

# 1 Biology of Soil Invertebrates

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## 1.1 Introduction

The soil is an important interface in nature which is influenced by different environmental spheres: the hydrosphere, the lithosphere and the atmosphere. The soil compartment has developed over eons, and passed through many stages of development and maturation. Soil is thus often described as an archive of earth history. All the spheres determine soil characteristics, but the influence of man and modern technology has increased significantly since the last ice age. It is therefore reasonable to add a fourth sphere influencing soil characteristics: the anthropo- or technosphere. This is a multifactorial web of human influences, the importance of which has increased greatly since the beginning of industrialization. Soil degradation and desertification are catchwords describing fundamental changes in natural soil functions which have led to an irreversible loss of high-quality soils worldwide. The key variables for the development of soils, the rocky subground, the climate and the vegetation have become more and more biased by modern soil tillage practices and inputs of contaminants and pollutants. Human impacts to soils have contributed much to the modification of the soil as a component of global change.

In this area of conflict and change we find a realm of organisms which have adapted to the specific conditions of life in the soil: the soil organisms. These are primarily microorganisms and invertebrates which play major roles in the soil community known as the edaphon and which are known to have specific adaptations to soil conditions. A wide range of life forms from euedaphic or endogeic species living within the soil profile up to epedaphic or epigeic species living mainly on the soil surface makes up the soil fauna. Between these main groups we can distinguish some intermediate life forms which are called hemiedaphic. Some authors also divide the edaphon into two major groups, the aquatic and the air-breathing organisms.

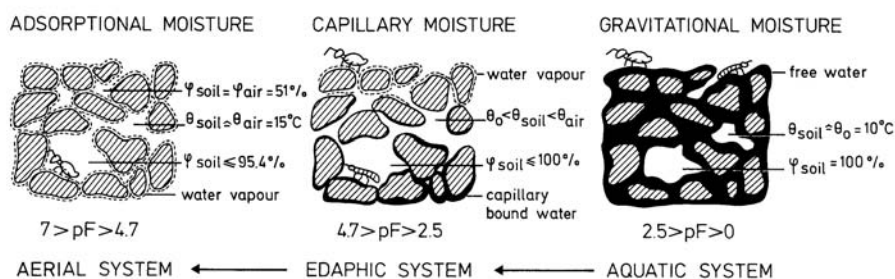
The French ecophysiologicalist Guy Vannier has characterized the soil habitat as a porosphere. It is composed of a hierarchy of micropores (fine,

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medium and large), of visually detectable macropores, and of megapore systems (i.e. larger cavities like corridors, tubes, crevices, clefts, and galleries). In this porosphere, Vannier differentiates three basic conditions depending on the water status of the soil: an 'aquatic system', an 'edaphic system' and an 'aerial system' as shown in Fig. 1.1. The best living conditions for soil organisms prevail in the 'edaphic system' with sufficiently high humidity within the pore spaces and capillary bound, residual water around the soil particles. The aquatic system, with its water filled pores, is unfavourable for all members of the air-breathing soil fauna, but all life forms which depend on free water or which are able to swim in water films will find good conditions there. Such organisms are the naked protozoans, the rotifers, and the nematodes often considered to be inhabitants of water films. According to Dunger (1983), most soil protozoans are the same species as occur in ponds and lakes, and only a small contingent can be classified as being endemic soil species. Many soil dwelling species differ from their free-living relatives only in their reduced body size. The aerial soil system, with its lower intrapore humidity is lethal for any soil organism with a highly permeable integument, and which lose body water rapidly. Generally, the atmosphere filling the soil pores differs from the free atmosphere above ground by its elevated humidity, relatively low temperature and increased concentration of  $\text{CO}_2$ .

The community of soil organisms forms the soil food web (Fig. 1.2), consisting of two subwebs (Beck 1993), which are composed of different trophic levels reflecting multiple relations and interactions between the soil fauna and micro-organisms. The main function of the food web is the processing of a variety of complex polymers, e.g. proteins and carbohydrates, to oligomers and monomers and finally to  $\text{CO}_2$ ,  $\text{H}_2\text{O}$  and minerals.



