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Methods of studying the feeding habits of saprophagous mites living in soil

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Abstract. The diversity of food eaten by soil saprophagous mites was misinterpreted for many years. Food selection by these mites was either neglected or simplified in the earliest papers. From 1956 onwards, however, several methods were developed for studying the food preferences of mites in laboratory and field studies. We carried out an histological study of the microanatomy of their gut contents, digestion and faeces, an experimental study of their food preferences and tested for different enzymes and presence of microorganisms. These analyses revealed that there are several categories of soil saprophagous mites ranging from obligatory forms, to specialized consumers up to ubiquitous mites that feed on a wide range of different foods. The adaptations of several species were also recorded under various conditions. The activities of the different enzymes seemed to be of crucial importance, in particular, the type and sources of these enzymes. Several studies indicate that they may be produced by mites however our results indicate they are the allochthonous chitinolytic enzymes of bacteria. In addition, their food preferences and feeding habits determine their movement between and colonization of different microhabitats and the stability of the community structure of mites.

Key words. Food offer, feeding habits, soil saprophagous mites, Oribatida, Acaridida, microhabitats.

INTRODUCTION

In the earliest papers the role of soil saprophagous mites was based on estimates or presented in terms of decomposition of plant litter, which included that decomposed by the microorganisms present. The present study revealed the very slow and poor efficiency of mite metabolism. Therefore, the general role of saprophagous mites in soils in terms of decomposition of organic matter and nutrient cycling would appear to be negligible. This study of food selection by several species and groups, however, indicate that this opinion was incorrect and the importance of saprophagous mites in soils is more significant. This is supported by their high abundances in soils – up to 500,000 specimens per m^2 (Wallwork 1976).

The methods used previously were various but changed over time from the very simple to more sophisticated. The mounting of mites in lactic acid is the oldest method and enabled taxonomists to identify the mostly dark and heavily sclerotized oribatid mites. Their gut contents may be visible, but only the corpuscular material (fungi and pieces of litter) and not the bacteria or liquid matter. The first association between the food consumed and the morphology of the mites was published by Schuster (1956) and subsequently Kaneko (1988). The morphology of their chelicera, especially the number and size of the teeth appeared to be associated with the type of food consumed. This resulted in mites generally being classified as either mycophagous, bacteriophagous, nematophagous or saprophagous. These different groups of mires differed in the number and size of the teeth on the digitus fixus and digitus mobilis that they used to capture, crush or cut their food.

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Then experiments were used to determine their food preferences, which usually involved rearing them in boxes in the laboratory in which they were offered different foods. These took the form of a one-way test or cafeteria test (Czajkowska 1970, Pankiewicz-Nowicka et al. 1984). Their remaining on the offered food was taken as indicating they consumed that food, which was confirmed by the subsequent production of excrement. These authors also used substrates consisting of fungi, e.g. artificially cultivated on a substrate (agar etc.) or growing naturally on a substrate (plant litter: Koukol et al. 2009). The counting of faeces has been used in studies on the feeding habits of oribatids in a black pine plantation (Pande & Berthet 1973). But, these studies did not provide any information on the digestion processes or contents of the faeces. Many foods are digested by mites but others pass through their guts undigested (Smrž & Soukalová 2012).

Luxton (1972) tested for enzyme activity in his basic ecological and biological study of oribatids. He tested for three enzymes – celullase, chitinase and trehalase and identified three nutritional groups of oribatid mites: *microphytophagous* – which consume the microorganisms – fungi, bacteria and algae, *macrophytophagous* – which consume plant litter and *panphytophagous* – which consume both types without any visible selection. His were the first studies on these topics in mites.

Enzyme activity was also studied by Zinkler (1972) and Haq (1981).

