZEGI, J., 1988: Cellulose decomposition and soil fertility. – Akadémiai Kiadó, Budapest.

SZLÁVECZ, K., 1993: Needle litter consumption by two terrestrial isopods, *Protracheoniscus amoenus* (CL Koch), and *Cylisticus convexus* (de Geer) (Isopoda, Oniscidea). – Pedobiologia **37**, 57-64.

SZLÁVECZ, K., MAIORANA, V.C., 1998: Supplementary food in the diet of the terrestrial isopod *Porcellio scaber* Latr (Isopoda: Oniscidea). – Israel Journal of Zoology **44**, 413-422.

TABACARU, I., DANIELOPOL, D.L., 1999: Contribution a la connaissance de la phylogénie des Isopoda (Crustacea). – Vie et Milieu **49**, 163-176

TAYLOR, E.C., 1982: Role of aerobic microbial populations in cellulose digestion by desert millipedes. – Applied and Environmental Microbiology **44**, 281-293.

TER-POGHOSSIAN, A., 1909: Beiträge zur Kenntnis der Exkretionsorgane der Isopoden. – Zeitschrift für Naturwissenschaften **81**, 1-50.

TEUBEN, A., 1991: Nutrient availability and interactions between soil arthropods and microorganisms during decomposition of coniferous litter: a mesocosm study. – Biology and Fertility of Soils **10**, 256-266.

TEUBEN, A., ROELOFSMA, T.A.P.J., 1990: Dynamic interactions between functional groups of soil arthropods and microorganisms during decomposition of coniferous litter in microcosm experiments. – Biology and Fertility of Soils **9**, 145-151.

THOMPSON, J.N., 1982: Interaction and Coevolution. – Wiley, New York.

THOMPSON, J.N., CUNNINGHAM, B.M., 2002: Geographic structure and dynamics of coevolutionary selection. – Nature **417**, 735-738.

THURSTON, C.F., 1994: The structure and function of fungal laccases. – Microbiology **140**, 19-26.

TOKUDA, G., SAITO, H., WATANABE, H., 2002: A digestive β-glucosidase from the salivary glands of the termite, *Neotermes koshunensis* (Shiraki): distributrion, characterization and isolation of its precursor cDNA by 5'- and 3'-RACE amplifications with degenerate primers. – Insect Biochemistry and Molecular Biology **32**, 1681-1689.

TOKUDA, G., YAMAOKA, I., NODA, H., 2000: Localization of symbiotic clostridia in the mixed segment of the termite *Nasutitermes takasagoensis* (Shiraki). – Applied and Envirnmental Microbiology **66**, 2199-2207.

TRAGER, W., 1932: A cellulase from the symbiotic intestinal flagellates of termites and of the roach, *Cryptocercus punctulatus*. – Biochemical Journal **26**, 1762-1771.

TREVES, D.S., MARTIN, M.M., 1994: Cellulose digestion in primitive hexapods: effect of ingested antibiotics on gut microbial populations and gut cellulase levels in the firebrat, *Thermobia domestica* (Zygentoma, Lepismatidae). – Journal of Chemical Ecology **20**, 2003-2020.

TROJANOWSKI, J., 2001: Biological degradation of lignin. – International Biodeterioration and Biodegradation **48**, 213-218.

TSUDA, M., TAN, H.M., NISHI, A., FURUKAWA, K., 1999: Mobile catabolic genes in bacteria. – Journal of Bioscience and Bioengineering **87**, 401-410.

UESBECK, M., TOPP, W., 1995: The effect of leaf litter, microorganisms and Collembola on the food allocation of *Oniscus asellus* (Isopoda), pp. 121-132. In: Terrestrial Isopod Biology (Alikhan, M.A., ed). – Balkema, Rotterdam.

ULLRICH, B., STORCH, V., SCHAIRER, H., 1991: Bacteria on the food, in the intestine and on the faeces of the woodlouse *Oniscus asellus* (Crustacea, Isopoda). – Pedobiologia **34**, 41-51.

VAN BORM, S., BUSCHINGER, A., BOOMSMA, J.J., BILLEN, J., 2002: *Tetraponera* ants have gut symbionts related to nitrogen-fixing root-nodule bacteria. – Proceedings of the Royal Society of London B **269**, 2023-2027.

VANDERMEER, J., 1983: The evolution of mutualism, pp. 221-232. In: Evoutionary ecology (23rd Symposium of the British Ecological Society Leeds 1982) (Shorrocks, B., ed). – Blackwell, Oxford.

VAN ELSAS, J.D., TURNER, S., BAILEY, M.J., 2003: Horizontal gene transfer in the phytosphere. – New Phytologist **157**, 525-537.

VAN WEMSEN, J., VERHOEF, H.A., VAN STRAALEN, N.M., 1993: Litter degradation stage as a prime factor for isopod interaction with mineralization processes. – Soil Biology and Biochemistry **25**, 1175-1183.

