

# Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior

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## Summary

Terrestrial isopods (Oniscidea) are the most successful crustacean colonizers of land habitats. From an evolutionary point of view, they are excellent examples of model organisms that have adapted to terrestrial life. The aquatic-terrestrial branching of the phylogenetic lines of the Oniscidea occurred in the marine littoral zone. The most oniscid species-rich areas are found in the circum-Mediterranean region. Studies on the morphology, physiology, ecology and biogeography of Oniscidea highlight the diversity of the group. They successfully colonized a wide range of terrestrial habitats by solving such ecological and physiological challenges as reproduction, respiration, excretion and protection against desiccation. During terrestrial adaptation, they evolved diverse morphological, ecological and behavioral traits. This review summarizes our present knowledge of some aspects of the morphology, physiology and behavior as it related to oniscidean adaptation to the terrestrial realm.

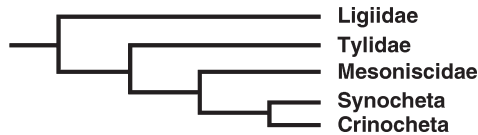
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## Keywords

Isopod cuticle; capillary system; lung; marsupium; oostegit; cotyledon; tegumental glands; behavior; life history

## Introduction

Oniscidean isopods (Malacostraca, Peracarida) are the most successful colonizers of terrestrial habitats among the Crustacea. There are around 3700 known species, representing the largest isopod suborder (Schotte et al., 1995- onwards; Schmalfuss, 2003). The cosmopolitan distribution of this monophyletic taxon (Schmidt, 2008) might indicate their ancient origin. Oniscidean isopods probably became terrestrial in the second half of Paleozoic (Cloudsley-Thompson, 1988). It is believed that the branching of the semi-terrestrial, terrestrial phyletic lines happened in marine littoral conditions without a freshwater stage (Schmalfuss, 2005). By the present classification, the Oniscidea are divided into five lineages (Figure 1): Ligiidae, Tylidae,



**Figure 1.** Schematic phylogenetic relationship among oniscidean lineages (Erhard, 1996).

Mesoniscidae, Synocheta and Crinocheta (Schmalfuss, 1989; Schmidt, 2008). Species of *Ligia* (Ligiidae) have morphological, physiological and behavioral characteristics that help us imagine what an intermediate form between ancestral marine and the modern terrestrial forms may have look like (Carefoot and Taylor, 1995; Schmidt, 2008).

Oniscideans are fascinating animals, both biogeographically and ecologically. While their dispersion ability is rather limited, they are cosmopolitan and are extremely diverse ecologically. The geographical distribution of the taxa is fully explored in southern and western Europe. Hot spots of high species' numbers, enriched with endemics, are found in the circum-Mediterranean region (Sfenthourakis et al., 2007), and a definitive latitudinal gradient in species richness has been shown from the Mediterranean to the northern regions in Europe (Hornung and Sólomos, 2007). The pattern is clear regardless of taxonomy: a gradual decrease of species richness towards the north is consistent in total species number and in species number within species-rich families, respectively (e.g. Philosciidae, Armadillidiidae, Oniscidae).

The ecological distribution of oniscideans ranges from supralittoral zones far into dry land, from sea level to high mountains and caves. Although most species of oniscideans are terrestrial, some are amphibious and live in littoral zones, such as *Ligia*, *Tylos*, *Littorophiloscia*, genera of the family Scyphacidae (*Scyphax* and *Actaecia*) as well as a number of other genera. Several species of Synocheta (mainly in the family Trichoniscidae) and some species of Crinocheta secondarily evolved into freshwater or cave dwelling forms (Schmalfuss, 2005). This evolutionary step has repeated itself several times independently and convergently in different groups (Tabacaru, 1999). Certain oniscideans live either in surface waters or under very wet conditions; they are stygobitic and live in hypersaline groundwater systems (*Haloniscus*), cave waters (*Cantabroniscus*) or submarine caves (*Utopioniscus*). Many species live in subterranean habitats and several of them are real troglobionts - troglobitic species found in tropical caves (e.g. lava tubes of Hawaiian Islands) (Taiti and Howarth, 1997; Taiti, 2004). Species adapted to desert environments represent the other end of a terrestrialization gradient (e.g. *Hemilepistus reaumuri* (Milne-Edwards, 1840), *Porcellio olivieri* (Audouin, 1826) or *Agabiformius obtusus* (Budde-Lund, 1909), Warburg, 1995; Baker et al., 1998; Baker 2005). Apart from these extreme exceptions, all oniscideans occur in moist microhabitats within terrestrial biotopes and show cryptic behavior, hide in shelter sites, such as under stones, logs in leaf litter (Schmalfuss, 1978). To inhabit so a wide range of habitats, isopods had to face several

ecological and physiological stressors. During their evolutionary adaptation, the oniscideans have developed different morphological, ecological and behavioral solutions to the terrestrial ways of reproduction, respiration, excretion and protection against desiccation.

The main trends of oniscidean morphological, physiological changes (compared to marine species) are: (1) reduction in size; (2) water-resistant cuticle (Bursell, 1955); (3) diverse surface morphology - increase in number of surface structures (Schmalfuss, 1978; Holdich, 1984); (4) pleodopodal lungs (Edney, 1954; Hoese, 1982a; Cloudsley-Thompson, 1988; Schmidt and Wägele, 2001); (5) water conducting system (Hoese 1981, 1982b; Horiguchi et al., 2007); and (6) closed brood pouch (Hoese, 1984) which was of key importance in the life of isopods on land. We can recognize the diverse trends on recent, living species. In addition, we will mention the ecomorphological and behavioral aspects of drought avoidance, habitat selection, foraging and life history characteristics.

A review and a comprehensive book by Warburg (1987, 1993, respectively) gives an overview of terrestrial adaptation in land isopods (Oniscidea). Several papers systematize and broaden our knowledge on different aspects of terrestrial isopods, all important in their land-adaptation. Such features include, phylogeny (Schmidt, 2008), reproduction (Warburg, 1994a, b; Kight, 2008), ultrastructure, calcium deposition and mineral distribution in the cuticle (Ziegler, 2004; Hild et al., 2009; Matsko et al., 2010), surface morphology (Schmalfuss, 1975, 1977, 1978; Holdich, 1984), water balance (Edney, 1977), water vapor absorption and ammonia volatilization (Wright and O'Donnell, 1995), respiratory structures (Hoese, 1982a, 1983a,b; Ferrara et al., 1991, 1994, 1997; Schmidt and Wägele, 2001; Paoli et al., 2002; Gruber and Taiti 2004), marsupial structure (Hoese, 1984; Hoese and Janssen, 1989), water conducting system (Hoese, 1981, 1982b), structure and development of digestive system (Milatović et al., 2010; Štrus et al., 2008), intestinal microbiota (Kostanjšek et al., 2006), nutritional and developmental aspects of isopod land adaptation (Štrus et al., 1995; Štrus and Blejec, 2001; Zimmer 2002), as well as eco-morphological (Schmalfuss, 1984) or evolutionary strategies (Schmalfuss, 1998).

However, our knowledge on oniscideans or isopods has increased significantly during the last decade. A complete bibliography of terrestrial isopod literature - containing publications on all biological aspects - was first published in 2002 (Schmalfuss and Wolf-Schwenninger). That bibliography was updated in 2004 and is available on the internet (<http://www.naturkundemuseum-bw.de/stuttgart/projekte/oniscidea-catalog/>). Since 2004, the publications of three Symposia proceedings, in Crete (Greece), Aveiro (Portugal) and Tunis (Tunisia) (Sfenthourakis et al., 2004; Loureiro et al., 2005a; Zimmer et al., 2008, respectively), and several additional papers – among them publications dealing with the above mentioned aspects of land adaptation – have enriched our present knowledge about oniscideans.

The present paper aims to summarize and update our knowledge on several structural, physiological and behavioral aspects of terrestrial isopods that have contributed to make them so successful in land colonization.

## Morphological and physiological adaptations

### *Cuticle*

The outer protective sclerotized tegumental cover, the cuticle or exoskeleton, is the main barrier between these small animals and their environment. In spite of the fact that their cuticle is relatively permeable to water (Quinlan and Hadley, 1983), woodlice can survive under a wide variety of terrestrial conditions by finding a locality with the appropriate humidity requirements.

The cuticle is composed of an organic matrix containing chitin and sclerotized proteins. Fabritius et al. (2005) describe the architecture of this organic matrix. The mineral phase consists of mainly calcium carbonate ( $\text{CaCO}_3$ ). Hild et al. (2008) summarized the known details on the finer cuticular structure and the forms of calcium carbonate. Recently, Matsko et al. (2010) proved experimentally the importance of silicon in the early stage of cuticle biocalcification in *Ligia italica* Fabricius, 1798.

The exoskeleton of isopods has four well-defined layers: the outer epicuticle, the exocuticle, the endocuticle and the innermost membranous layer (Figure 2A; see also Figure 6A below). Individual layers may have sublayers, depending on species (Hild et al., 2008). The first three layers are calcified and contain calcite crystals and amorphous calcium carbonate (Roer and Dillaman, 1984). Compere (1991) has described the fine structure of the thin superficial epicuticle on *Oniscus asellus* Linnaeus, 1758. Compere stated that the overall structure of the isopod cuticle follows that of crustaceans, the mineralized exoskeleton has an additional waxy and a cement layer. These two layers might be the consequences of terrestrial adaptation.