**Fig. 1.1.** The soil pore system (called the porosphere by Vannier 1983). It is classified into three main stages with relation to the soil water regime.  $pF$  Logarithm of the height in centimetres of a column of water corresponding to the water suction power of the soil,  $\varphi$  relative humidity,  $\theta$  temperature (e.g.  $\theta_{\text{air}}$  dry temperature,  $\theta_0$  wet temperature due to the cooling effect of evaporation of a water-saturated soil)

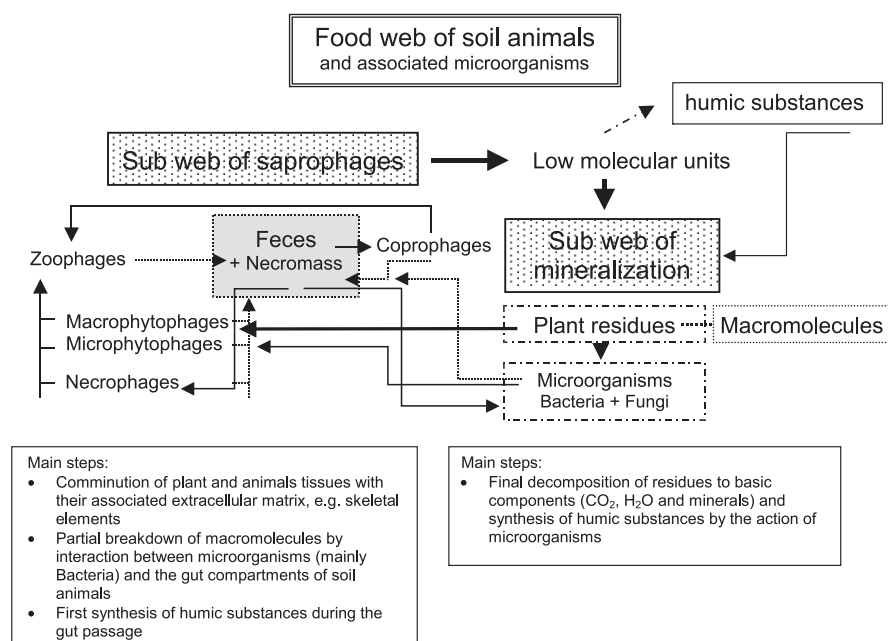


Fig.1.2. Components of a dual soil food web (food web of saprophages and food web of mineralizers) derived from Beck (1983) and different authors

Only the indigestible fraction of carbon (20% in carbohydrates and 75% in lignins, tannins, aromatic amino acids, fats, and waxes) enters into the formation of humic matter.

For pragmatic reasons the classification of the soil fauna is based on the body length of the animals resulting in the following groups: the microfauna (< 0.2 mm), the mesofauna (0.2–4 mm), the macrofauna (4–80 mm), and the megafauna (> 80 mm). Whereas most soil invertebrates can be ranked among the smaller groups (micro- to macrofauna), the larger soil animals (> 80 mm), e.g. insectivores, rodents and hamsters, are mostly vertebrates. It must be noted that there is no correlation between the size of a soil animal and its trophic position in the food web. To carry out such an assessment, the life style and feeding habits must be known. A new method for detecting lines of food processing along food chains by primary and secondary consumers or by predators, has recently been introduced: the analysis of stable isotopes (Ehleringer et al. 1986; Eggers and Jones 2000; Scheu and Falca 2000). The ratio of a heavy to a light isotope of a given element (e.g.  $^{14}\text{N}/^{15}\text{N}$  or  $\text{C}^{13}/\text{C}^{14}$ ) within a sample is compared with a known standard sample, giving a difference ( $\delta$ ) in ‰. As a rule, the heavier isotope component is enriched as the organic material pass from a lower to a higher trophic level. Thus, if plant biomass (e.g. litter material) is transferred

into the body mass of a plant (litter) feeder, then the  $\delta$ -value for  $^{14}\text{N}/^{15}\text{N}$  commonly is about 3.4 ‰ (Eggers and Jones 2000).

According to Anderson (2000) the smaller soil animals contribute disproportionately to the metabolic activity of the edaphon, and there are many interactions between them and the microflora, e.g. by grazing. Conversely the larger soil animals are more important in the modification of the physical properties of soils, e.g. by geophagy, comminution of dead plant biomass and by promoting both vertical and horizontal translocation by the process of bioturbation or bioturbation. Therefore the larger soil animals are often called 'soil engineers' because they have a strong input to such overall soil parameters as infiltration capacity and texture.