VEIVERS, P.C., MÜHLEMANN, R., SLAYTOR, M., LEUTHOLD, R.H., BIGNEL, D.E., 1991: Digestion, diet and polytheism in two fungus-growing termites: *Macrotermes subhyalinus* Rambur and *M. michaelseni* Sjøstedt. – Journal of Insect Physiology **37**, 675-682.

VINOT, C., DURAND, P., LECLERCQ, M., BOURGEAY CAUSSE, M., 1987: Studies on the biochemical composition of *Undaria pinnatida* with a view to its utilization in human feeding. – Science of Alimentation **7**, 589-601.

WADA, M., AZUMA, N., MIZUNO, N., KUROKURA, H., 1999: Transfer of symbiotic luminous bacteria from parental *Leiognathus nuchalis* to their offspring. – Marine Biology **135**, 683-687.

WÄGELE, J.W., 1989: Evolution und phylogenetisches System der Isopoda – Stand der Forschung und neue Erkenntnisse. – Zoologica **140,** 1-262

WANG, J., DING, M., LI, Y.-H., CHEN, Q.-X., XU, G.-J., ZHAO, F.-K., 2003: Isolation of a multifunctional endogenous cellulase gene from mollusc, *Ampullaria crossean*. – Acta Biochimica et Biophysica Sinica **35**, 941-946.

WANG, Y., BRUNE, A., ZIMMER, M., in review: Molecular identification of hepatopancreatic symbionts in the freshwater isopod, *Asellus aquaticus* (Crustacea: Asellota).

WANG, Y., STINGL, U., ANTON-ERXLEBEN, F., GEISLER, S., BRUNE, A., ZIMMER, M., 2004b: '*Candidatus* Hepatoplasma crinochetorum', a new, stalk-forming lineage of Mollicutes colonizing the midgut glands of a terrestrial isopod. – Applied and Environmental Microbiology, **70**, 6166-6172.

WANG, Y., STINGL, U., ANTON-ERXLEBEN, F., ZIMMER, M., BRUNE, A., 2004a: '*Candidatus* Hepatincola porcellionum' gen. nov., sp. nov., a new, stalk-forming lineage of Rickettsiales colonizing the midgut glands of a terrestrial isopod. – Archives of Microbiology, **181**, 299-304.

WANG, Y., STINGL, U., BRUNE, A., ZIMMER, M., in review: Symbiotic bacteria in the midgut glands of isopods (Crustacea: Isopoda): phylogeny and evolution.

WARBURG, M.R., 1965: The evolutionary significance of the ecological niche. – Oikos **16**, 205-213.

WARBURG, M.R., 1987: Isopods and their terrestrial environment. – Advances in Ecological Research **17**, 187-242.

WATSON, R.A., POLLACK, J.B., 2003: A computational model of symbiotic composition in evolutionary transitions. – BioSystems **69**, 187-209.

WHITE, J.J., 1968: Bioenergetics of the woodlouse *Tracheoniscus rathkei* Brandt in relation to litter decomposition in a deciduous forest. – Ecology **49**, 694-704.

WIESER, W., 1966: Copper and the role of isopods in degradation of organic matter. – Science **153**, 67-69.

WIESER, W., 1968: Aspects of nutrition and the metabolism of copper in isopods. – American Zoologist **8**, 495-506.

WILKINSON, D.M., SHERRATT, T.N., 2001: Horizontally acquired mutualisms, an unsolved problem in ecology? – Oikos **92**, 377-384.

WILKINSON, T.L., DOUGLAS, A.E., 1996: The impact of aposymbiosis on amino acid metabolism of pea aphids. – Entomologia Experimentalis at Applicata **80**, 279-282.

WILKINSON, T.L., ISHIKAWA, H., 2000: Injection of essential amino acids substitutes for bacterial supply in aposymbiotic pea aphids (*Acyrthosiphon pisum*). – Entomologia Experimentalis et Applicata **94**, 85-91.

WILKINSON, T.L., ISHIKAWA, H., 2001: On the functional significance of symbiotic microorganisms in the Homoptera: a comparative study of *Acyrthosiphon pisum* and *Nilaparvata lugens*. – Physiological Entomology **26**, 86-93.

WILSON, B.A., SALYERS, A.A., 2003: Is the evolution of bacterial pathogens an out-of-body experience? – Trends in Microbiology **11**, 347-350.

WOOD, D.A., 1980: Production, purification and properties of extracellular laccase of *Agaricus bisporus*. – Journal of General Microbiology **117**, 327-338.

WOOD, S., GRIFFITHS, B.S., 1988: Bacteria associated with the hepatopancreas of the woodlice *Oniscus asellus* and *Porcellio scaber* (Crustacea, Isopoda). – Pedobiologia **31**, 89-94.

WOOD, T.M., GARCIA-CAMPAYO, V., 1990: Enzymology of cellulose degradation. – Biodegradation **1**, 147-161.

YAMAMURA, N., 1993: Diversity and evolution of symbiotic interactions, pp. 75-82. In: Biodiversity: an ecological perspective (ABE, T., LEVIN, S.A., HIGASHI, M., eds). – Springer, New York.