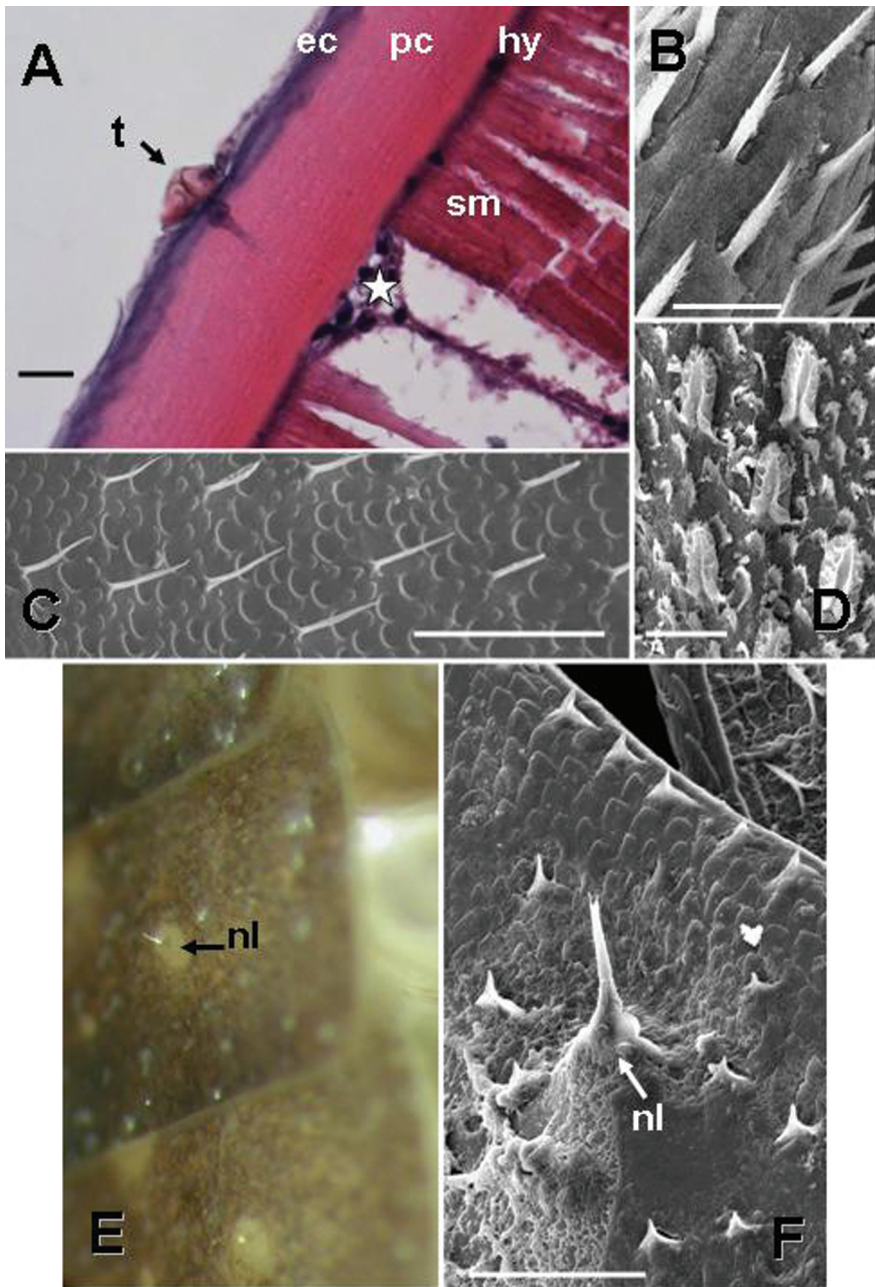
To be able to grow in size, terrestrial isopods molt frequently throughout their lives. Molting has two phases: the first is the shedding of the posterior part of the cuticle. After one day, this is followed by the molt of the exoskeleton's anterior half (Figure 3). Before molting, calcium (in the form of calcium carbonate or calcium phosphate) is reabsorbed first from the posterior half of the cuticle. It is stored in deposits partially located in the anterior region, in the ecdysial space, and in the haemolymph. After molt, animals reuse these stocks for mineralization of the new cuticle (e.g. Steel, 1993; Ziegler et al., 2007). There is a high interspecific variation in the method and location of calcium deposition (Ziegler, 2004). The molting individual often consumes the exuvia to regain mineral content (Steel, 1993; personal observation in the field, Figure 3C).

Several valuable papers have been published recently concerning the mysterious and exciting processes of calcareous deposition, calcariferous transport processes and the anatomic changes in the cuticle, especially during molting, (e.g. Neues et al., 2007; Ziegler et al., 2005, 2007; Hild et al., 2009; Štrus and Blejec, 2001).

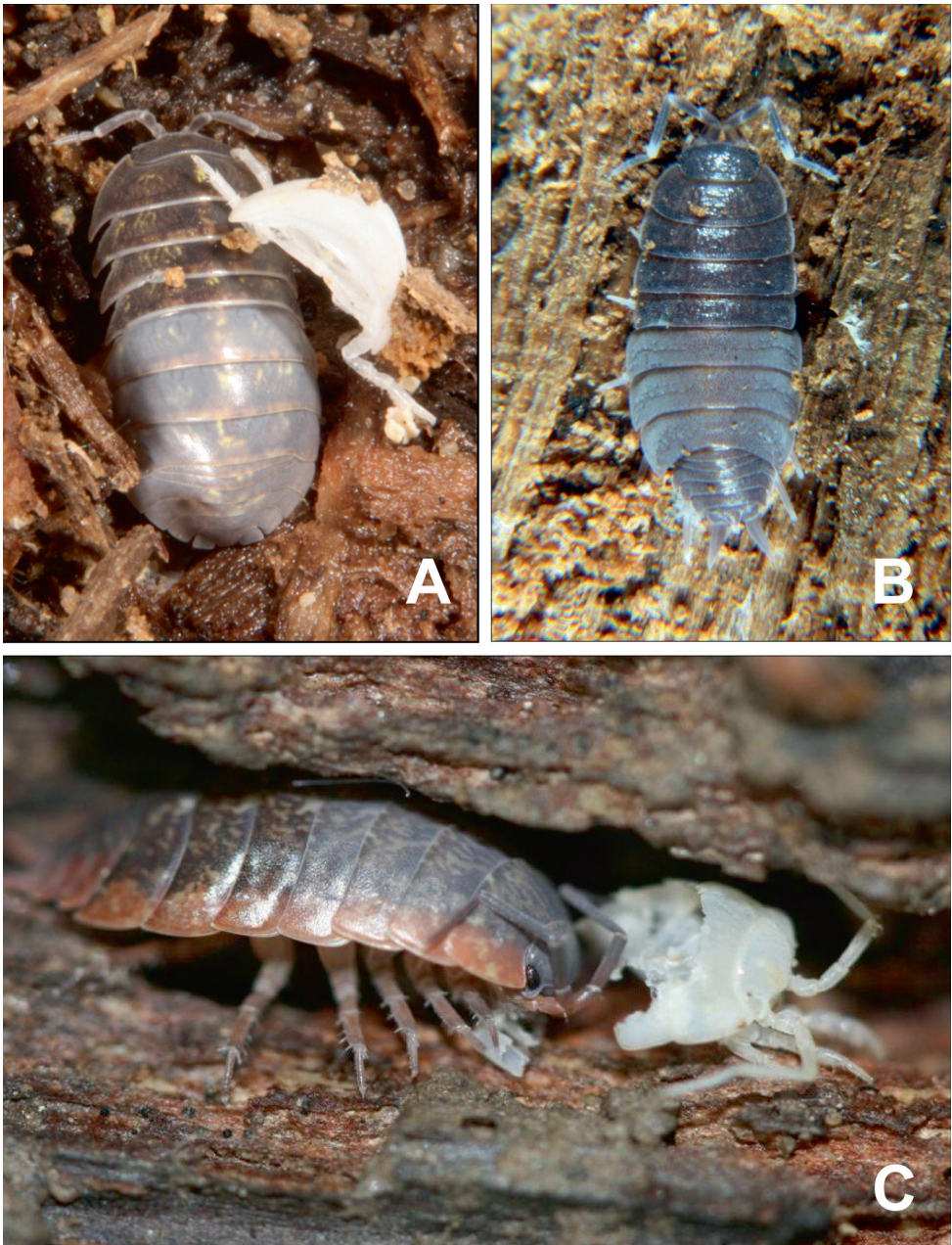
### *Surface morphology, perception*

Electron microscopic (SEM) scanning is a splendid method of studying the morphology of isopod cuticular surfaces. A great variety of surface ornaments are present on the dorsal surface of terrestrial isopods (Figures 2B-F and 4), such as sensory and





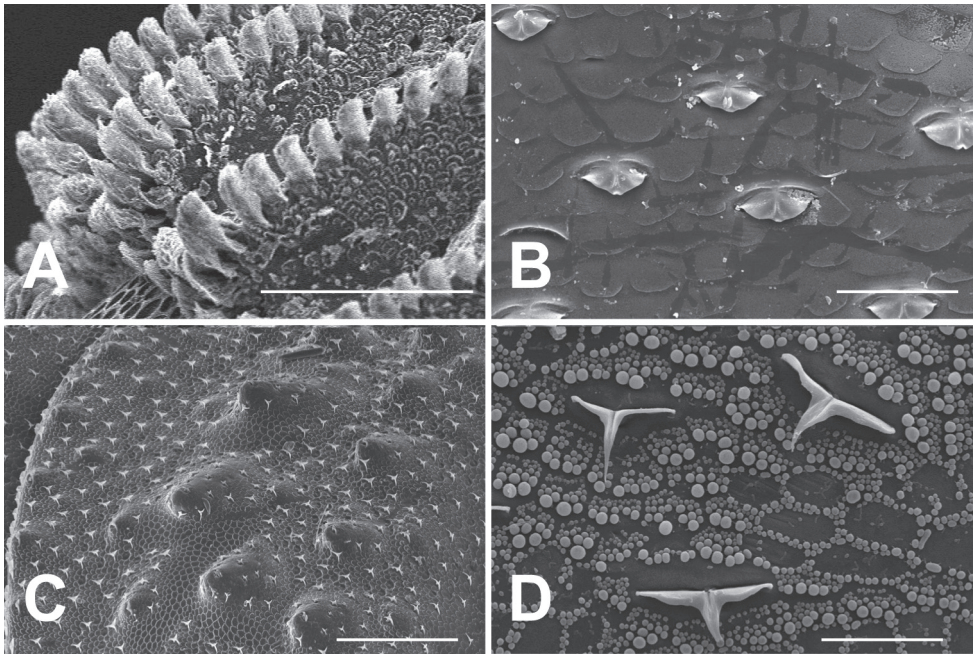
**Figure 2.** (A) Cross section of *Armadillidium vulgare* tergite: layers of the cuticle with an innervated cuticular extension (photo by D. Csonka); ec: epicuticle; pc: procuticle; hy: hypodermis; sm: skeletal muscle; t and black arrow: exteroceptor ('tricorn'); star: nuclei of supporting cells around a nerve (scale bar = 20  $\mu$ m). (B) Antennal setae of *Platyarthrus schoblii* Budde-Lund, 1885 (20  $\mu$ m). (C) *Protracheoniscus major* (Dollfus, 1903) tergal surface with plaques and sensory setae (100  $\mu$ m). (D) *P. hoffmannseggii* Brandt, 1833 tergite surface (20  $\mu$ m). (E) Noduli laterales (nl) in *Protracheoniscus politus* (approximate length of isopod is 12 mm). (F) The same by SEM (100  $\mu$ m). All illustrations in this and other figures were prepared by the author unless another name is mentioned (parenthetically).



**Figure 3.** Molting. (A) *Armadillidium vulgare* after shedding the posterior part (pale and soft); approximate length of isopod is 17–20 mm. (B) *Porcellionides pruinosus* (12 mm), after shedding the posterior part; note the freshly molted posterior being much wider and grayish than the anterior (“old”) one. (C) Freshly molted *Protracheoniscus politus* (C. Koch, 1841) (anterior part) feeding on exuvia.

non-sensory structures, including papillae, setae, tricorns, microscales, pits, minute plaques, tubercles, ridges, pores (Powell and Halcrow, 1982). Innervated cuticular extensions mediate sensory information (Holdich, 1984) of behavioral responses.