The main function of the soil food web (Fig. 1.2) is the processing and recycling of the dead biomass (litter) which is added annually to the soil. There are two main pathways of input. I: Above ground (exogenous) by (1) all sorts of vegetation products (e.g. leaves, remnants of sprouts, twigs and logs), (2) remnants of dead animals, large and small, (3) remnants of micro-organisms, e.g. the dead fruiting bodies of some fungi, and (4) animal excrement, e.g. the faeces of herbivores (phytophages) and carnivores (zoophages), and II: within the soil (endogenous) by (1) dead microbial biomass, e.g. bacteria and fungal hyphae, (2) dead roots, (3) root exudates, (4) animal carrion, and (5) the excrement of edaphic and hemiedaphic animals. The process of decomposition in a wider sense includes a cascade of steps resulting in both mechanical and chemical breakdown (comminution and reduction/mineralization) of complex structures and molecules (polymers) to basic units which are added again (recycled) to the pool of usable materials ( $\text{CO}_2$ ,  $\text{H}_2\text{O}$  and minerals). The basic role of the animals in this context is the initial comminution of the litter by their feeding, but some of them are also involved in regulating the density of microorganisms, e.g. by grazing bacterial colonies and mycelia, and by cleaning up dead micro-organisms. It is known that parts of the microbial populations in a soil survive in a dormant stage; such dormant stages constitute an enormous pool of species. They are able to survive hard times and may be reactivated by better conditions and/or new substrates. Often they need a strong change within their milieu. Such hot spots of microbial biodiversity are considered to occur, e.g., during the gut passage of the biomass or within carrion and faecal deposits.

The basic ecological function of saprophytophagous soil animals is comminution of the dead plant biomass followed by incubation during gut passage. There under specific and constant conditions in succeeding gut compartments, the fine grained food particles are attacked by enzymes at high pH. It is assumed that most of the soil animals cannot digest the litter material using their own enzymes but need the help of the gut microflora. Therefore the incubation of food material in the gut takes place

in a close contact with micro-organisms which provide some of the enzymes for digestion, especially those for the breakdown of polymers like cellulose, lignin and their derivatives. But micro-organisms are themselves a further source of food for soil animals, both those which have colonized the food material before entering the gut and those which live permanently as endosymbionts within the gut.

In the case of non-specific soil feeders which ingest a mixture of organic material and mineral particles, both the gut milieu and the close contact of components insure that faeces leave the body enriched with organo-mineral (clay-humus-) complexes. These are regarded as valuable constituents of a healthy soil texture which minimizes soil erosion and improves the porosity and stability of the soil matrix.

Soil animals which are involved in the first steps of comminution of litter are classified as primary decomposers or saprophytophages. The key members of this group are the lumbricids, the diplopods, the isopods and the larger dipteran larvae. They produce large numbers of faecal pellets with a high proportion of undecomposed material. Such deposits in the soil which are more or less colonized by gut microorganisms are submitted to further colonization by free living micro-organisms. This stage, the material is ready to enter the next stages of decomposition. These are mainly the task of those soil animals which are classified as secondary decomposers. Here the key groups are mites, collembolans and enchytraeids, which feed on the pellet material. Isopods are also known to feed on their own faeces. This type of nutrition is called coprophagy. This transformation of litter into a fine grained stage increases the relative surface area of the material and improves the colonization and penetration of micro-organisms. Soil litter in a recalcitrant stage has to pass through the gut of soil animals several times, which increases the chance that different functional types of micro-organisms can colonize it. During these gut passages, first steps of humification are performed by micro-organisms which can synthesize cyclic (aromatic) compounds.

Other soil animals are less dependent on their own gut micro-organisms as the main food source. Their strategy of foraging is to graze bacterial colonies and fungal hyphae directly from soil substrates. This grazing of micro-organisms is thought to stimulate the metabolic activity and the renewal of microbial populations. Therefore it must be noted that all the activities of both soil animals and the micro-flora increase the overall activity of a soil resulting in high decomposition rates and rapid turnover of matter.

The spectrum of soil the fauna includes many groups of soil dwellers from Protozoa up to the Vertebrata. Vertebrates like rodents and hamsters are well-known for digging in soil and storing large amounts of food in subsoil cavities. This improves both soil aeration and soil mixing, but generally

they are regarded to be only locally active. Soil invertebrates, on the other hand, are more active over the whole soil area and their main task is litter processing and the promotion of basic cycling of elements like carbon and nitrogen. In the following the focus is turned to selected groups of soil invertebrates which are known to be very active in the soil or to share the soil life with interesting biological features.

## 1.2

### The Microfauna

The most important microfaunal groups ( $< 0.2$  mm) are the Protozoa and the smaller Nematoda. Other semiaquatic soil dwellers include the Rotatoria and the Tardigrada, which have evolved sophisticated mechanisms of anabiosis, which enable them to resist extreme conditions of drought and cold. They have commonly been neglected in soil studies because their role in the soil food web is considered to be less important.