A similar approach was adopted by Siepel & Ruiter-Dijkman (1993) who identified the following so-called nutritional guilds:

- herbivorous grazers – with cellulase, which digest the walls and contents of plant and algal cells);
- herbivorous browsers – lack cellulase or chitinase, which digest animal tissues, including carrion and bacteria;
- fungivorous grazers – with trehalase and chitinase, which digest the walls and contents of fungi;
- fungivorous browsers – with only trehalase, which digest not only the cell contents of fungi, but also lichens rich in algal tissues;
- herbo-fungivorous grazers – with chitinase and celullase, which digest the walls and contents of fungal and plant cells and lichens;
- oportunistic herbo-fungivores – with trehalase and celullase, which digest the walls and contents of plant and fungal cells and lichens;
- omnivorous mites – with celullase and chitinase, which digest the walls and contents, other than trehalose, of fungal and plant cells. These authors thought these mites might also be predators of arthropods but trehalose is present in insect haemolymph (Wigglesworth 1978).

Except for the study of Luxton (1972) these studies only record the presence of enzymes without any reference to the biology or ecology of the mites (microhabitat, community structure, long term observations).

Coleman & McGinnis (1970) used the fungus *Geotrichum* sp. isolated from old field soil and labelled with a radioisotope to determine whether this fungus is eaten by mites of several groups. Only a few species of mite became radioactive. The authors thought they had a minor role in grazing soil fungi. Of the mites tested some were saprophagous and others were either mycophagous or predacious (*Amblyseius* Berlese, 1904). The validity of their results and conclusions is therefore

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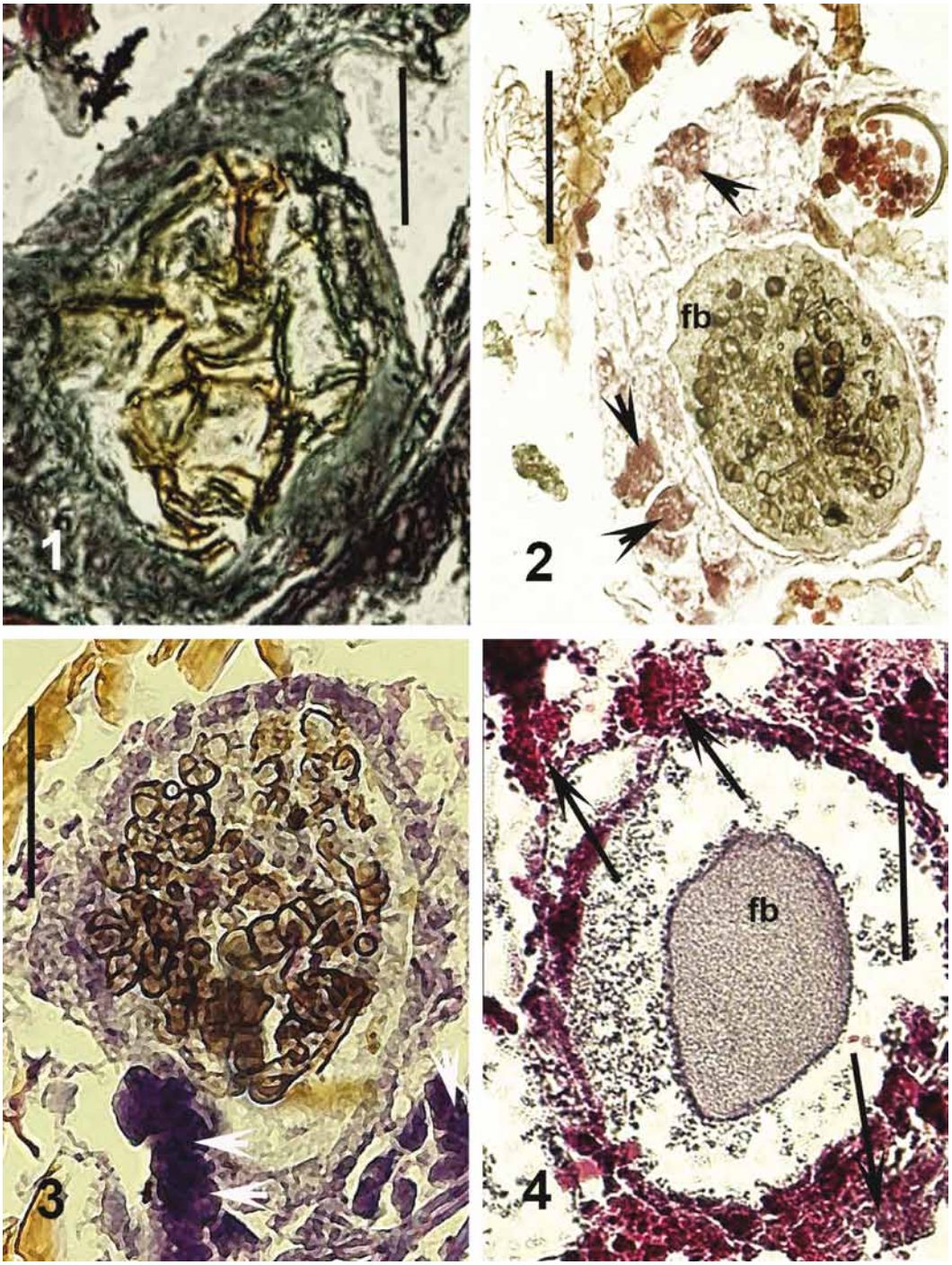
Figs 1–4. Mesenteron: 1 – litter eater, *Melanozetes meridianus* Sellnick, 1928, with fragments of moss leaves; 2 – mycophagous mite, *Belba pseudocorynopus* Markell et Meyer,1960, with conidia, black arrowheads point to hemocytes; 3 – *Tectocepheus velatus* (Michael,1880), juvenile, white arrowheads point to hemocytes; 4 – bacteriophagous *Liebstadia similis* (Michael,1888), with a food bolus of bacteria enclosed in a membrane, arrows point to glycogen rosettes. Stained using Masson's trichrome. Abbreviation used: fb – food bolus. Scale bars: 0.05 mm.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questionable. Moreover, the method used was indirect and there were no details of the biology of the accompanying phenomena.