**Figure 4.** Tergal surfaces of (A) *Platyarthrus schoblii*: tergal ridges (scale = 100  $\mu\text{m}$ ), (B) *Armadillidium versicolor* (50  $\mu\text{m}$ ), (C) *Porcellio scaber*: tubercles covered by sensory tricornes (250  $\mu\text{m}$ ), and (D) *Porcellionides pruinosus*: tricornes and waxy spheres (250  $\mu\text{m}$ ).

Holdich and Lincoln (1974) found no sexual differences in this morphology in their studies on *Porcellio scaber* Latreille, 1804. Dorsal scale-setae in different forms, antennal, uropodal spikes are unique to oniscideans presumably accompanying terrestrial adaptation (Figures 2 and 4; Holdich, 1984).

Scale like, circular or polygonal micro-ridges (Figure 4A) provide anti-adhesive qualities, preventing small, wet particles from sticking to the animals' cuticle (Schmalfuss, 1975, 1977, 1978). The dorsal surface of the exoskeleton is adapted to the microhabitat type (Schmalfuss 1984). There is great variation in surface structures, from very smooth surfaces to rather ornate ones with depressions, groves, ridges, tubercles, plaques, scales etc. (Schmalfuss, 1978; Holdich, 1984) (Figures 2B-F and 4). These surface formations, together with other external characteristics, were categorized by Schmalfuss (1984) into five eco-morphological strategies to show the high correlation between body-construction and habitat, and microhabitat features (i.e. ecological preferendum and antipredator strategies), detailed below (see also Figure 13 below).

1. The real epigean forms are either slow moving animals with flat and broad bodies, strong and short pereopods ('clingers' like *Trachelipus*, *Porcellio*, *Nagurus*), or fast moving, narrow and elongated bodied ones with a smooth surface and long pereopods, 'runners' (families Ligiidae and Philosciidae, genus *Trichoniscus*, *Protracheoniscus*, *Porcellionides*). The latter type is thought to represent the most

ancient type of terrestrial forms (see below Figure 13F-I and C-D, respectively; Schmidt, 2008).

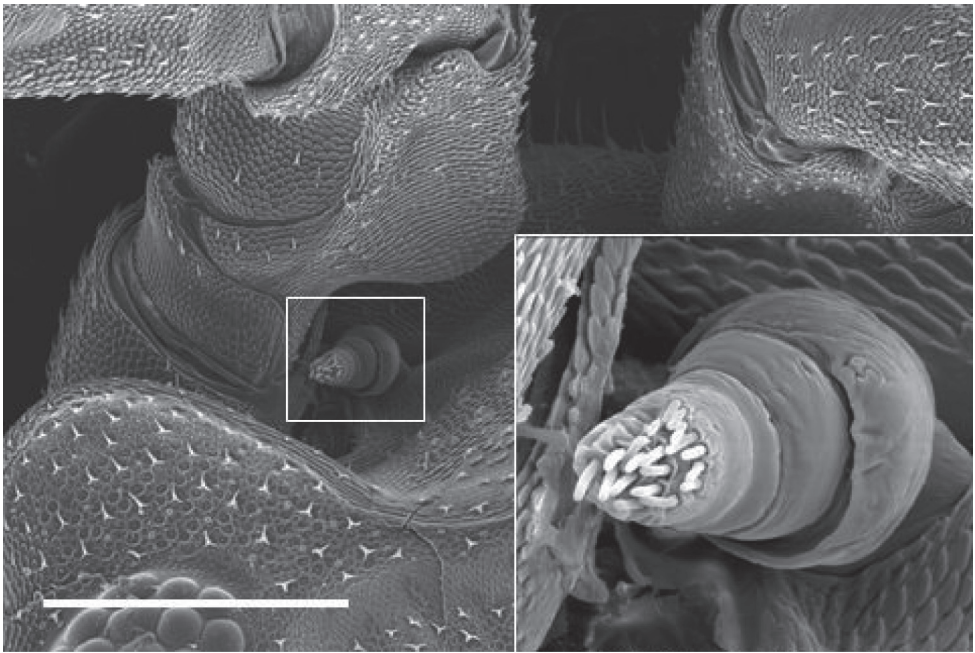
2. True soil dwelling, endogean species, ‘creepers’—Oniscidae, such as *Bathytropa*, Trichoniscidae as *Graeconiscus*, Plathyarthridae as *Platyarthrus*, Stenoniscidae as *Stenoniscus*—are mostly pygmy forms with convex, elongated body, short appendages. They do not conglobate, or roll forming a sphere. They depend strongly on conditions of high humidity because of their high cuticular evaporation rates. However, they have dorsal longitudinal ribs to prevent passive captivity inside water drops due to decreased surface and thereby decreased surface tension (see Figure 13A-B below; Schmalzfuss, 1984).
3. The conglobating forms are called ‘rollers’ (Armadillidae, Eubelidae, Armadillididae, Sphaeroniscidae, and Tylidae). Their body is highly convex and they are able to roll up into a ball (see Figure 13J-M below).
4. There are ‘spiny’ forms that live outside the litter layer (Eubelidae such as *Panningillo*; Armadillidae such as *Acanthoniscus*, *Echinodillo*, *Tridentodillo*). These are mainly tropical, subtropical species.
5. The so-called ‘non-conformists’ (about 10%) that do not fit into the previous categories (e.g. commensalists in ant nests as *Plathyarthrus* spp., *Schoebelia*; soil diggers as *Hemilepistus*, *Leptotrichus*). For further details and examples, see Schmalzfuss (1984). The eco-morphological defense strategies of land isopods are strengthened by the species specific mineral distribution in their exoskeleton (see Figure 13N-P below; Hild et al., 2008).

Humidity is a key factor limiting the distribution of terrestrial isopods. The function of ‘moisture monitoring’ is provided by flagellar aesthetascs found on the apical article of the first antennae and on the flagellar articles of the second antennae (Schmalzfuss, 1998). Extreme diminution of the first antennae in terrestrial species was a vital evolutionary development in favour of protection against predators (Figure 5). The sensory function of the minute antenna is essential in the task of finding suitable humidity conditions for short and long-term survival (Schmalzfuss, 1998).

Isopods are less resistant to desiccation than insects, and their behavioral reactions to humidity changes have enabled them to colonize a great variety of land habitats (reviewed by Edney, 1968; Lindqvist, 1968). Their existence, distribution on different scales (from global to microscales) depends on the species’ ecological tolerance and on the suitable habitat conditions (e.g. Hornung et al., 2008).

### *Cuticular transpiration*

Cuticular lipids and /or hydrocarbons are supposed to reduce transcuticular water loss (Hadley and Warburg, 1986). They are also able to maintain the water level of the cuticle against desiccation by a supposed active regulating mechanism (Lindqvist, 1968, 1972). For instance, early transpiration studies of Bursell (1955) suggested that the cuticle of isopods is a highly efficient barrier to water loss. The values calculated closely approximate those of other terrestrial arthropods. The permeability of the oniscidean cuticle is limited by the lipoids impregnating the endocuticle, such that when



**Figure 5.** The minute first antenna of *Porcellio scaber* with flagellar sensory appendages (aesthetascs) is covered and protected by the second, large antenna (scale bar = 500  $\mu\text{m}$ ).

the temperature is raised above the lipid melting point, there is a marked increase in permeability to water and water loss (Bursell, 1955). However, Hadley and Quinlan (1984) think that lipids, although present in the cuticle, do not provide an effective barrier to water loss. Quinlan and Hadley (1983) measured cuticular permeability on dead isopods, where the regulating mechanism cannot act. They found, in *Porcellio laevis* Latreille, 1804 and *Porcellionides pruinosus* (Brandt, 1833) at 30°C, that water loss through the cuticle was rather high (55–75%) during the first 3 hours of exposure, in  $\text{mg}/\text{cm}^2$  surface area and permeability increased with higher temperatures (from 25°C to 50°C).

Although cuticular dehydration is a major issue in isopod life, water can be taken up by cutaneous absorption (Coenen-Stass, 1981). Terrestrial isopods are capable of active water vapor absorption (WVA) (Wright and Machin, 1990, 1993a, b). Different species vary in integumental permeability and have different lethal relative humidity (RH) limits: the loss rate is different for species adapted to diverse habitat types on a humidity scale (Edney, 1977). All species are able to replenish tolerable water losses under given humidity conditions and they can be classified by their tolerance limits into hygric, mesic, xeric categories, in accordance to phylogeny and habitat requirements. Representatives of Synocheta appear to have no WVA capability, as was shown gravimetrically by Wright and Machin (1990, 1993a). Their cryptozoic way of life and close ties with wet habitats, may explain this (Wright and O'Donnell, 1995).

### *Tegumental glands*

There are tegumental glands, with openings widely distributed either on the surface of the cuticle or on the lateral surface/edges of the thoracic and abdominal segments, and on the uropods, respectively (Figures 6 and 7; Gorvett, 1951, 1952). These dermal glands have a secretory function, occur only in land isopods, and are probably connected to terrestrial adaptation (Gorvett, 1951, 1956). Weihrich and Ziegler (1997) described the unique, lobed structure of these exocrine glands (Figure 6A). They found that the smaller lateral plate glands and the larger uropod glands are very similar in anatomy. The functional significance of these lobed type glands perhaps is antipredator defense. Gorvett (1956) experimentally tested his “limited defence hypothesis”. According to this hypothesis, the main potential predators of woodlice are spiders. The hardened, drawn-out threads of uropod gland secretum (Figure 6C) can be used as an attachment to the substratum (e.g. in the case of wind-blown juveniles, Hornung, pers. obs.). Gruner (1966) suggested that these glands evolved first as excretory structures and developed into defense ones later (Figures 6 and 7). The development of lobed glands might be correlated with the evolutionary position and the ecological conditions (habitat) of the isopod species.