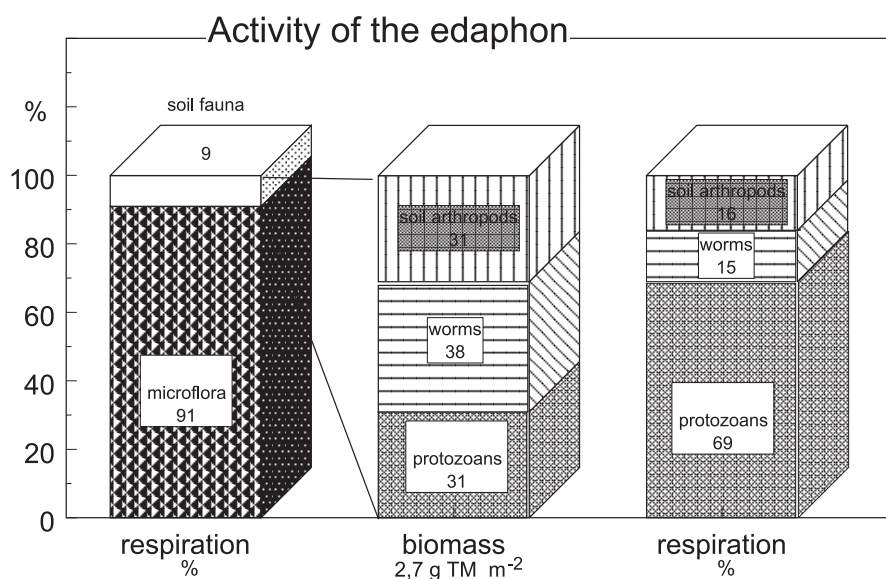
#### 1.2.1

##### Protozoa

Size: 5 to 500  $\mu\text{m}$  in diameter; species number:  $> 15,000$ , about 10% are restricted to soil habitats; abundance:  $\approx 10,000$  per gram soil; key literature: Lousier and Bamforth 1990; Foissner 1994

Since the 1970s, the soil protozoans have received greater attention from soil biologists in the context of large-scale ecosystem studies (e.g. the Solling project in Germany) even though their study requires the experience of a well-versed expert (Weigmann 1998). For a good introduction into their systematics, biology and ecology with a fantastic visualization of their cell bodies, see Foissner (1994) and Darbyshire (1994).

Most relevant are the rhizopods including both testate (Testacea) and naked forms (Amoebina), the flagellates, the ciliates and parasitic sporozoans (Sporozoa). Foissner (1994) gives some good tips for the extraction, the fixation and the staining of protists. Further chapters treat their use as bioindicators and discuss a special phenomenon known from ciliates, and which has been termed the stasis phenomenon. It refers to extreme competition among species and the production of inhibitors by micro-organisms which result in a low population density of ciliates in a normal moistened soil, termed by Foissner ciliatostasis. Indeed, many ciliates are encysted in a dormant stage, especially in deeper soil layers. However, after a soil sample is dried and then rewetted, there is an explosion of the ciliate population as many of the cysts are activated. Foissner (1994) recommended this



**Fig. 1.3.** The respiratory activity of: soil fauna, soil microorganisms, and of the major soil fauna groups according to Meyer et al. (1989)

procedure to survey the species pool of a soil sample. Analysis of 14 ecosystem studies revealed that the protozoa of a forest soil, regardless of their apparently low level of activity, make up nearly one-third of the biomass of the soil fauna (Fig. 1.3; Meyer et al. 1989). This high proportion doubles once again if their contribution to soil respiration is considered. More than two-thirds of soil respiration by animals is contributed by protozoans, and the share of worms and arthropods is overshadowed.

Protozoans feed mainly on bacteria, and thus accumulate in the rhizosphere. Foster and Dormaar (1991) used transmission electron microscopy to show the ingestion of bacteria by pseudopods of naked amoebae which were grazing close to the root surface called rhizoplane. Amoebae have been estimated to ingest about 10,000 bacteria per day. A further spectacular interaction between ciliates and fungal hyphae was described by Foissner (1994). The protoplasm of fungal hyphae is sucked out via a channel created by the ciliate, which penetrates the chitinous cell wall of a hypha. The same behaviour has been observed in amoebae of the family Vampyrellidae, which use enzymes to penetrate the cell wall and to suck out the nutritious protoplasm.

In summary, some important functions are attributed to protozoans in the soil food web, primarily within the inner zone of the rhizosphere, including:



- Regulation of bacterial and fungal populations by grazing.
- Mobilization of nutrients, especially of N (because the C/N ratio of their body is more extended (10:1) than that of bacteria (3:1 to 10:1). In turn, if they share a high biomass then nutrients are also immobilized by themselves.
- Protozoans do exert suppressive effects by downregulation of pathogenic microbial populations.
- They serve as an important food source for other soil organisms, e.g. nematodes.