YAMIN, M.A., TRAGER, W., 1979: Cellulolytic activity of an axenically-cultivated termite flagellate, *Trichomitopsis termopsidis*. – Journal of General Microbiology **13**, 417-420.

YAN, Y., SMANT, G., STOKKERMANS, J., QIN, L., HELDER, J., BAUM, T., SCHOTS, A., DAVIS, E., 1998: Genomic organization of four β-1,4-endoglucanase genes in plant-parasitic cyst nematodes and its evolutionary implications. – Gene **220**, 61-70.

ZACHARY, A., COLWELL, R.R., 1979: Gut-associated microflora of *Limnoria tripunctata* in marine creosote-treated wood pilings. – Nature **282**, 716-717.

ZIMMER, M., 1998: Wechselwirkungen zwischen Vertretern der saprophagen Bodenmakrofauna und saprotrophen Mikroorganismen. – Cuvillier, Göttingen.

ZIMMER, M., 1999: The fate and effects of ingested hydrolyzable tannins in *Porcellio scaber*. – Journal of Chemical Ecology **25**, 611-628.

ZIMMER, M., 2001: Why do male terrestrial isopods (Isopoda: Oniscidea) not guard females? Animal Behaviour **62**, 815-821.

ZIMMER, M., 2002a: Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. – Biological Reviews **77**, 455-493.

ZIMMER, M., 2002b: Is decomposition of woodland leaf litter influenced by its species richness? – Soil Biology and Biochemistry **34**, 277-284.

ZIMMER, M., BARTHOLMÉ, S., 2003: Bacterial endosymbionts in *Asellus aquaticus* (Isopoda) and *Gammarus pulex* (Amphipoda), and their contribution to digestion. – Limnology and Oceanography **48**, 2208-2213.

ZIMMER, M., BRUNE, A., 2005: Physiological properties of the gut lumen of terrestrial isopods (Isopoda: Oniscidea) – adaptive to digesting lignocellulose? – Journal of Comparative Physiology B, **175**, 275-283.

ZIMMER, M., TOPP, W., 1997a: Does leaf litter quality influence population parameters of the common woodlouse, *Porcellio scaber* Latr., 1804 (Crustacea: Isopoda)? – Biology and Fertility Soils **24**, 435-441.

ZIMMER M, TOPP W. 1997b: Homeostatic responses in the gut of *Porcellio scaber* (Isopoda: Oniscidea) optimize litter degradation.

– Journal of Comparative Physiology B **167**, 582-585.

ZIMMER, M., TOPP, W., 1998a: Do woodlice (Isopoda: Oniscidea) produce endogenous cellulases? – Biology and Fertility of Soils **26**, 155-156.

ZIMMER, M., TOPP, W., 1998b: Microorganisms and cellulose digestion in the gut of *Porcellio scaber* (Isopoda: Oniscidea). – Journal of Chemical Ecology **24**, 1397-1408.

ZIMMER, M., TOPP, W., 1998c: Nutritional biology of terrestrial isopods (Isopoda: Oniscidea): Copper revisited. – Israel Journal of Zoology **44**, 453-462.

ZIMMER M, TOPP W. 1999: Relations between woodlice (Isopoda: Oniscidea), and microbial density and activity in the field. – Biology and Fertility of Soils **30**, 117-123

ZIMMER, M., TOPP, W., 2000: Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea). – Journal of Animal Ecology **69**, 1071-1082.

ZIMMER, M., KAUTZ, G., TOPP, W., 1996: Olfaction in terrestrial isopods (Isopoda: Oniscidea): the responses of *Porcellio scaber* to the odour of litter. – European Journal of Soil Biology **32**, 141-147.

ZIMMER, M., KAUTZ, G., TOPP, W., 2003: Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for *Porcellio scaber* (Isopoda: Oniscidea)? – European Journal of Soil Biology **39**, 209-216.

ZIMMER, M., GEISLER, S., WALTER, S., BRENDELBERGER, H., 2002c: Fluorescence in *Asellus aquaticus* (Isopoda: Asellota): a first approach. – Evolutionary Ecology Research **4**, 181-187.

ZIMMER, M., PENNINGS, S.C., BUCK, T.L., CAREFOOT, T.H., 2002b: Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. – Functional Ecology **16**, 596-607.

ZIMMER, M., DANKO, J.P., PENNINGS, S.C., DANFORD, A.R., ZIEGLER, A., UGLOW, R.F., CAREFOOT, T.H., 2001: Hepatopancreatic endosymbionts in coastal isopods (Crustacea: Isopoda), and their contribution to digestion. – Marine Biology **138**, 955-963.

ZIMMER, M., DANKO, J.P., PENNINGS, S.C., DANFORD, A.R., CAREFOOT, T.H., ZIEGLER, A., UGLOW, R.F., 2002a: Cellulose digestion and phenol oxidation in coastal isopods (Crustacea: Isopoda). – Marine Biology **140**, 1207-1213.

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