Use of stable isotopes can provide important information on the food of mites and using them Schneider et al. (2004) also identified four groups:

– carnivores, scavengers and omnivores, which consume living or dead animals and fungi;
– secondary decomposers, which consume fungi and some litter;
– primary decomposers, which consume fresh litter that is poorly colonized by fungi and bacteria;
– phycophages and fungivores, which consume lichens and algae.

As regards more detailed specialization, Maraun et al. (2003) record a higher grazing preference of mites for pigmented fungi due to several factors (their content of nutritive substances, ease of digestion etc.). The fungal feeders are assumed to be generalists rather than specialists. Mites also show a greater specialization for grazing on pigmented fungi (Schneider & Maraun 2005). The evidence for this preference, however, is according to these authors only weakly supported. Their idea that the preference results from the lower toxicity of certain fungi is wrong, e.g. both *Alternaria* and *Penicilium* produce large quantities of toxins (patulin, alternariol, griseufulvine etc.). There is an exponential increase in the abundance mites on, e.g., the fungus *Alternaria alternata*, which produces many toxins. On the other hand, Maraun et al. (2011) used such methods too rapidly and precicely separate mycophagous mites, even although the fungal taxa cannot be delineated. A preference for saprophytic conidial fungi (*Altenaria*, *Trichoderma*) over the mycorrhizal *Glomus macrocarpum* is reported by Klironomos & Kendrick (1996). Such interpretations are based on faecal counts. The authors account for this result in terms of the mites tested living in deeper soil layers and the generally poor co-evolution between mycorrhizal fungi and microathropods.

An analysis of fatty acids is also a useful tool in such studies (Ruess et al. 2002, 2005a,b), as the offered food is transformed into specific fatty acids by soil animals (springtails, mites, nematodes). Based on the typical fatty acid present in an organism one can identify the food it consumed and digested. This method gives accurate results in studies on predacious animals but it is not as accurate for identifying othe food sources, such as, fungi or bacteria.

The following topics were studied: (1) What methods can be used to determine the feeding habits of mites? (2) Is the selection of food in soil by mites specific or general? (3) What significance can be placed on the results of offering particular types of food for determining the feeding habits of mites in soil? (4) Does the selection of food by mites affect the structure of the soil communities in microhabitats or over large areas?