## 1.2.2

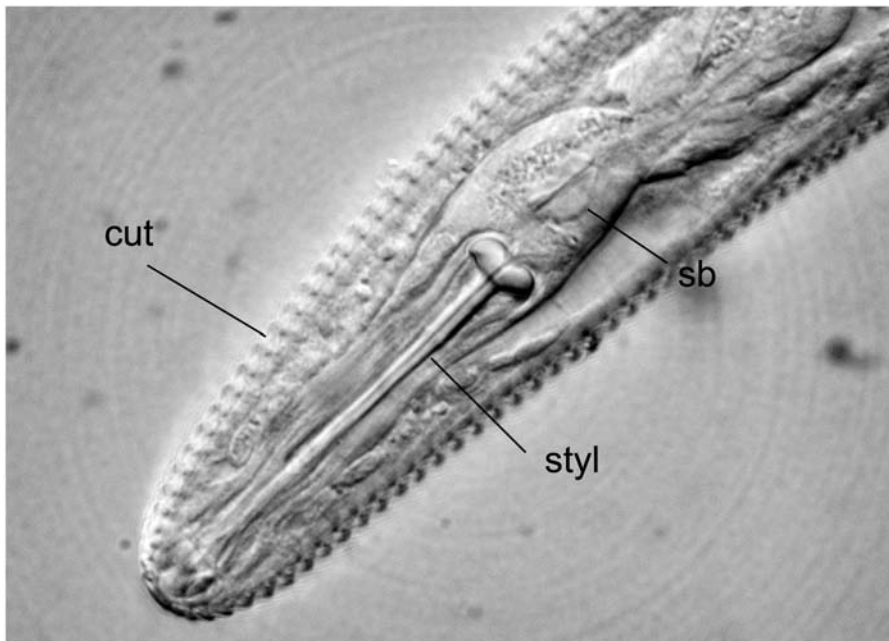
### Nematoda – Roundworms, Eelworms

Size: typically 50  $\mu\text{m}$  in diameter/2 mm in length; species number: described 20,000, estimated half a million; abundance:  $1\text{--}100 \times 10^6 \text{ m}^{-2}$ ,  $10\text{--}1,000 \text{ g}^{-1}$  soil; body mass: 1.6  $\mu\text{g}$  (0.03 to 15  $\mu\text{g}$ ); key literature: Freckman 1982; Freckman and Baldwin 1990; Lee 2002

Nematode worms are some of the most common and widely distributed invertebrates on earth. They inhabit the soils in huge numbers and are often associated with plants and other animals or attack them as parasites. They are worms with a simple body construction consisting mainly of a monolayer muscle tube allowing them to move like a snake. Despite their simple body construction they exert key functions in the food web due to their high density and short life cycles. They take part in litter decomposition and colonize the rhizosphere or decaying animals in large numbers. Consequently, they are involved in nutrient cycling (e.g. release of  $\text{NH}_4^+$ ), which stimulates microbial populations and plant growth. They contribute to the dispersal of microbes, and they attack and penetrate the root tissues. According to structural and behavioural differences they show a high diversity in feeding types (Yeates et al. 1993). These are classified mainly according to the external micro-morphological structures lining the mouth region, but the internal construction of the pharyngeal region is also very important distinguishing the type of nutrition. Ideally, the feeding-group-specific structures should reflect the type of food (e.g. spines, papillae, stylets). The following types of feeding have so far been described:

- Bacterial feeders
- Fungal feeders
- Plant feeders
- Predatory nematodes





**Fig. 1.4.** Anterior body of a nematode with ribbed cuticle (*cut*), pharyngeal stylet (*styl*) and sucking bulb (*sb*)

- Omnivorous nematodes
- Plant associated nematodes
- Entomopathogenic nematodes

Those nematodes which penetrate plant tissue are provided with a stylet which is retracted with its base into the pharyngeal pocket (Fig. 1.4). To attack a target, it is protruded to open a channel in the food source. Predators which feed on nematodes include not only other predatory nematode species but also fungi which are specialized to catch nematodes, as well as predatory groups of mites, collembolans, protozoans, insect larvae and some bacteria. The fungi trap the nematodes in adhesive loops of their hyphae, which are exposed as sticky traps.

Since nematodes are indicators of soil changes in soil environments, due to their high density and high reproductive rate, they are used as bioindicators. For this purpose, the Maturity Index (MI) was introduced by Bongers (1990). It is primarily applied to the free-living forms, but later on it was modified to serve as a Plant Parasite Index (PPI) to characterize better the specific communities of parasitic species. The MI attempts to reflect the strategy of nutrition and reproduction of nematodes. It is

based on a so-called ‘colonizer-persister-scale’ (c-p). The colonizers are ranked as nematode species which are able to increase their population rapidly and to disperse, if soil conditions and food supply improve. They are able to colonize new substrates very quickly (r-strategists) and they tolerate greater disturbances of soil environments, such as mechanical and chemical stresses, e.g. tillage, eutrophication and anoxibiosis. On the other hand, there are the so-called persisters, which are less able to adapt when subjected to changing conditions. Their reproductive rate is low and their ability to disperse is reduced. They need a relative stable environment and their species are classified as K-strategists. The ranking along the c-p-scale starts with the value of 1 for the colonizers and ends with the value of 5 for the most specialized persisters. The intermediate values are assigned to intermediate forms. The classification is mostly based on the taxonomic level of families and genera and the MI emerges as the weighted mean of the specific c-p values according to the following formula:

$$MI = \sum_{i=1}^n v(i) * f(i) \quad (1.1)$$

where  $v(i)$  = c-p value of the taxon  $i$ ,  $f(i)$  = relative frequency of the taxon  $i$ .

