Feeding biology of oribatid mites: a minireview

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Summary

The aim of this review is to summarize the existing knowledge on the feeding biology of oribatid mites. Understanding their feeding habits may help in solving the problem of the large number of animal species that co-exist in soil, and it may contribute to a better understanding of the functioning of oribatid mites in the decomposer subsystem. It could be shown (1) that oribatid mites prefer dark pigmented fungi (Dematiacea) over most other soil fungi, (2) that some Dematiacea (Alternaria alternata, Ulocladium sp.) were preferrentially ingested compared to others, (3) that some ectomycorrhizal fungi are accepted as food substrates (Hymenoscyphus ericae, Boletus badius) whereas others are rejected (Amanita muscaria, Paxillus involutus). Stable isotope studies (¹⁵N) indicate that oribatid mites form a gradient from phytophagous species over primary and secondary decomposers to predators and scavengers. Molecular methods appear to be a promising tool to study the gut content of oribatid mites in the future. Overall, findings of this review indicate that there is niche differentiation concerning oribatid mite feeding habits but that the feeding preferences of oribatid mites are rather small and therefore are insufficient to explain the high diversity of oribatid mites in soil. We conclude that oribatid mites are generalists with a certain degree of specialization concerning their food resources.

Key words: oribatid mites, feeding biology, fungi, stable isotopes, review.

Introduction

The number of species living above the ground probably exceeds the number of soil living animal species. However, while the high diversity of above-ground species is partially understood and at least in part can be explained by niche differentiation (Chesson, 2000) the species number of soil living animals is difficult to understand (Anderson, 1975; Schaefer, 1991; Giller, 1996). Typical mechanisms that drive speciation processes such as co-evolution, bottleneck events, adaptive radiations after colonization events, the

heterogeneity of the habitat, strong biotic interactions and niche differenti-
ation appear to lack in the soil animal community or seem to be of minor im-
portance (Scheu, 2002; Scheu and Setälä, 2002). Therefore, the diversity of
soil animal species is considered as being enigmatic (Anderson, 1975; Ma-
raun et al., 2003).

One of the potential mechanisms that may contribute to the under-
standing of large species numbers of soil animals is trophic niche differentia-
tion. Surprisingly, however, this topic received little attention (Hartenstein,
1962; Siepel and de Ruiter-Dijkman, 1992) and results were not conclusive. It
still is not clear if soil living animals are specialist or generalist feeders
(Schneider and Maraun, 2005).

To contribute to the understanding of food as a potential niche dimen-
sion for soil living animals we studied the feeding biology of oribatid mites,
using a variety of methods, including food choice experiments, stable isotope
analysis and molecular methods. Oribatid mites are mainly soil living de-
composer animals; about 10,000 species are described until now and a total
of 50,000 - 100,000 species may exist (Schatz, 2002).

The main aim of this review is to summarize the present knowledge on
food relationships of oribatid mites, to present results of ongoing experi-
ments and to outline ideas for future studies on trophic relationships in soil
living animals in general.

Historic perspective

The studies of Jacot (1930, 1936, 1939) were the first investigations on
the feeding biology of oribatid mites. He showed that oribatid mites do not
just feed randomly on dead organic matter but that some species have spe-
cific requirements, e.g. that juvenile Ptyctima live and feed inside leaf and
needle litter material. Mining in litter has been shown more recently for
other oribatid mite species, such as Adoristes ovatus (Gourbiere et al., 1985;
Lions and Gourbiere, 1988). Forsslund (1938) studied the gut content of ori-
batid mites and found a range of fungal hyphae and spores. He concluded
that oribatid mites mainly live on fungal material. He also showed that ori-
batid mites are unable to digest lignin and cellulose. More recent studies
suggest that oribatid mites also feed on mosses, lichens, algae and pollen
(Harding and Stuttard, 1974) but these food components may be of minor
importance in the field.

Riha (1951) was the first who showed that oribatid mites are not just
decomposer animals but also feed on dead animals. Hypochthonius rufulus
has been observed to feed on dead collombolans and was reluctant to feed on
plant litter material. Additionally, she observed Belba pulverulenta to feed
on ‘dead worms’ (Riha, 1951). Later Galumnidae, Fuscozetes sp., Nothrus
sp., Scheloribates sp., Oppiella nova and Tectocepheus velatus were observed
when feeding on nematodes (Rockett and Woodring, 1966; Muraoka and
Ishibashi, 1976; Rockett, 1980) and Oppia nitens on conspecifics (Stefaniak
Schuster (1956) separated oribatid mites in different feeding guilds. He distinguished (1) macrophytophagous species (feeding mainly on dead wood, roots and litter material, e.g. Ptyctima, some Liacaridae, several Galumnidae), (2) microphytophagous species (feeding mainly on fungi, lichens, algae and pollen, e.g. Damaeidae, Oppiidae, T. velatus, Oribatula tibialis, Amerus troisi), and (3) non-specialised species that feed on dead organic material as well as on fungi, lichens and pollen, e.g. Nothrus silvestris, N. palustris, Xenillus tegaeocranus and Adoristes ovatus. A similar grouping was presented later by Wallwork (1958) and modified by Luxton (1966, 1972).