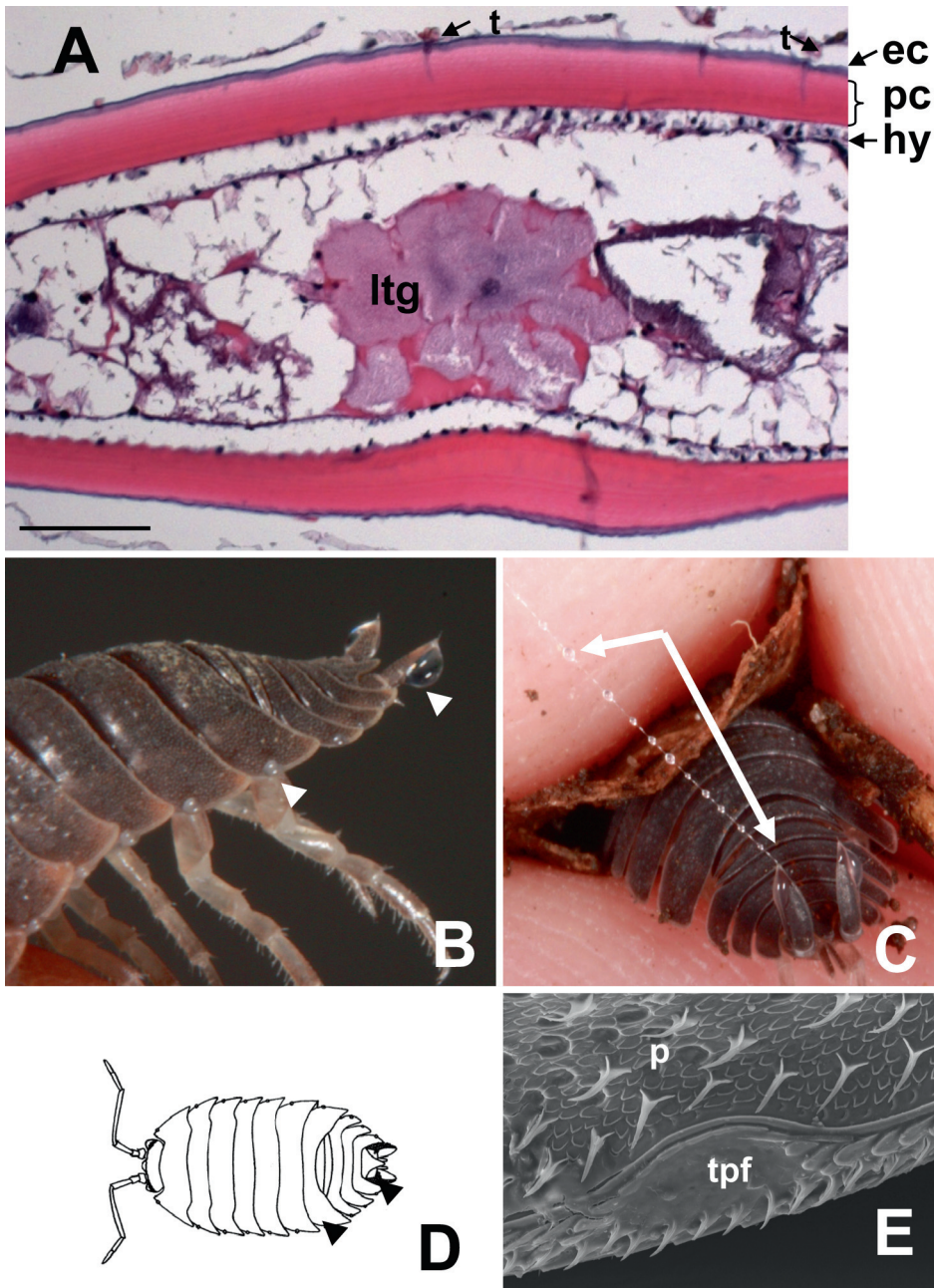
### *Water conducting system: a solution to multiple regulation problems*

An important problem for life on land in isopods was to evolve an adaptive solution for thermoregulation, excretion, osmo- and ion-regulation under terrestrial conditions. The evolution of a water conducting system (WCS) is important in overcoming these problems (Hoese, 1984). This system consists of scale rows (Figure 8A-B) holding water by capillary forces (Hoese, 1981, 1982b). WCS or capillary conducting system (Hoese, 1984) allows also nitrogenous waste to be excreted as ammonia gas, after water resorption. Such a phenomenon is unique to oniscid isopods. Hoese (1981) gives a detailed account of the development of theories on the water conducting system, which was first described by Verhoeff in 1917 (c.f. Hoese, 1981).

In vivo and SEM investigations of 56 isopod species (ranging from marine and freshwater to terrestrial types) resulted in distinguishing two structurally different types of water conducting systems for oniscideans (Hoese 1981). These are the ‘*Ligia*’- and the ‘*Porcellio*’-types.

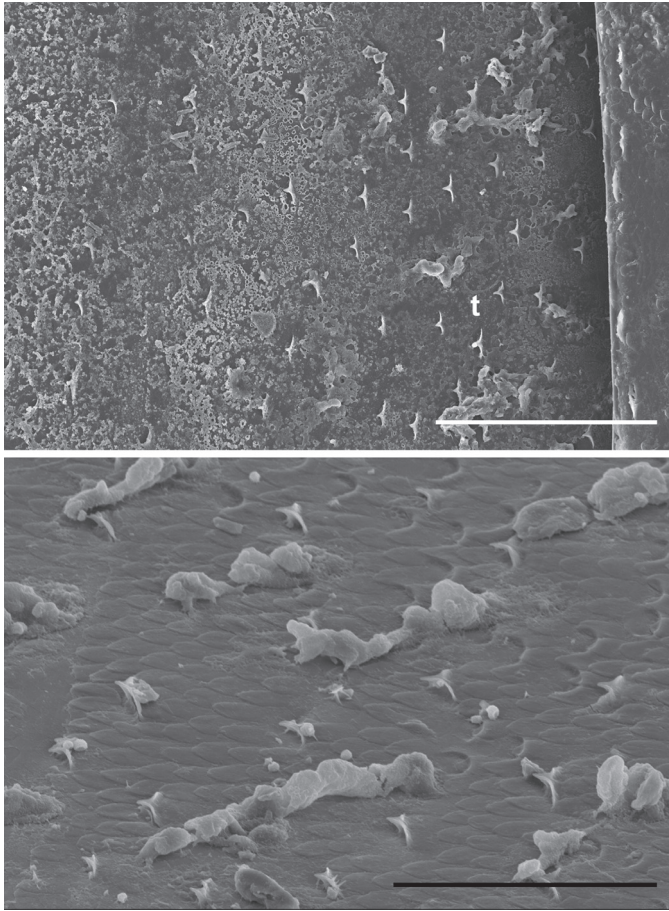
The ancient form (‘*Ligia* type’, named by Hoese, 1981) is an open system, that uptakes water and excretes diluted nitrogenous waste, urine. This system allows water uptake by capillary forces through the 6-7th pereopods. Water is forwarded to other body parts by a water conducting system. The WCS consists of belts of scale-rows on sternites along the insertions of the legs, the antennae and partly the sixth and seventh walking leg. These structures are considered homologous and must have evolved in the common ancestor of all Oniscidea (Schmalfuss, 2005). The group possessing *Ligia* type system includes mainly amphibious isopods, some members of Ligiidae and few species of Trichoniscidae families. The exact details of its structure and the precise functioning of this system were recently studied in *Ligia exotica* Roux, 1828 (Horiguchi et al., 2007). Horiguchi and co-workers succeeded in demonstrating the function and role of each part of 6th and 7th pereopod in the process (see figure 5 therein).





**Figure 6.** (A) Cross section of an epimeron (*Armadillidium vulgare*): structure of cuticle (see also Figure 2; ec: epicuticle, pc: procuticle, hy: hypodermis) and tegumental lobed gland (ltg) (Photo: D. Csonka), t: tricorn (scale bar = 100  $\mu$ m). (B) Each tergite and the uropods have a pore-field, here with secretum drops in *Porcellio scaber* (size of the animal is 14–18 mm). (C) *P. scaber* uropodal gland secretum with drawn-out thread (arrows). (D) Schematic figure of *Porcellio scaber* showing the location of tegumental (anterior arrowhead) and uropodal glands (posterior arrowhead). (E) SEM of a tegumental gland pore-field (tpf) covered by secretum (*Porcellio scaber*) located on the margin of the tergite; p: plaques (scale bar = 100  $\mu$ m).

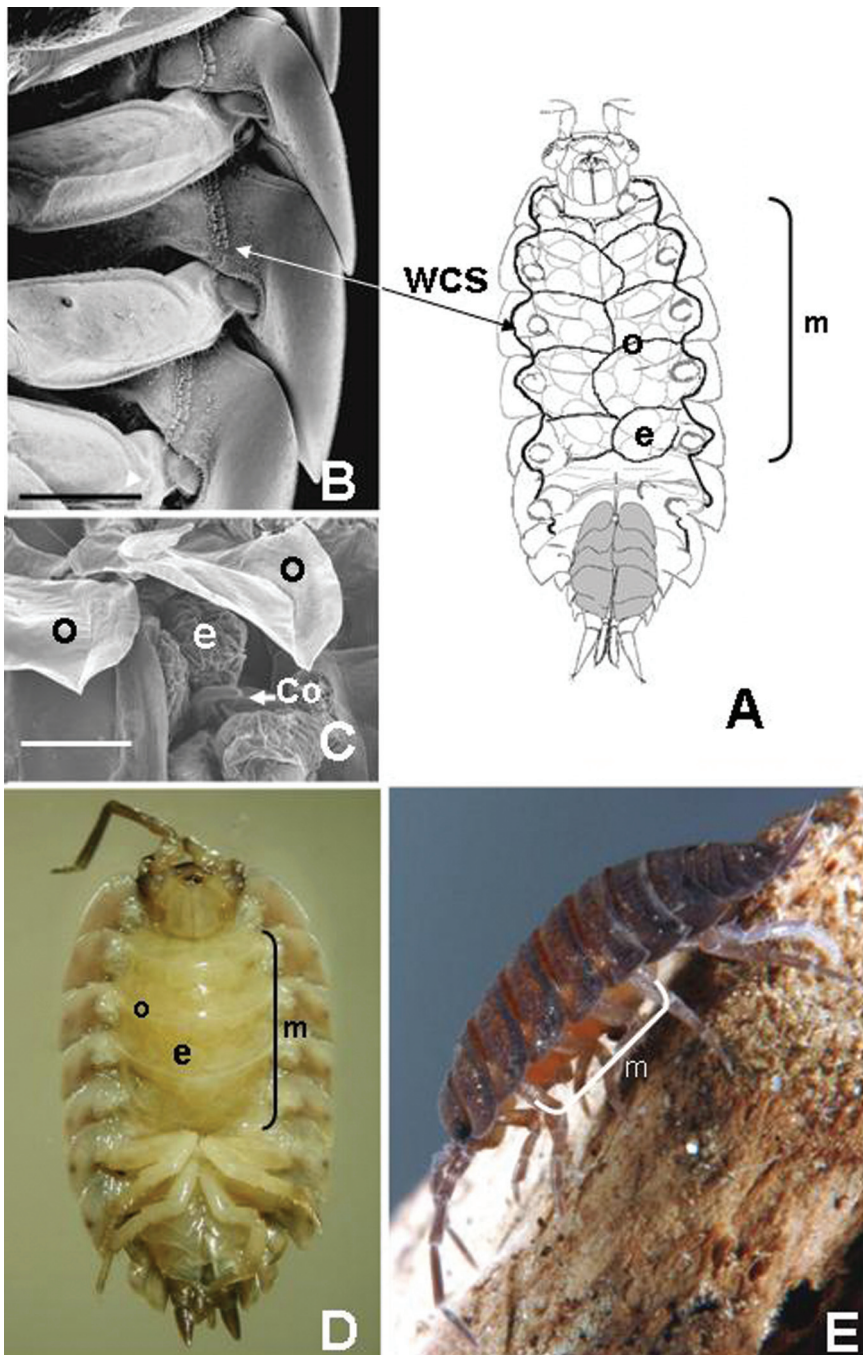




**Figure 7.** (A) Tergal surface of the of *Protracheoniscus politus* covered by secretum (scale bar = 200  $\mu\text{m}$ ). (B) The same surface in higher magnification with precipitated secretum (scale bar = 100  $\mu\text{m}$ ).