The calculation includes either the free-living or the parasitic taxa, although sometimes a mix from both groups has been used. In the literature one can find some modifications of the MI, e.g. Yeates (1994), Bongers and Ferris (1999) and Neher (2001). There is abundant literature available about the MI which can be downloaded via <http://www.dpw.wageningen-ur.nl/nema>.

### 1.3

## The Mesofauna

The mesofauna of a soil includes invertebrates with a body diameter under 2 mm and a length under 4 mm. Important mesofaunal soil dwellers are the smaller Enchytraeidae, the Pseudoscorpionida, the Acari, the Symphyla, the Paupoda, the Collembola, the Protura, the Diplura as well as some smaller groups of pterygote insects, e.g. Psocoptera, Hymenoptera (not included in this chapter, just the smaller Araneida). Collectively, the arthropods within this group are often called micro-arthropods. The populations of the mesofauna exceed those of the macrofauna by several orders of magnitude. However, if a soil environment becomes extreme, e.g. in the course of increasing soil acidification, mesofaunal groups become more and more dominant, resulting in a so-called ‘mesofauna soil’.

### 1.3.1

#### **Pseudoscorpionida – False Scorpions, Book Scorpions**

Size: 1 to 5 mm, min 0.89, max 12 mm; species number: 2,400; abundance:  $50 \text{ m}^{-2}$ ; body mass: 1–5 mg; key literature: Weygoldt 1966, 1969; Muchmore 1990a; Moritz 1993a

The small pseudoscorpions of the order *Pseudoscorpionida* are tiny arachnids which are rarely longer than 8 mm. They are clearly different from true scorpions because they do not terminate in a long segmented tail tipped with a robust venomous stinger. Biologically they are very interesting because they skilfully hunt other micro-arthropods and nematodes. Eyeless, or equipped only with one or two pairs of eyes (ocelli), they move very quickly forwards, backwards or sideways, and changing their direction very quickly. The most conspicuous appendages of their body are the long chelate pedipalps which are equipped with superlong sensory hairs (trichobothria) (Eisenbeis and Wichard 1987; Fig. 1.5). These are used to detect the location of prey, which is attacked and rapidly caught. The prey is grasped with the help of the long chelate pedipalps and subdued by venom from glands which open at the sharp tip of one or both fingers. The prey is then turned over to the chelicerae and crushed to small pieces which enter the mouth.

In a German beech forest soil, Beck (1983) found a correlation between the numbers of the pseudoscorpion *Neobisium* and the density of



Fig. 1.5. SEM photograph of a pseudoscorpion, in frontal view. Magnification:  $22\times$

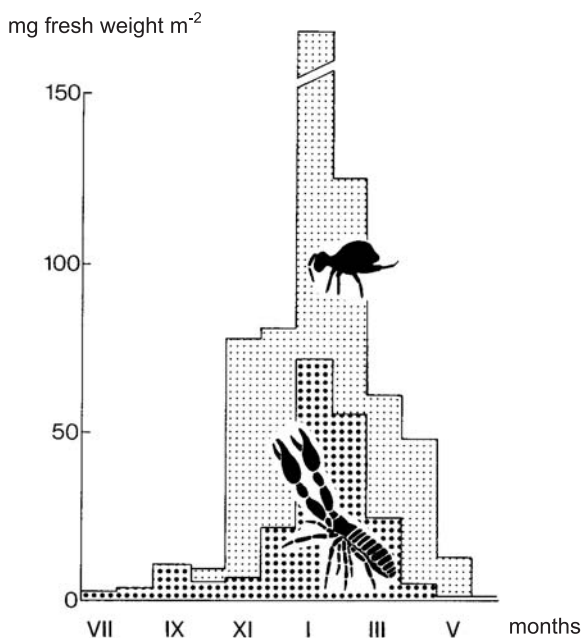


Fig. 1.6. Pseudoscorpions as predators of Collembola. (According to Beck 1983)