METHODS

The basic method used in this study was histology (Smrž 2002b). The mites were extracted using Berlese-Tullgren funnels and collected in modified Bouin-DeBosque-Brasil fluid (Smrž 1989). The sections were cut using a Leica 2155 rotation microtome (thickness of sections 5 μm) and stained with Masson's trichrome. Some specimens were stained with Pianese stain or orange G fluorescence stain. The stained sections were observed under a Provis AX-70 microscope (Olympus) and some of them under a Nomarski DIC prism. Some mites were fixed in cacodylate-buffered glutaraldehyde (4%), embedded in Poly/Bed epoxy resin (Polysciences) and sectioned using a Leica 2155 rotation microtome with a tungsten carbide knife (thickness of section 1 μm) and observed under TEM Philips EM 300.

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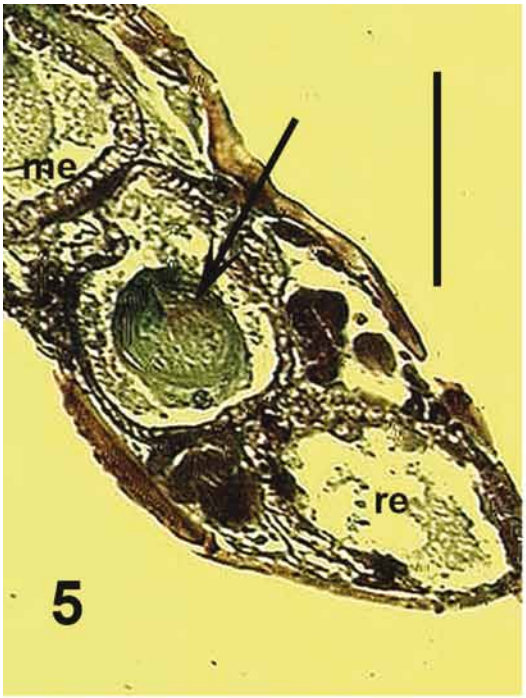
Figs 5–8. Alimentary tract: 5 – *Hypochthonius rufulus* Koch,1840, colon with concentric food bolus (arrow); 6 – *Gustavia fusifera* (Koch,1841), rectum with faecal pellet (arrow), arrowhead points to microvilli on the rectal wall; 7 – *Punctoribates punctum* (Koch,1839), starving mite with only a bacterial lining (arrowheads) to its mesenteron; 8 – *Metabelba pulverosa* Strenzke,1953, colon with conidia. Stained using Masson's trichrome. Abbreviations used: fb – food bolus; me – mesenteron; re – rectum. Scale bars: 0.05 mm (5, 7, 8), 0.02 mm (6).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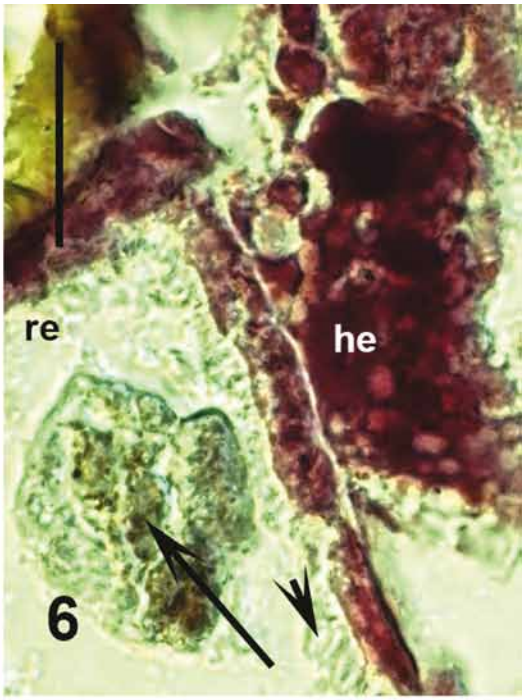