They demonstrated that the two superimposed pereopods form a gutter for capillary action. The different surface formations complement one another and they cannot act separately. Also, the system has regulatory ability precluding unnecessary passive water uptake (Horiguchi et al., 2007). Water forwarded by this system also supplies pleopods for respiration. Interestingly, uptake of stained water proved that the anus (but not the oral cavity or the foregut, contrary to the suggestion of Hoese, 1981) is involved in this putatively ancestral water conducting system.

The more derived ‘*Porcellio* type’ WCS was stated to be a closed one, not involving pereopods in the process. Urine excreted by the maxillary nephridium and glands is forwarded caudally. In higher terrestrial isopods (‘*Porcellio*’-type), liquid water can be taken up by mouth (Hoese, 1981), by the rear appendages, or uropods (Spencer and Edney, 1954) and, as water vapor, through the pleoventral space (Wright and Machin, 1990, 1993a, b; Wright and O’Donnell, 1992, 1995). Meanwhile, diluted



**Figure 8.** (A) Schematic representation of the water conducting system (WCS) and marsupium with oostegites (o) and eggs (e) (redrawn after Schmidt, 2008). (B) SEM photo of the WCS: *Porcellio laevis* (by courtesy of H. Schmalfuss). (C) Detail of the brood-pouch (*Porcellionides pruinosus*) with eggs (e), oostegites (o) and cotyledon (Co). (D) Marsupium of *Trachelipus rathkii*: oostegites (o) and eggs (e) (pereipods 1-5 removed). (E) Gravid *Porcellionides pruinosus*. Note inflated venter (m).

ammonia is excreted. Using well-hydrated *Porcellio scaber* individuals exposed to a moistened substratum and saturated air, Drobne and Fajgelj (1993) showed that water is uptaken both by mouth and through the uropod endopodites. Thus, they modified Hoese's (1981) model and proved that the *Porcellio* type water conduction system - and most probably that of *Armadillidium* - is also open. The main difference between the two WCS types is in the route by which the external water is taken up: In *Porcellio*, the water is taken up by uropods and not by 6th and 7th pereopods, as is the case with *Ligidium* and *Ligia*. Subsequently, this water is also distributed along the water conducting system, but it appears first in the pleoventral space (Drobne and Fajgelj, 1993).

The more developed the lung is, the less watering is needed as the animal is relatively more water independent. The WCS is a multifunctional system that (1) aids in respiration by wetting the lung epithelia (the activity of WCS is in negative correlation with the development of pleopodal lungs); (2) supports thermoregulation through water conduction – the two types have different function in this respect: the *Ligia* type shows water uptake and water distribution on the whole body surface while in *Porcellio* type there is a hydrophobic surface (scales filled with air); (3) is essential for excretion: similarly, to true aquatic organisms, they are ammoniotelus or excrete their waste nitrogen principally as ammonia. Urine, excreted by the maxillary nephridium and glands, is channeled into WCS. Faeces contain only about 10% of the N excretum, the rest is eventually evaporated as  $\text{NH}_3$  gas through the WCS (Hoese, 1981).

### *Pleopodal lungs*

In isopods, oxygen uptake happens mainly through the abdominal appendages. In aquatic species these take the form of gills, but the oxygen uptake organs in land (mainly mesic and xeric habitats) isopods evolved in several ways on the pleopod exopodites for aerial respiration during terrestrial adaptation (Hoese, 1982a). In addition, endopodites keep their gill-like structure and function in most of the terrestrial species (Becker, 1936; Cloudsley-Thompson, 1975). The efficiency of aquatic respiration depends on the extent of their adaptation to land: less adapted, littoral species (e.g. *Ligia pallasii* Brandt, 1833) survive for a long time under (sea) water (Taylor and Carefoot, 1993).

The evolution of the respiratory surface on the pleopodal exopodites parallels the phylogeny and adaptations to colonize terrestrial habitats along a humidity gradient. The anatomy, the structure, and the functional principles show different evolutionary routes (Figure 9; Hoese, 1981, 1982a, 1983a, 1983b, 1984; Ferrara et al., 1991, 1997; Paoli et al., 2002; Gruber and Taiti, 2004). Taiti et al. (1998) as well as Schmidt and Wägele (2001) discussed the evolution of oniscidean respiratory structures in the context of phylogenetic relationships, based on morphological characters. In the most primitive oniscideans, the thin ventral integument of the exopodites is the place of respiration. Respiration takes place through a folded surface, which makes up a significant part of the dorsal wall of the pleopodal exopodite (Figure 9Aa, C).

These foldings vary depending on species (Gruber and Taiti, 2004). This simple, open and folded epithelial surface on the exopodites of pleopods could be the first stage of the morphological phylogenetic developmental line. The next phylogenetic stage is a weakly wrinkled surface followed by a partly covered respiratory field (Figure 9Aa, D) with strongly wrinkled surface and the last stage is a completely internalized lung with spiracles and water-repellent surface (Figures 9Ac, E-H and 10). During evolution, the respiratory surface becomes increasingly separated from the atmosphere as its surface area is expanded by inward foldings. It becomes progressively more covered and is connected to the environment through respiratory apertures or spiracles of decreasing size during adaptation (Figures 9E-G and 10) in the most advanced closed lungs, spiracles are surrounded by a water-repellent perispiracular area (Hoese, 1982a; Ferrara et al., 1991; Schmidt and Wägele, 2001). The respiratory epithelium within a pleopodal lung is folded with many small branches (Figure 11). The surface morphology of the perispiracular region has a modular, microsculptured structure (Figure 9B) (e.g. Mödlinger, 1931; Ferrara et al., 1994; Schmidt and Wägele, 2001; Paoli et al., 2002). Mödlinger (1931) described a species-specific difference in shape of this structure in species of *Porcellio* based on cross-sections viewed under a light microscope (LM). A similar, species-specific feature can be recognized in species of *Armadillidium* (Figure 9B; Csonka et al., pers. comm.).

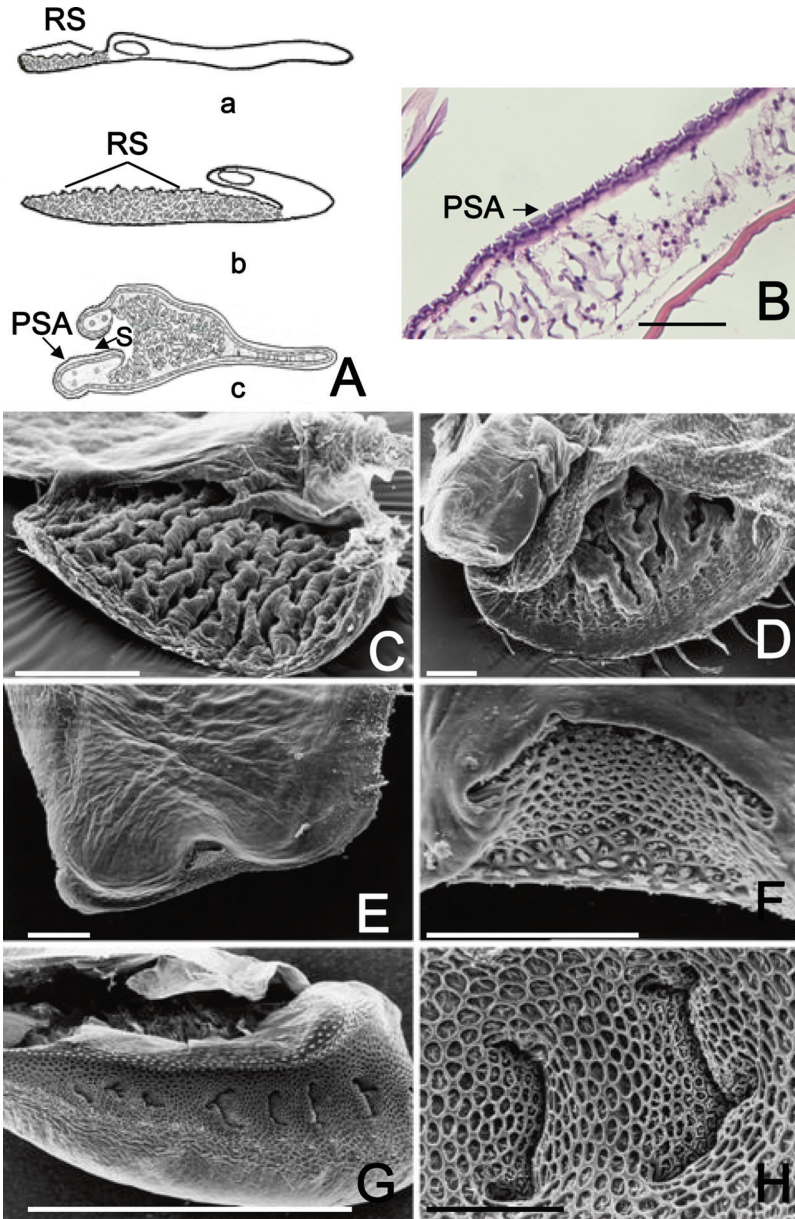
The highest level of development appears in species inhabiting extreme dry habitats, mainly deserts: the tubular structure inside, penetrates into the body cavity ending in so called “lacunae laterales”, as in species of *Periscyphis* (Ferrara et al., 1997). In the desert-living genera (*Periscyphis*, *Hemilepistus* and probably more), the spiracle is closeable (Ferrara et al., 1991, 1997).

Covered lungs can be polyspiracular or monospiracular, depending on the number of openings: monospiracular lungs (Figures 9E-F and 10A, B, D) are the most common type of lungs. Polyspiracular lungs are characterized by several spiracles going into respiratory trees within the pleopodal exopodites (Figures 9G-H and 10C, E, F). The number of spiracles usually decreases from the first to the last pleopod (Gruber and Taiti, 2004). A single spiracle is followed inside the exopod by an atrium which gives rise to narrow lacunae in a compact tissue or branches out into many respiratory tubules (Figure 11) of decreasing diameter (Paoli et al., 2002).