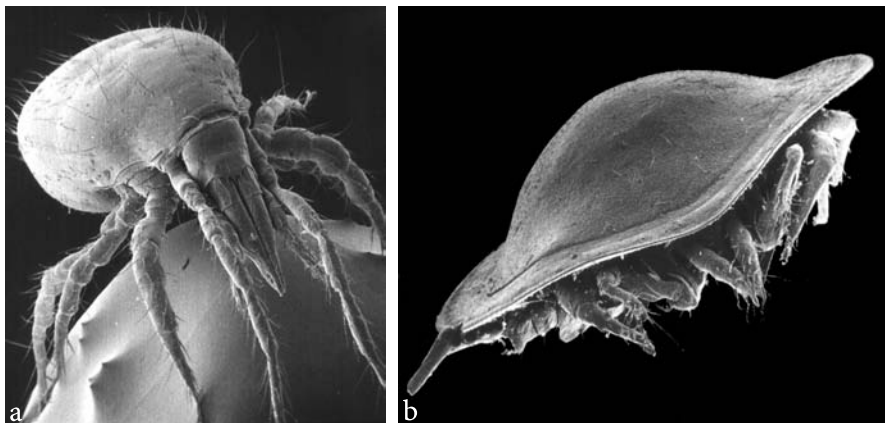
Collembola suggesting a trophic relation between them (Fig. 1.6). However, it must be noted that the importance of pseudoscorpions in the soil food web should not be overestimated since their population density is low.

### 1.3.2

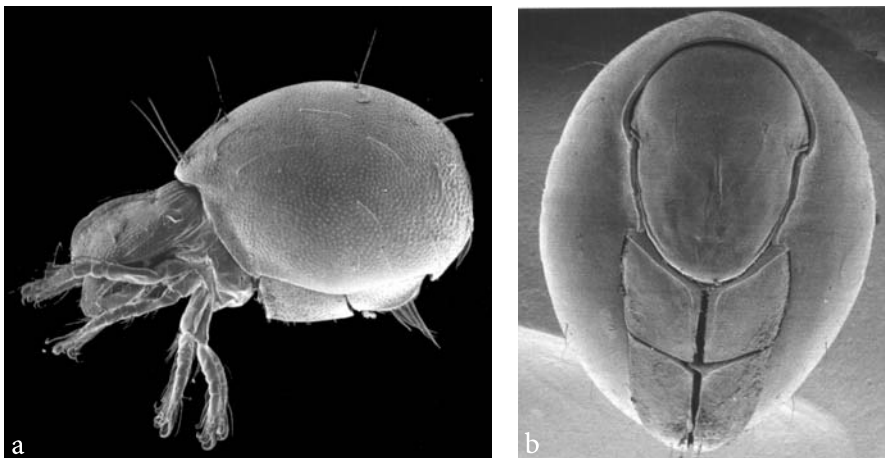
#### Acari – Mites

Size: 200 nm to 2 mm; species number: > 40,000; abundance: 80,000 to > 1 million m<sup>-2</sup>; life body mass: 8–600 µg; key literature: Wallwork 1983; Kethley 1990; Krantz and Ainscough 1990; Norton 1990; Philips 1990, Moritz 1993b; Karg 1994, Karg and Freier 1995; Alberti and Coons 1999; Maraun and Scheu 2000

The Acari (mites) are an extremely diverse group of arachnids which have successfully adapted to a wide range of habitats. They are divided into two main lines: the Parasitiformes and the Acariformes, which are distributed through the soil and the different layers of vegetation. Well known groups include the Gamasina and Uropodina (predatory mites, turtle mites; Fig. 1.7), and the Oribatida (cryptostigmatid mites, moss mites; Fig. 1.8), which are very important in soil environments. Karg (1994) assessed the predatory mites as valuable regulators of the natural environment and



**Fig.1.7.** SEM photographs of **a** a gamasid mite in frontal view with extended chelicerae; **b** a turtle mite with helm-shaped soma in frontal view. Magnification:  $80\times$ ,  $120\times$



**Fig.1.8.** SEM photographs of an oribatid mite – Phthiracaridae with **a** exposed prosoma; **b** closed prosoma, flexed like a jack-knife. Magnification:  $80\times$ ,  $100\times$

Karg and Freier (1995) consider them to be bioindicators for the status of ecosystems.