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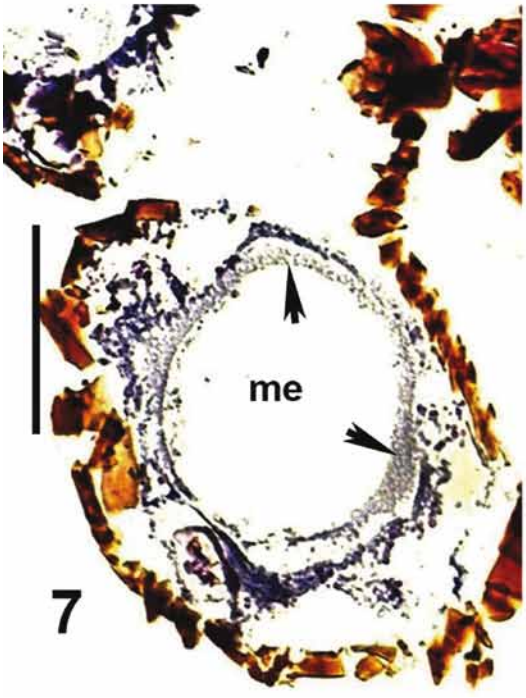
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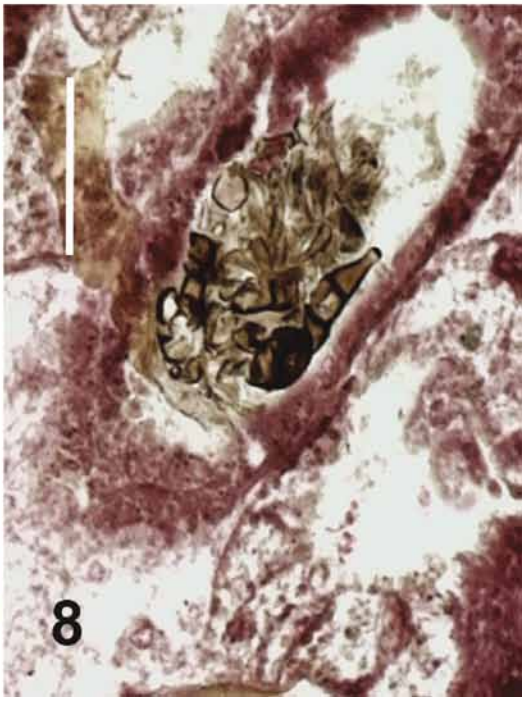
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We used living mites collected in the field in addition to those from rearing boxes. In addition to the effect of food on reproduction and changes in population we studied the activities of different enzymes when the mites were fed on various foods. This was done using homogenates of whole mites. The plating of homogenates on MPA agar or malt agar in Petri dishes and the purification and isolation of microorganisms, especially bacteria, resulted in pure strains that were identified by CCM Brno (Czech Collection of Microorganisms of Masaryk University Brno, internationally certified laboratory). Moreover the chitinolytic activity of homogenates and isolated bacteria was done using a thin film of soluble chitin on microscope slides and staining with basic fuchsin (Smrž 2000). The homogenates and isolated bacteria were tested also on living fungi (*Alternaria*, *Fusarium*, *Verticillium*, *Penicillium*, *Mucor*) (Smrž & Soukalová 2008).