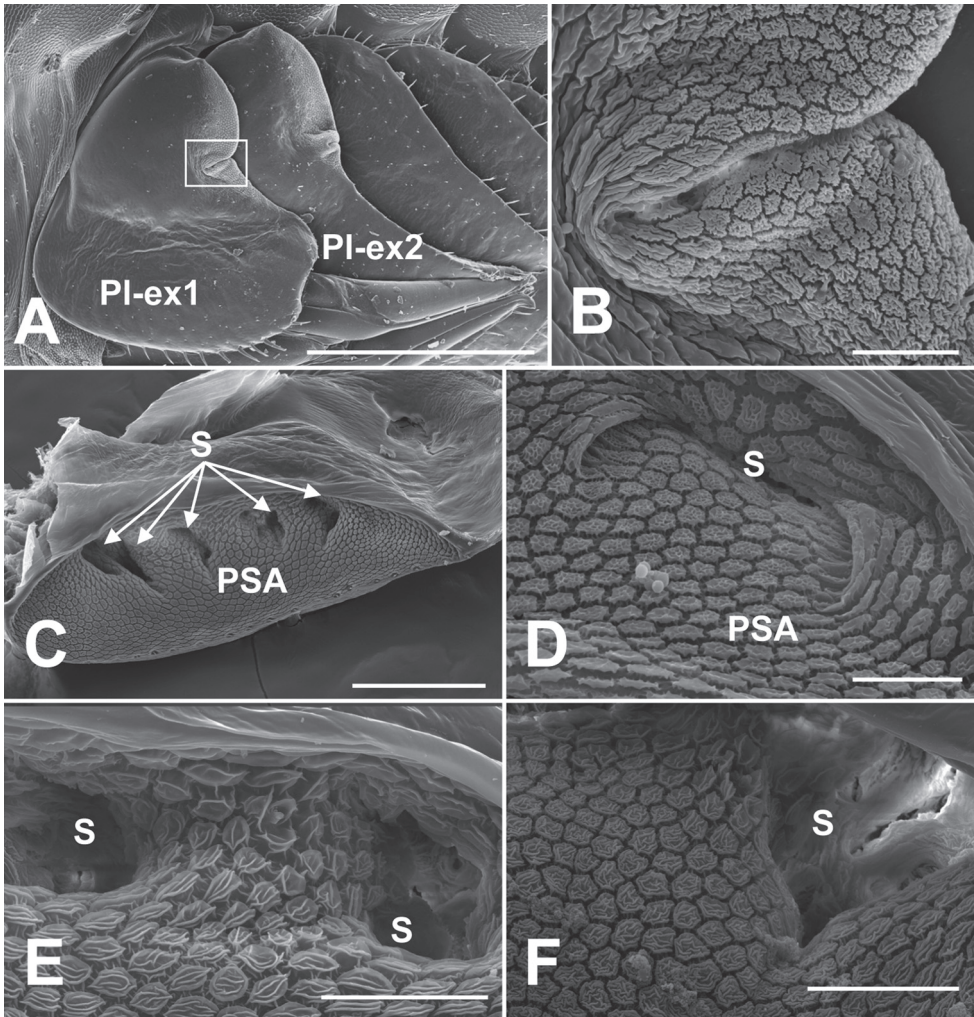
The structural and correlating functional adaptations of respiratory organs might be the main factor in successful colonization of diverse types of land habitats. The developmental stages of lungs have evolved several times convergently during evolution of isopod lineages. At each stage, at least six fold analogous branching steps have evolved. The independent evolution of different types of pleopodal lungs has been demonstrated in the Armadillidae, Eubelidae, Philosciidae, and Tyliidae (Hoese, 1983a; Ferrara et al., 1991, 1994; Taiti et al., 1998; Paoli et al., 2002).

The pleopodal lungs vary not only in structure but also in number. For example, in the Eubelidae (216 species) a phylogenetic series of intermediates can be found, beginning with no lungs (secondary reduction) through 1, 2, 3 and 5 pairs of lungs (detailed schematic presentation in Ferrara et al., 1991). A study of 90 species of Armadillidae





**Figure 9.** Lungs (pseudotracheae). (A) The main evolutionary steps of the development of terrestrial respiratory organs terrestrial isopods; RS: respiratory surface, PSA: perispiracular area, S: spiracle; (a) Open, folded respiratory surface of pleopodal exopod; (b) partly covered type; (c) internal, closed respiratory area, opening (spiraculum) surrounded by perispiracular area. (B) Cross section of perispiracular area of *Armadillidium vulgare* (scale bar = 100 µm). (C-H) SEM images of the different lung types, Photos' courtesy of S. Taiti; (C-D) Uncovered lungs; (C) *Atracheodillo marmorivagus*, 1st exopod; (D) *Synarmadilloides pila*, 2nd exopod; (E-F) Covered, monospiracular lung (*Aethiopopactes nigricornis*, 3rd exopod); (G-H) Covered, polyspiracular lung (*Somadillo taramassoi*, 3rd exopod); Scale bar in C, D, E, F and H = 0.1 mm, in G = 1 mm.

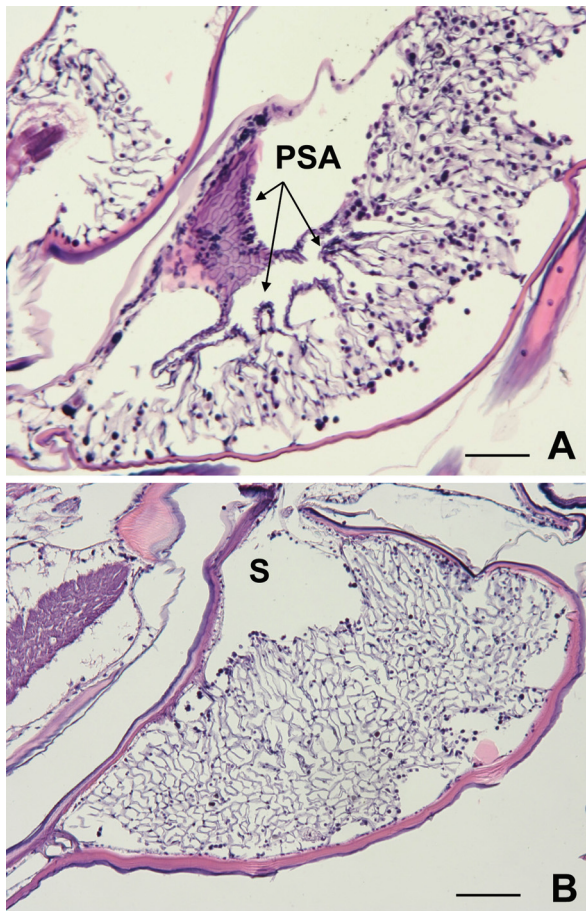


**Figure 10.** (A) First and second pleopodite exopodite with lungs (Pl-ex 1 and Pl-ex 2, respectively) in *Porcellio scaber*, ventral view (scale bar = 1 mm; covered, monospiracular lung type). (B) Close-up of (A) (50  $\mu$ m). (C) Perispiracular area and spiracles of a polyspiracular lung type in *Armadillidium vulgare* (200  $\mu$ m). (D) Spiracle (S) and PSA in a monospiracular type lung, such as *P. scaber* (25  $\mu$ m). (E) Close-ups of spiracles of *A. versicolor* and (F) of *A. nasatum* (both scale bars = 50  $\mu$ m; covered, polyspiracular lung types).

(57 genera) strengthened the descriptions and statements above: all forms of respiratory organs known in Oniscidea are present at family level (Gruber and Taiti, 2004). The primitive uncovered form and the advanced covered pleopodal lungs (including mono- and polyspiracular ones) are present.

The morphological development is in close correlation with the ecological steps of colonization of drier and drier habitats.





**Figure 11.** Light microscopy cross sections of the lung of *Armadillidium vulgare*. The perispiracular elements (PSA) follow the major branches of the ‘lung’ behind the spiraculum (S). (Photos taken by D. Csonka) (Scale bars = 100  $\mu\text{m}$ ).

### *The marsupium*

Brood care is widespread in crustaceans but the temporally existing marsupium appears only in the superorder Peracarida (e.g. isopods, amphipods, and other shrimp-like animals). The marsupium originally evolved for the mechanical protection of eggs and developing embryos under marine conditions. While in aquatic forms, the marsupium protects the eggs, under land conditions it has evolved into a progressively closer brood pouch. The brood pouch is “not just a simple container, but protects eggs against desiccation and microbes, ensures ‘sea conditions’ – aquatic milieu, fluid (water) and oxygen and allows females to remove their brood from dangerous places and carry them into favorable zones (e.g. thermal optima for embryogenesis)” (Linsenmair, 1989). This sexual female character is the speciality of gravid females. They carry their fertilized eggs on their ventral side in this brood pouch (Figure 8A, C-E) and habitually look for places with optimal temperature and humidity conditions for embryogenesis



(Dangerfield and Hassall, 1994; Hassall and Tuck, 2007). Eggs develop into embryos and manca or post-larval juveniles in peracarid crustaceans, regardless of the environmental water supply.

Terrestrial isopods exhibit extensive parental care providing protection and nutrition for developing progeny under marsupial conditions. Ovigerous females show a lower ingestion rate, lower capacity for energy acquisition (Lardies et al., 2004a).

Duration of marsupial development is influenced by light and temperature and has a great plasticity depending on weather conditions and environmental stresses (Hornung and Warburg, 1993, 1994). Both increased light and/or temperature accelerated oocyte maturation, appearance of brood pouch, shortened duration in egg, embryo, and manca development in *Porcellio ficulneus* Budde-Lund, 1885 (Hornung and Warburg, 1993). Oocyte or egg resorption as well as embryo or manca abortion signals the cost of accelerated development (Hornung and Warburg, 1994) resulting in fewer offspring. Increased locomotory activity as well as physical stress has the same effects: reduced fecundity and shortened duration in marsupial development (Hornung and Warburg, 1993; Lardies et al., 2004a).

*Structure of the marsupium.* In semi-terrestrial and terrestrial isopods, the marsupium evolves into a partly or totally closed brood pouch and it is a key component of terrestrial adaptation. Some time after fertilization, isopod females undergo a parturial molt and develop oostegites on the 2nd–5th thoracic segments (Figure 8A, C–E). Within the marsupium, we can recognize the cotyledons, hanging from the venter and penetrating among developing eggs (Figure 8C). The chamber of the brood pouch is filled with marsupial fluid.