Saprophytic fungi

The first laboratory feeding experiments using soil fungi indicated that oribatid mites mainly live on fungi rather than on litter material (Luxton, 1966; Martin, 1979). Hartenstein (1962) found preferences of oribatid mites for fungal species such as Cladosporium cladosporioides, Phialophora mustea and Stemphylium sp. whereas fungal genera such as Rhodotorula, Aspergillus, Epicoccum, Pachybasium (synonym of Trichoderma), Penicillium and Sporotrichum were usually rejected as food substrate. Other studies regarding the food preferences of oribatid mites were those of Mitchell and Parkinson (1976), Behan and Hill (1978), Behan-Pelletier and Hill (1983), Hubert et al. (1999, 2001), Maraun et al. (1998a, b, 2003) and Schneider and Maraun (2005).

In a large number of studies it could be shown that oribatid mites preferentially feed on fungi with dark melanised hyphae and/or spores (collectively named Dematiacea) such as Cladosporium, Alternaria and Ulocladium (Luxton, 1966; Mitchell and Parkinson, 1976; Hedlund et al., 1991; Klironomos and Kendrick, 1996; Maraun et al., 1998a, b, 2003). Similar preferences have been shown for other soil animal taxa such as collembolans (Verhoef et al., 1988; Klironomos et al., 1992) and enchytraeids (Dash and Cragg, 1972). The preferences are unlikely due to the melanin itself because melanin is hard to digest (Scheu and Simmerling, 2004; Scheu and Folger, 2004). Other mechanisms such as fungal exoenzyme production may be related to food preferences of oribatid mites; decomposer animals may use exoenzymes for their own digestion purposes (external rumen, Swift et al., 1979).

Despite the preference of oribatid mites for dark pigmented fungi selective feeding on different species of Dematiacea is little studied. We therefore conducted a laboratory food choice experiment where we offered a number of different dark pigmented fungi (Alternaria alternata, Aureobasidium pullulans, Bipolaris spicifera, Chloridium sp., Cladosporium sp., Codinea sp., Oidiadendron sp., Phialophora verrucosa, Ulocladium sp.) to different species of oribatid mites (Achipteria coleoptrata, Carabodes sp., Eupelops torulosus, Hypochthonius rufulus, Liacarus subterraneus, Nothrus silvestris, Oribatella quadricornuta, Oribatula tibialis, Platynothrus peltifer, Platythelphusa...
Steganacarus magnus). Only some of the dark pigmented fungi were preferentially ingested (Alternaria and Ulocladium) others were of intermediate food quality (Phialophora, Aureobasidium, Codinea, Cladosporium) and some were rejected (Oidiodendron, Mortierella, Bipolaris, Chloridium). Obviously, it is not the melamin itself that is responsible for the feeding preferences of the oribatid mites (Schneider and Maraun, 2005).

Mycorrhizal fungi

Mycorrhizal fungi in soil often belong to the arbuscular mycorrhizal fungi (=AMF) of the phylum Glomeromycota, or to the ectomycorrhizal fungi which are represented by many Basidiomycota, but also by some Ascomycota and some Zygomycota of the Endogonales. Additionally, there are some mycorrhizal types, the orchid mycorrhizae, formed by basidiomycete imperfects in the genus Rhizoctonia, and the ericoid mycorrhizae, formed by ascomycetes of the genus Oidiodendron and Hymenoscyphus (see Smith and Read, 1997).

Studies on feeding preferences of oribatid mites and collembolans for AMF have been carried out by Klironomos and Kendrick (1996) and Klironomos et al. (1999). The results of these studies indicate that oribatid mites and collembolans preferred saprophytic fungi (especially Dematiacea) over AMF. However, the effect of soil microarthropods on AMF is still controversial (Gange, 2000) and remains to be studied in more detail in the future (Gange and Brown, 2002).

No studies investigated feeding of oribatid mites on ectomycorrhizal fungi exist but results of Hiol Hiol et al. (1994) using collembolans indicate that endomycorrhizal fungi (Rhizoctonia solani) are preferred over ectomycorrhizal fungi (e.g. Laccaria laccata, Suillus luteus). Results of recent studies indicate that some ectomycorrhizal fungi (Hymenoscyphus ericae and Boletus badius) may be as good as Dematiacea (Alternaria alternata) whereas others are rejected as food substrate (e.g. Amanita muscaria and Paxillus involutus; Schneider, unpubl.).