RESULTS AND DISCUSSION

Traditional studies on the feeding habits of soil saprophagous mites (Oribatida, Acaridida) resulted in us developing several new approaches to this problem. The first and basic way – histology – has revealed several characteristics:

Type of food (litter, bacteria, fungi, algae, mixtures of several types). As food can be present in all three parts of the gut of mites its palatability is confirmed by the presence of the same type of food in the whole gut (Figs 1–6) and its digestability by the changes in the structure of the food that occurs between the mesenteron and rectum (see below).

The presence of a particular type of food in all parts of the gut, mesenteron, colon and rectum, indicates the food is digestible (Smrž & Norton, 2004). If it is indigestible it occurs only in one or two parts with other part(-s) empty or their contents do not undergo any changes.

The palatability of food is illustrated also by the presence of a *food bolus* in the mesenteron, which is especially conspicuous in bacteriophagous mites. Bacteriophagous species form a compact bolus, frequently enclosed in a membrane (Fig. 4), which in some papers is described as peritrophic (Šobotník et al. 2008). But some mites consume bacteria as so-called *hermit's* food. In this case the alimentary tract of the mite seems to be empty or contains only a small amount of bacteria, which line the gut walls rather than fill the gut (Fig. 7). This type of food is hardly palatable or digestible. This phenomenon is very frequent in soil mites. These species graze mainly on bacteria and only partially fill their gut and only for a short time. Subsequently, they search for more suitable food in other microhabitats. On the other hand, bacteriophagous species form a compact central bolus (e.g. *Gustavia fusifera* (Koch, 1841): Drobná 1999; *Liebstadia similis* (Michael, 1888): unpubl.) or a concentric bolus as in *Hypochthonius rufulus* Koch, 1840 (Figs 4–6). Bacteriophagous oribatids are uncommon. For other types of food, however, the situation seems to be similar, but not so conspicuous. Other types of food (fungi, plant litter) if present, are consumed and digested by mites.

The presence of same type of food in the mesenteron and rectum, however, only indicates consumption, not digestion. For this the food must undergo visible changes, such as the digestion of the walls of fungal propagules and plant cells, or a reduction in the size of the particles etc., (Figs 8–9).

Activity of gut walls is indicated by the following phenomena:
– thickening of walls of the *mesenteron* accompanied by the formation of number of vacuoles and many dark granules of enzymes in the cells in the walls and apocrine secretion of enzymes