*Oostegites.* Trevianus and Trevianus (1816, cited by Hoese, 1984) first described the structure of this brood-pouch. The oostegites are leaf like, overlapping appendages, basally fused with the pereomeres. They project medially from the coxae of the anterior pereopods. Five pairs of oostegites form the marsupium, which is tightly sealed ventrally, and laterally (Figure 8C, D; further details and illustrations in Hoese, 1984; Hoese and Janssen, 1989).

The oostegites are formed under the control of an ovarian hormone during vitellogenesis. An extract of vitellogenic ovaries induced oostegite development in ovariectomized females (Suzuki and Yamasaki, 1989). In *Porcellio dilatatus* Brandt, 1833, fresh or accumulated sperm induces their formation (Loyola e Silva and Coraiola, 1999). *Ligia oceanica* (Linnaeus, 1767) develops oostegites during maturation and keeps them throughout its whole life, which is unusual among isopods (Willows, 1984). The outer wall of oostegites possesses a rather thick and impermeable cuticle that prevents water loss from the marsupium and thereby avoids desiccation (Hoese and Janssen, 1989).

*Cotyledons.* Cotyledons are fingerlike extensions of the intersegmental membrane of the 2nd–5th thoracic segments (Figure 8C). They appear in the marsupium of gravid females after parturial molt and have an excretory function. Their cuticle is extremely

thin. Cotyledons supply the eggs, embryos and manca with water, oxygen and nutritive fluids (Hoese and Jansen, 1989; Lewis, 1991). In *Porcellio olivieri* (Audouin, 1826), a fossorial desert species, a cotyledon (Warburg and Rosenberg, 1996; see figures therein) connects each egg. Aquatic forms and the ancient, supralittoral, amphibian species (e.g. Tylidae, Ligiidae and Trichoniscidae), have no cotyledons, reminiscing of ancestral marine species (Lewis, 1991).

Cotyledons vary in shape and size with species, and with the age of the brood, growing in length, thickening with embryo growth and shrinking before manca release. Their length may also be related to the characteristic humidity of the species' habitat (Hoese and Janssen, 1989). Cotyledons occur singly or in groups of 2-3 along the ridges of the thoracic membrane. The shape of these cotyledons might be single or divided into branches (Hoese, 1984; Hoese et Janssen, 1989; Lewis, 1991). They are usually located in three areas of the body: at mid-line and on each side towards the lateral margin of the marsupium (Lewis, 1991). The arrangement of the cotyledons varies with the family or subfamily oniscids. Ridges in some cases (e.g. *Porcellio scaber*) can enlarge their surface (Hoese, 1984). The number of cotyledons ranges widely within the Oniscidea; this might be correlated with the aridity of habitats (Hoese and Janssen 1989; Lewis, 1991). Lewis (1991) studied over 60 species of Oniscidea belonging to 20 families and found between 4 and 28 cotyledons per individual; a higher cotyledon number was found in species living in increasingly arid habitats and more inferred derived species. Species with the highest number of cotyledons belong to the most advanced members in the Armadillidae that are found mainly in arid regions (Lewis, 1991).

*Marsupial fluid.* Eggs of terrestrial isopods undergo development in the female's brood-pouch. There, they are surrounded by marsupial fluid excreted by the cotyledons. This fluid contains nutritive components essential for embryogenesis, such as oxygen, and provides protection against desiccation, as well as bacterial infection (Hoese 1984; Hoese and Janssen, 1989; Linsenmair, 1989). During marsupial development, the offsprings also need calcium ions ( $\text{Ca}^{+2}$ ) for cuticle mineralization. Ouyang and Wright (2005) have found that the total calcium increased 17-fold in *Armadillidium vulgare* (Latreille, 1804) during embryogenesis. They measured a further 35-fold increase in calcium during the manca stage while they drink and ingest marsupial fluid.

All development stages developing (eggs, embryos and manca; detailed descriptions in Surbida and Wright, 2001) face physiological stress during marsupial development -such as potential desiccation, high ammonia concentrations and changes in osmotic concentrations. Surbida and Wright (2001) studied osmotic conditions, possible osmoregulation in the marsupium and osmotic tolerance, osmoregulatory capacity of marsupial juvenile stages in *A. vulgare* finding that marsupial forms have a wide tolerance and physiological adaptability to land conditions.

*Types of terrestrial marsupium.* Besides the aquatic type, the land colonizing semiterrestrial and terrestrial isopods (Oniscidea) evolved two main types of marsupium: the amphibian type and the terrestrial type. These are –depending on evolutionary

stages and correspondence with habitats— the amphibian and the real terrestrial brood pouches. These marsupia differ in structure (Hoese, 1984; Hoese and Janssen, 1989 illustrate the structures).

The amphibian type marsupium (basic type in species of *Ligia*) is similar to that in aquatic species: open at both ends, anteriorly and posteriorly, and water –taken up by the water conducting system– can pass slowly through the brood pouch on a caudal to apical direction. This type of brood pouch is characteristic of phylogenetically more ancient species, living under extremely wet conditions (Hoese, 1984; Hoese and Janssen, 1989).

The terrestrial type of marsupium (Figures 8A, C, E), is the inferred most advanced type of marsupium and it is characteristic of the Crinocheta or ‘higher’ Oniscideans. There is no connection between the water conducting system and the marsupium being completely enclosed. The marsupium contains a nutritive fluid with mucus and blood cells secreted by the cotyledons. The terrestrial type of marsupium can be regarded as an extension of the body cavity or a kind of uterus (Hoese, 1984). There is no exchange of fluids (*Porcellio* type water-conducting system; no capillary action).

A special form of terrestrial marsupium was described by Warburg and Rosenberg (1996) using SEM and TEM. It raises the possibility of a ‘sac’ type marsupial structure in *Armadillo officinalis* Dumeril, 1816 and *Schizidium tiberianum* Verhoeff, 1923. Eggs, embryos and manca are grouped into monolayered sacs suspended by a chord from the ventral integument of the female’s marsupium. No cotyledon-like structure could be seen, although the structure of sac-epithelium showed similarities with cotyledons.

## **Behavioral and ecological adaptations**

A wide range of behavioral adaptations enables isopods to live on land. Their behavior is in response to environmental factors such as light, humidity, temperature and chemical stimuli. Intrahabitat behavior, alterations in microhabitat use, resource utilization, breeding phenology, sheltering strategy and ecomorphological differences provide ways to avoid competition and support coexistence for sympatric woodlice populations (Schmalfuss, 1984; Zimmer and Brauckmann, 1997; Zimmer and Kautz, 1997; Zimmer, 2003).

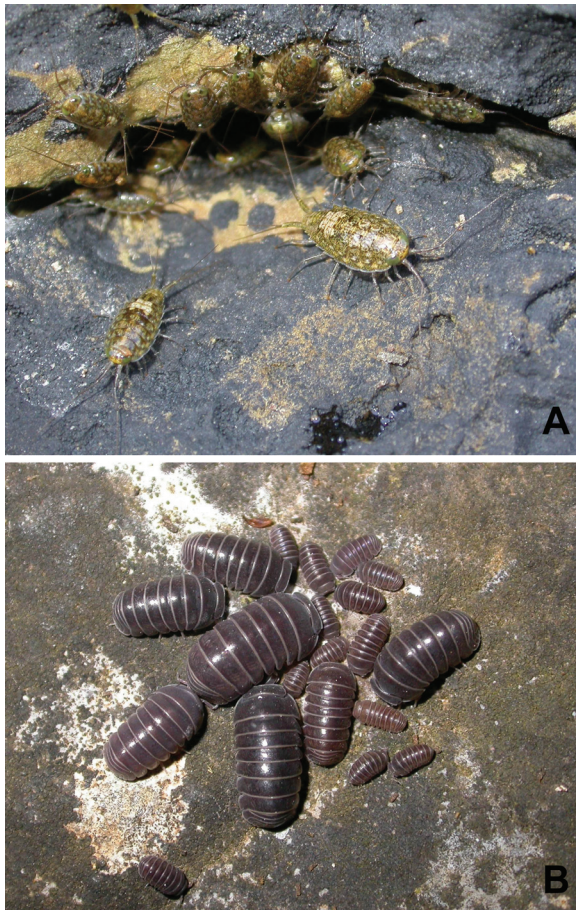
### *Dispersion, surface activity*

Most surface-active terrestrial isopods are typically nocturnal (e.g. Tuf and Jeřábková, 2008), and exhibit seasonal rhythms that follow changes in key environmental factors. These changes result in seasonal changes in surface activity and dispersion patterns (mainly clumped; Figure 12; Hornung 1989, 1991; Hornung and Warburg, 1995, 1996; Farkas, 1998). The presence of suitable humidity conditions is critical and has a basic role in determining tolerance ranges at a habitat and microhabitat scale. Humidity can be more important than any other environmental conditions or resources – such as food, temperature, light or oxygen support (Heeley, 1941). Dispersal and migration

are critical elements of the behavior of individuals and populations in response to changing environmental conditions, such as e.g. seasonal dynamics in favourable habitat patches or, on a greater scale, in response to habitat change or loss. Dispersal might be determined by higher quality food patches (Hassall et al., 1992; Hassall, 1996) under humid conditions, or for higher humidity shelter sites (Hornung, 1989, 1991) in habitats with extreme seasonality. A special activity pattern is shown by desert-dwelling isopods. Detailed studies of *Hemilepistus reaumuri* proved that the active period of the population is determined by their annual rhythm and phenophase. Individuals maintain their heat and water exchange within their physiological tolerance limits by their diurnal activity (Shachak et al., 1979; Nashri-Ammar and Morgan, 2005).

### Sheltering

To avoid desiccation, isopods shelter, depending on species-specific tolerance, humidity and time of the day (Hassall and Tuck, 2007). Shelter site use can be seasonal



**Figure 12.** Aggregating isopods; (A) *Ligia italica* (life size 12 mm); (B) *Armadillo officinalis* (19 mm).

and/or sex-dependent. Males are more active early in the season during mating while soliciting receptive females. Later in the season, gravid females are looking for shelter sites that are optimal for incubation, decreasing the overall cost of reproduction (Dangerfield and Hassall, 1994; Hornung et al., 2009, 2010).

Above the general habits, there are special cases, such as troglobitic, troglophilic forms or desert dwelling species. Caves are real ecological refuges for such hygrophilous invertebrates as terrestrial isopods. Around 300 species of terrestrial isopods are troglobiotic and additionally many others are troglophilic (Taiti, 2004). Numerous species of terrestrial woodlice are adapted to hypogeian and endogeian habitats (Manicasterri and Argano, 1989).