Gut enzymes

Zinkler (1971) and Luxton (1972, 1979) studied the enzymatic abilities of oribatid mites. They found cellulase, glucanase, chitinase (for the digestion of fungal cell walls) and trehalase (for digestion of fungal cell content) in the gut of different species of oribatid mites. Later Urbasék and Starý (1994) detected activities of amylase, xylanase, laminarinase and lichenase. Siepel and de Ruiter-Dijkman (1993) grouped 49 oribatid mite species in seven feeding guilds according to their enzymatic abilities. Gut enzyme activities suggest which compounds actually are digested, however, the data have to be interpreted with care since gut enzyme activities may vary with the actual food ingested. Furthermore, it is difficult to separate enzymes produced by the mites themselves and those taken up from the environment (e.g. from soil fungi).
Stable isotopes

Analysis of the natural variation in stable isotope ratios in animal tissue has been shown to be a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada, 1984; Wada et al., 1991; Ponsard and Arditi, 2000; Scheu and Falca, 2000). In contrast to gut content analyses and food choice experiments, stable isotope ratios reflect the long-term trophic relationships of animals. Animal tissues are more enriched in $^{15}$N than their food source (DeNiro and Epstein, 1981), on average by 3.4 $\delta$ units (Post, 2002). Scheu and Falca (2000) and Ponsard and Arditi (2000) were the first to analyse soil animal communities using stable isotopes. They found e.g. that the soil food web comprises of two to four trophic levels, that Uropodina are predators (probably on nematodes) and that the trophic levels in soil are not distinct. Scheu and Falca (2000) for the first time included nine oribatid mites in a stable isotope analyses but the first detailed analyses of a large number of species (36) was presented by Schneider et al. (2004). In that study signatures of $\delta^{15}$N formed a gradient spanning over 12 $\delta$ units suggesting that different species occupy different trophic niches and oribatid mites span four trophic levels including a group that feeds on dead or living animals (fig. 1). The finding that some taxa are predators or scavengers (probably on dead bodies of collembolans but presumably also on living nematodes) confirmed earlier findings by Riha (1951), Rockett and Woodring (1966) and Muraoka and Ishibashi (1976). The study of Schneider et al. (2004) also suggests that species of the same genus (e.g. N. silvestris and N. palustris) cannot be aggregated into the same functional group, since their $^{15}$N signatures may differ strongly. The study supported the view that juveniles and adults of oribatid mite species feed on similar food resources. Also, oribatid mite trophic niches appear to be independent of the habitat/forest the animals live in. The results suggest that trophic niche differentiation within taxonomic groups significantly contributes to the high diversity of soil animal taxa. However, care is necessary in interpreting stable isotope data of fungal feeding taxa since little is known on the variation in $^{15}$N signatures of fungal species in soil (Scheu and Folger, 2004).

Molecular analyses

The most recent technique that has been used to study food relationships of animals is the analysis of the gut content using molecular markers (Symondson, 2000). Until now, the method has not been used to investigate the food of oribatid mites. The advantage of this method (especially for soil animals such as oribatid mites) compared with other methods is that (1) fungi which are difficult to cultivate in the laboratory can be analysed, (2) animal remains of putative oribatid mite prey which are difficult to be detected by microscopy, such as nematodes and collembolans, and (3) even small amounts of prey (e.g. fungi, lichens or animal remains) can be detected.
However, there are also disadvantages of this method, e.g. (1) the method is not quantitative because the amount of DNA of the respective prey remains unknown, (2) similar to microscopic analysis of the gut content it remains unclear if the detected diet is in fact digested and therefore contributes to animal nutrition.

The first studies that have been carried out with oribatid mites indicate that a large number of fungal species are associated with oribatid mites.

Fig. 1 - Schematic representation of the trophic structure of oribatid mites from four different beech forests, as indicated by $^{15}$N/$^{14}$N ratios. Species that belonged to similar taxa and also had similar $^{15}$N signatures were grouped at higher taxonomic levels: Galumnidae (incl. Pilogalumna spp., Galumna spp., Galumna lanceata), Damaeidae (Paradamaeus davipes, Hypodamaeus riparius), Oribatulidae/Scheloribatidae (Hemileius initialis, Scheloribates spp., Oribatula tibialis), Chamobatidae (Chamobates volgtsi, Ch. cuspidatus, Ch. borealis), Phthiracaridae/Euphthiracaridae (Steganacarus magnus, Phthiracarus spp., Atropacarus striculus, Rhysotritia duplicata).
(e.g. Beauveria bassiana, Penicillium ssp., Mortierella ssp., Mucor ssp.; Renker, unpubl.). However, it remained unclear if the detected fungi originated from the surface of the animal or from the gut. The results indicate that there are much more fungal species associated with oribatid mite bodies than previously assumed. Future studies are necessary that establish reliable washing methods that eliminate the spores from the bodies of oribatid mites. Alternatively, the guts of oribatid mites may have to be dissected to exclude contamination by fungi from the body surface.

Summary and prospects

There has been considerable progress in understanding the feeding biology of oribatid mites in the last years. Oribatid mites are generalists able to feed on a wide variety of resources but they do not indiscriminately feed on materials offered in laboratory food choice experiments. They preferentially feed on dematiaceous fungi but not on all species; additionally, they ingest non-Dematiacea and also feed on ectomycorrhizal fungi. Therefore, they have been termed ‘choosy generalists’ (Schneider and Maraun, 2005). However, a number of questions on food relationships of oribatid mites remain to be answered. Recent methodological developments including stable isotopes and molecular markers are promising tools for uncovering trophic relationships in oribatid mites and help in understanding evolution and coexistence of species in this hyperdiverse soil animal group.

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