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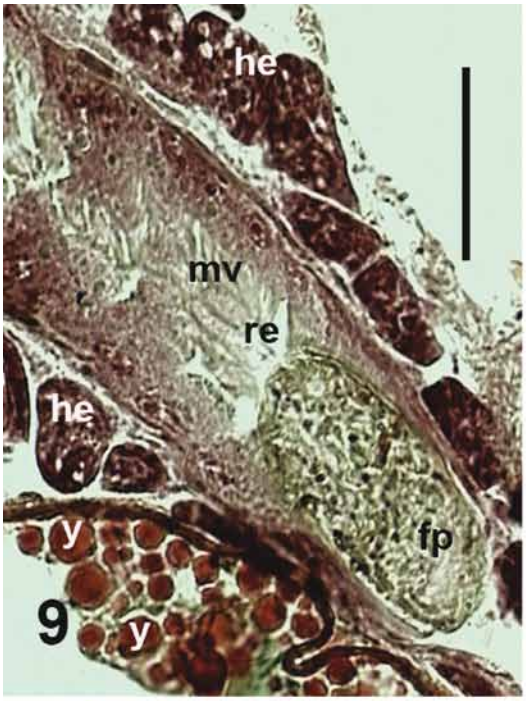
Figs 9–12. Alimentary tract: 9 – *Metabelba pulverosa*, the same specimen as in Fig. 8, rectum; 10 – *Scutovertex minutus* (C. L. Koch,1836), secretion of mesenteral walls, dark granules of enzyme (arrows), microvilli (arrowheads); 11 – *Archegozetes longisetosus* Aoki, 1965, mesenteral caecum wall, apocrinne secretion (arrowheads), hemocytes (arrows); 12 – *Hermannia gibba* (Koch, 1839), mesenteral caecum with apocrine secretion (arrows) and with incorporated hemocytes (arrowheads). Stained using Masson's trichrome (9, 12), Masson's trichrome inverted colours (10), confocal microscope, autofluorescence (11). Abbreviations used: fp – faecal pellet; mv – microvilli; re – rectum; ro – glycogen rosettes; y – yolk granules in egg. Scale bars: 0.05 mm (9, 11), 0.02 mm (10, 12).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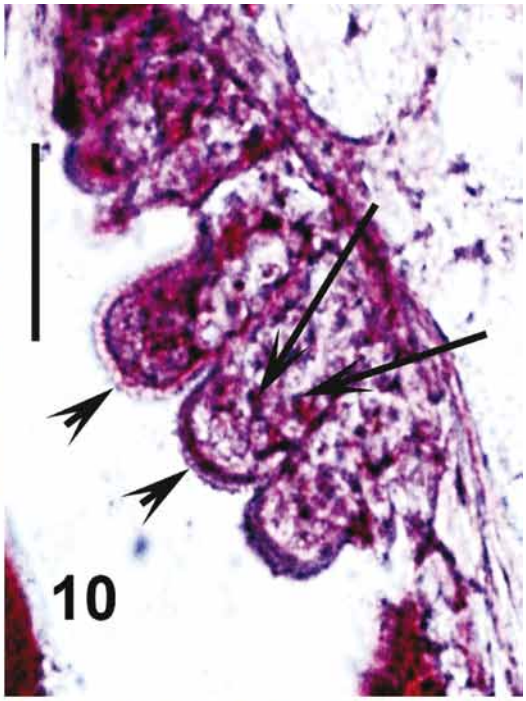
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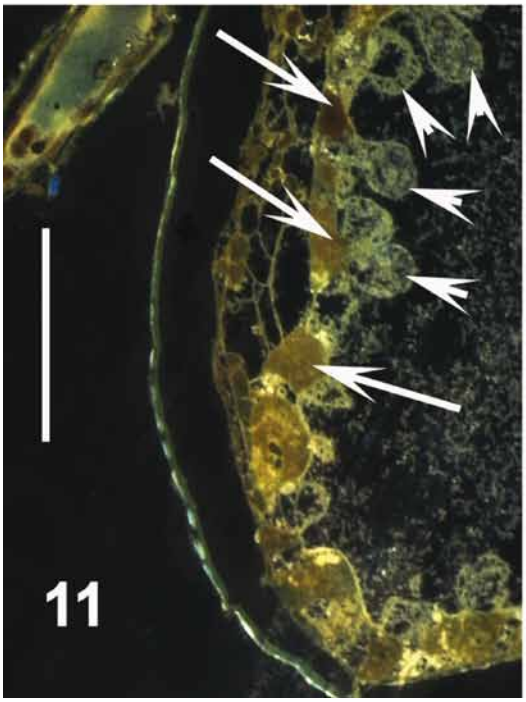
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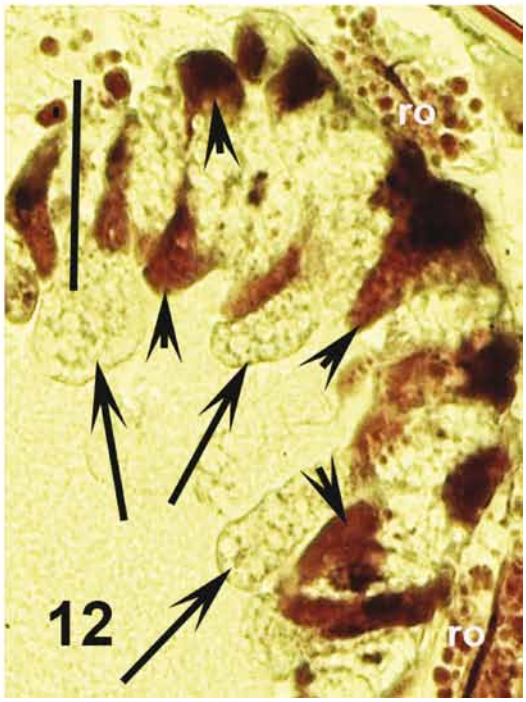
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into the lumen (Fig. 10). There are also hemocytes attached to the external surface of the mesenteron. Thin walls, however, indicate little or no digestive activity.

– in active *mesenteral caeca* apocrinne secretion of enzymes occurs and the cells in the walls are large and vacuolized. Those activities are very clearly visible when viewed under a confocal microscope (Fig. 11). Moreover, there are hemocytes between the cells in the walls of the mesenteral caeca (see below) (Fig. 12). The cells in the walls are transparent and the hemocytes are a dark colour. No food is present in mesenteral caeca.

In the *colon* water and simple substances are absorbed. Therefore, the food bolus gradually becomes more concentrated (Fig. 8).

The food bolus in the rectum is called a "*fecal pellet*" and is much more concentrated as the remainig water has been resorbed via the microvilli inside the rectum (Fig. 6). A compact pellet in the rectum confirms the food is palatable.