Probably the most amazing example of adaptation and tolerance in the Oniscidea is the genus *Hemilepistus* that inhabits loess deserts. *Hemilepistus reaumuri* (Figure 13R) is the best-known species that has adapted to these harsh conditions with its monogamous, subsocial behavior, 'family life', diurnal activity, and semelparous reproduction strategy (Linsenmair, 1985, 1987; 2008; Shachak, 1980; Shachak and Newton, 1985; Warburg, 1992; Nashri-Ammar and Morgan, 2005). This animal emerges at the end of the Mediterranean winter and is active on the surface from the beginning of spring to autumn. During the heat of the day, it remains in its burrow, but it is active above ground in the morning and evening (Nasri-Ammar and Morgan, 2005). *Hemilepistus* shows prolonged brood care, investing higher costs in reproduction and gaining higher survival of progeny under the extreme desert conditions (Linsenmair, 2008). In an experiment on the settling behavior of *H. reaumuri*, Baker (2005) has shown that specimens experiencing poor, degraded habitat conditions became less selective and settled in poor quality areas while those from good quality habitat patches did not disperse in spite of overcrowding.

### *Conglobation, aggregation*

Conglobating isopods ('pill bugs') can influence water balance and prevent predation by rolling-up (Figure 13J-L). Water loss rate and CO<sub>2</sub> release were decreased significantly (by about 35% and 37%, respectively) by this behavior, depending on relative humidity (Smigel and Gibbs, 2008). Non-conglobating forms may have the advantage of effective locomotory activity to avoid desiccation and for finding suitable microhabitat as was shown with *Porcellio laevis* (Dailey et al., 2009).

The spatial pattern of isopod distribution at the habitat scale proved to be aggregated in most ecological studies (Hornung, 1989, 1991; Hornung and Warburg 1996; Farkas, 1998). This clumping behavior may have a temporal pattern in seasonal environments and correlates with above ground humidity conditions. Aggregation is an adaptive behavior (Figure 12) against desiccation and it correlates intraspecifically with latitude (Caubet et al., 2008): southern populations show a higher level of aggregation. Aggregation may also be a stimulating trigger for reproduction in females, speeding up their vitellogenesis (Caubet et al., 1998) and accelerating body growth (Takeda, 1980). An aggregation pheromone is secreted in the mid- and/or hindgut and it is excreted with the faeces (Takeda, 1980).



### Food choice, feeding strategy

Isopods are saprophagous invertebrates important in plant litter decomposition. Their function has a key role in ecosystems and is strongly influenced by environmental factors, including climate and so, thus by global climatic changes (David and Handa, 2010). They may have a key regulatory function in the decomposition of dead plant material in certain habitat types (e.g. arid regions of North Africa and Asia – Shachak and Yair, 1984; Linsenmair, 2008; tropical and temperate ecosystems – David and Handa, 2010). Terrestrial life also requires adaptation also to the quality of available food sources. Evolution of behavioral adaptations includes food source choice and feeding strategies.

Second antennae of terrestrial isopods help not only orientation but function as gustatory organs in food localization. In case of loss of the second antennae, the minute first antennae (Figure 5) substitute them by using their aesthetascs, or chemoreceptors (Schmalfuss, 1998). The odor of metabolites emitted by food colonizing microbiota (Zimmer et al., 1996) directs the food choices of isopods. Microbes produce extracellular enzymes and/or trace nutrients, first of all essential amino acids (Ullrich and Storch, 1991). Isopods use exo-enzymes gained from consumed microbita for digestion of plant material. Kostanjšek et al., (2010) found the first evidence for cellulose degrading endogenous enzymes in peracarid crustaceans, namely in *Porcellio scaber*. Enzyme activity was shown in hepatopancreatic extract.

Zimmer (2002) reviewed knowledge of terrestrial isopod nutrition from an evolutionary ecological view. Food quality influenced food choice in the laboratory experiments of Szlavecz and Majorana (1991). Nitrogen rich leaves were preferred by all investigated species, either cosmopolitans (*Porcellio scaber* and *Armadillidium vulgare*) or more restricted, central European species (*Protracheoniscus amoenus* (now *P. politus*) and *A. zenckeri*). Dicotyledons mean high quality food that is preferred (Rushton and Hassall, 1987). Increasing patchiness of high quality food distribution and isopod abundance changes foraging behavior of individuals. At high density, woodlice spend more time searching for food and spend more time on low quality food (Hassall et al., 2001). Food choice and consumption are often used as endpoints of toxicological tests. Zidar et al. (2003, 2005) found on *Oniscus asellus* that food quality is reflected in the behavior of woodlice. Animals avoided both Cadmium contaminated and sterilized food in the presence of uncontaminated or molded food.

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**Figure 13.** Examples of different eco-morphological types (Schmalfuss, 1984). ‘Creepers’: (A) *Haplophthalmus danicus* Budde-Lund, 1880 (size 2.5–4 mm), and (B) *Androniscus dentiger* Verhoeff, 1908 (7–8 mm); ‘Runners’: (C) *Hyloniscus riparius* (C. Koch, 1838) (4–6 mm), (D) *Porcellionides pruinosus*, (E) *Protracheoniscus politus*; ‘Clingers’ (F) *Porcellio dilatatus* (12–15 mm), (G) *Trachelipus ratzeburgii* (Brandt, 1833) (12–15 mm), (H) *Porcellio scaber* (14–18 mm), and (I) *P. spinicornis* Say, 1818 (12–15 mm); ‘Rollers’: (J) *Armadillidium vulgare*, (K) *A. nasatum* Budde-Lund, 1885 (13 mm), (L) *A. versicolor* Stein, 1859 (14 mm), and (M) *Cylisticus convexus* (De Geer, 1778) (12–14 mm); ‘Non-conformists’: (N) *Platyarthus hoffmannseggii* (2–4.5 mm), (O) *Buddelundiella cataractae* Verhoeff, 1930 (2 mm; courtesy of F. Vilisics), (P) *Trichorchina tomentosa* (Budde-Lund, 1893) (3.5–4 mm), and (R) *Hemilepistus reaumuri* (‘true digger’; 10–19 mm).





Faeces consumption (allo-, autocoprophy) is a general phenomenon in terrestrial isopods although the interpretation of its function is inconsistent (Hassall and Rushton, 1982; Wieser, 1984; Ullrich and Storch, 1991). In default of coprophagy, survival, body weight increase might be negatively influenced. That might be due to shortage of microbiota reconsumed. The extent of faeces eating is in correlation with food quality (Hassall and Rushton, 1982). A previous hypothesis of Wieser (1966, 1984) presumes copper regain as the function of coprophagy.

Hassall and Rushton (1984) discussed the adaptive significance of selective feeding. Food quality may play a crucial role in population dynamics of terrestrial isopod assemblages.

### *Life history strategy*

Phenotypic plasticity in life history traits is an adaptive response to environmental conditions (photoperiod, temperature). Timing of breeding (about 2 days time lag increase per degree of latitude) in *Armadillidium vulgare* (Souty-Grosset et al., 1988) or increase in reproductive output and offspring size in *Porcellio laevis* Latreille, 1804 (Lardies and Bozonovic, 2008) with higher latitude. *Ligia exotica* Roux, 1828 produced larger offspring in inland population under unpredictable aridity conditions than living in littoral zone under constant humidity (Tsai and Dai, 2001). There is a clear trade-off between offspring number and size. Most terrestrial isopods show extensive parental care contributing to increased fitness of their offspring. Larger juveniles favor colonization and enables invasion from littoral to inland habitats. Diet quality, high protein content of food resulted in a significant increase in offspring number and decrease in offspring size in *Porcellio laevis* (Lardies et al., 2004b).

Sutton et al. (1984) divided the life history characteristics of terrestrial isopods into steno- and eurydynamic types, more or less similar to r-K strategies. The observed life history traits are in close relationship to the eco-morphological strategies suggested by Schmalzfuss (1984) (Table 1). Soil dwelling ('creeper') species belong to stenodynamic ones ('K' strategy) while surface-active species ('runners', 'clingers', 'rollers') belong mainly to the eurydynamic ('r' strategy) species group. All these variation of strategies occur also among cave-living species (Taiti, 2004). Additionally, troglobiotic species show the characteristic adaptive traits of troglobiotic invertebrates, such as reduction or shortage of eyes and pigmentation, long appendages, thin cuticle, specialization of sensory organs, loss of rhythmicity, reduced fertility, and low number of offspring (Manicasterri and Argano, 1989).

### **Future directions**

The diverse group of terrestrial isopods offers an excellent opportunity to study the diversity in land adaptations, morphologically, physiologically and ecologically. Specimens of several species can easily be reared under laboratory conditions and used as experimental models.

A series of research questions can be raised covering a wide range of biological disciplines (Hornung et al., 1992). Most of the questions were grouped by subdisciplines

**Table 1.** Life history characteristic of terrestrial isopods (compilation based on Sutton et al., 1984; Schmalzfuss, 1984) and represent broad relative tendencies.

Characters	Stenodynamic ('K') strategy	Eurodynamic ('r') strategy
	Soil active species ('creepers')	Surface active species ('runners', 'clingers', 'rollers')
Size	small	large
Number of ocelli	a few	many
Pigmentation	light	extensive
Maturity	late	early
Number of offspring	small	large
Manca's size	large	small
Growth rate	slow	fast
Locomotion	slow	fast

and published as an outcome of the plenary discussion at the 6th Symposium of Isopodologists (Hassall et al., 2005). The topics range from molecular and physiological questions to ecological and biogeographical ones. The issues concern life history and reproductive strategies, plasticity at the individual level, such as pair choice, number of successive broods, reproductive investment of specimens, etc. In addition, the problem of correspondence between ecological tolerance, adaptive morphological characters and the environmental conditions of species and their distribution on regional and habitat/microhabitat level are waiting for further elucidation. The correlation between ecomorphological features and environmental tolerance/habitat requirements in determining geographical distribution as well as life history traits and their association to successful establishment, distribution, especially in the case of invasive species, needs to be further addressed.

In the last decade, new research trends in isopodology have also emerged. A more functional approach in ecological investigations is needed, such as studies on the significance and mechanisms of population interactions within a decomposing system; the efficiency of their contribution to ecosystem services also need further investigations: the importance of species richness, functional diversity and redundancy in decomposing subsystems (Heemsbergen et al., 2004). Isopods also became favorite models for ecotoxicological studies: e.g. investigating the effects of heavy metals (Hopkin, 1993; Drobne, 1997; Vijver et al., 2005), insecticides (e.g. Drobne et al., 2008; Santos et al., 2010), endocrine disruptors (e.g. Lemos et al., 2009; 2010), or general methodological problems (Drobne and Hopkin, 1994; Loureiro et al., 2005b).

In addition, the increasing global problem of urbanization, the functional role of alien species, and the homogenization of the urban fauna also need urgent research (Magura et al., 2008a, b; Pouyat et al., 2008; Vilisics and Hornung, 2009).

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