Like other true soil animals, the predatory mites (Gamasina) lack eyes and commonly avoid light. To catch their prey they use a mechanism like a catapult. The chelicerae, normally held in a retracted position in a pocket of the gnathosome, are protruded very quickly and the prey, e.g. a nematode or another micro-arthropod, is very quickly grasped with the pincers of the chelicerae. Their main prey are nematodes and collembolans; the many species of mites have adapted to attack the different prey types living in

the different soil horizons. Karg (1994) has observed how the predatory mites use their pincer-like chelicerae very skilfully and are able to eat a large number of nematodes within minutes. The chelicerae of some of these mites have been transformed into stylets. They use the extraintestinal mode of digestion and suck in the liquid food with the help of a pharyngeal pump. Other predatory mites feed on particulate food in the form of minute fragments of the tissue of their prey. The uropodid mites are also predatory, particularly on nematodes. They are often used to monitor the progress of compost formation. The distribution of predatory mites in soil is believed to be more uniform than that of the oribatids, which are often found to have a tendency to aggregate. This corresponds more to the behaviour of predators which try to increase the spectrum of their prey by being more mobile. Both the biomass and metabolism of predatory mites have been found to be comparatively high in a forest. Consequently they play a major role in the energy flux of the soil fauna.

The oribatids, frequently termed moss mites (in German, *Hornmilben*), live in dense clusters in the decomposing litter within the upper soil layers. More than 6500 species are known worldwide, but in central Europe soil habitats are populated only by about 20 to 80 species. The more increased is their density with up to  $5 \times 10^5$  counts per  $\text{m}^2$  (Table 1.1). Key factors which determine the occurrence of the oribatids are the thickness of the organic horizons, the quality of the litter and the pH values of the soil. Both acidified soils and a recalcitrant litter material improve the dominance of this mesofaunal group. In contrast to the Gamasina, none of the oribatid species is parasitic. They feed on a variety of material, mainly of plant debris and carrion, but also on fungi, bacteria, lichens and living plants. Their metabolic rates are low reflecting more the consumption of low quality food, slow development and reduced fecundity. Of course this may be compensated for by the high population density of thousands of the mini-shredders. Therefore it is obvious that they must play a key role in the food web of mesofauna-dominated soils.

**Table 1.1.** Abundance and species numbers of oribatid mites in selected habitats of central Europe (adapted from different authors)

Habitats	Density $\text{m}^{-2}$ ( $\times 10^3$ )	Species
Fields	$20 \pm 10$	20
Meadows	$25 \pm 15$	30
Fen	$45 \pm 20$	50
Deciduous forest	$56 \pm 20$	70
Mixed forest	$123 \pm 50$	80
Spruce/fir forest	$212 \pm 100$	40
Pine forest	$425 \pm 200$	60

According to Rusek (1975), their faecal pellets are different from those of Collembola. Because oribatids do not take in mineral particles with their food the micro-pellets produced are round and with a smooth surface. In contrast, the pellets of Collembola have sharper edges in profile, indicating the presence of mineral particles.

Oribatids are eyeless, but have a pair of large, conspicuous sensilla (trichobothria), which are inserted into deep cups in the prosomal carapace. They should be able to detect vibrations of the air and to receive sensory inputs from their nearby surroundings. Their body is commonly covered with a thick cuticle giving a bizarre, armoured appearance. It has been found that the integument can be used as a store for minerals, e.g. calcium. Species of the family Phtiracaridae are able to shield their body against drought by rolling into a wall. All the free exposed appendages are then retracted and completely covered by the hood-like prosomal shield (Fig. 1.8).

### 1.3.3 Symphyla

Size: 2 to 9 mm; species number: 170; abundance:  $< 100 \text{ m}^{-2}$  (forest soils),  $1000 \text{ to } 20,000 \text{ m}^{-2}$  (cultivated soils); body mass: 0.5–1 mg; key literature: Edwards 1990; Dunger 1993b

Symphylans are elongated and unpigmented true soil animals divided into head and trunk, consisting of 14 segments and 12 pairs of legs (Fig. 1.9). Together with the pauropods and diplopods they form the Progoneata which have genital openings just behind the head region. The symphylan body terminates with two conical appendages called 'cerci' which contain spinning glands. Dorsally, the body is covered with overlapping smooth tergites. The lateral and ventral integument is covered with a felt of tiny microhairs above which project sensory hairs or scales.

Though the animals are eyeless they have thousands of sensory hairs. It is likely that most of them are mechanoreceptors, but some are thought to function as chemoreceptors. Most spectacular is the Tömösváry or post-antennal organ, which has been thought to be hygroreceptor. It is found near the antennal base in an open cavity of the head capsule (Eisenbeis and Wichard 1987). Symphylans require high humidity. Under completely dry conditions *Scutigereilla immaculata* loses about 80% of its body water per hour (Eisenbeis, unpublished). To compensate for water loss by transpiration, the animals are provided on their ventral side with nine ventral, eversible pairs of coxal vesicles which are commonly used in arthropods to absorb water and ions from moist substrates.

Very remarkable in symphylans is their special mode of sperm transfer from an attached spermatophore to an egg. The female first opens the sper-



<http://www.springer.com/978-3-540-28180-1>

Intestinal Microorganisms of Termites and Other  
Invertebrates

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