The *content of a faecal pellet* is a good indicator of the palatability or digestibility of the food. As said above, food is frequently eaten as *hermit's food* and not used as a source of energy, for growth or reproduction. Therefore, sectioning faeces in the rectum or examining smears of those excreated under a fluorescent light gives a good indication of the digestibility of the food. Staining with orange G, for example, results in red colour if pieces of fungi have been digested or green colour if not (Fig. 13). A similar difference in colour is recorded when algae or bacteria are eaten (Fig. 14). Hence, defecation does not indicate the food is either palatable or digestible unless this is confirmed by examining the contents of the faeces using fluorescent light (Smrž 2002a).

The active digestion results in the production of metabolites. Guanine is the terminal one in mites, as in all arachnids (Vitzhum 1943). Crystals of guanine are reported deposited in the walls of the gut (Fig. 15) or in mesenchymal tissue between the internal organs. These crystals have a concentric structure (Fig. 16). A thorough analysis reveals that these crystals contain not only guanine, but also amino acids, peptids or other simple substances in concentric layers. Of course, digestion results in the metabolism of nitrogen and subsequently in deposits of guanine. An excess of nitrogen, e.g., this often occurs when fungi is fed to mites in the laboratory and can result in massive depositions of guanine. These crystals may damage the internal organs and muscles of mites by crushing. As a consequence mite populations decline due to poor reproduction, which is followed by a decrease in consumption and digestion and a reduction in the locomotory activity of the mites. The mites die in spite of the apparent sufficient supply of food. This phenomenon, is called "white body syndrome" (Smrž & Čatská 1989), however, it occurs mainly in experiments or mass rearing and is very rare in nature.

The palatability of food can be confirmed by the presence of deposits of *glycogen*. When suitable food is abundant excess nutrients are stored. Granules of glycogen are very easily detected (Woodring & Cook 1962) using histological stains (Best carmine, Masson's trichrome, haematoxyline – eosin). These granules are deposited in clusters, so-called "rosettes" (Smrž & Materna 2000) around the internal organs (Fig. 17). The number of rosettes indicates the quality of the food, mainly in terms of its carbon content. Many substances are transported in mites via their vascular system including by the specialized cells called *hemocytes*. These cells are conspicuous because they are strongly vacuolized and have various contents in their vacuoles (Fig. 18).

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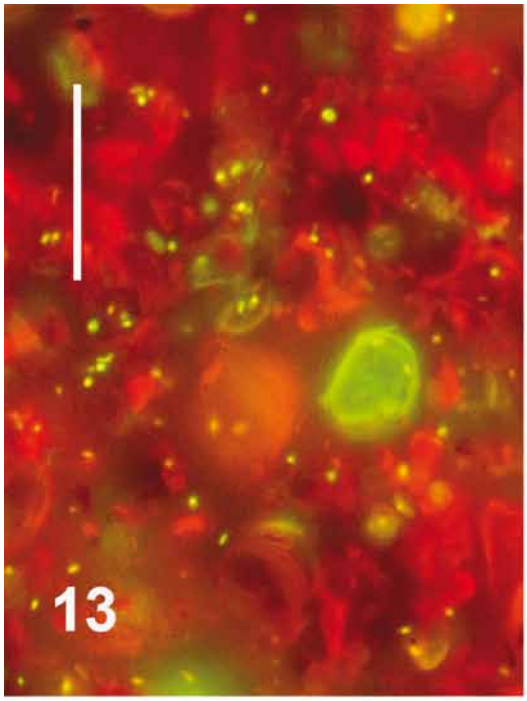
Figs 13–16. Faeces and metabolites: 13 – *Archegozetes longisetosus*, smear of faeces, great red objects = digested particles of fungi, great green object = living fungal particle (spore), small pale green objects = bacteria; 14 – faeces of mite that has consumed algae, *A. longisetosus*, red spots in cells = digested cell contents; 15 – *Scutovertex minutus* (Koch,1836), mesenteral wall, secreted guanine crystals in lumen (arrows); 16 – *Tyrophagus putrescentiae* (Schrank, 1781), TEM, inverted colors. Fluorescence microscope, orange G, (13, 14), stained using Masson's trichrome (15), TEM (16). Abbreviations used: fp – faecal pellet; me – mesenteron. Scale bars: 0.02 mm (13, 14, 15), 0.002 mm (16).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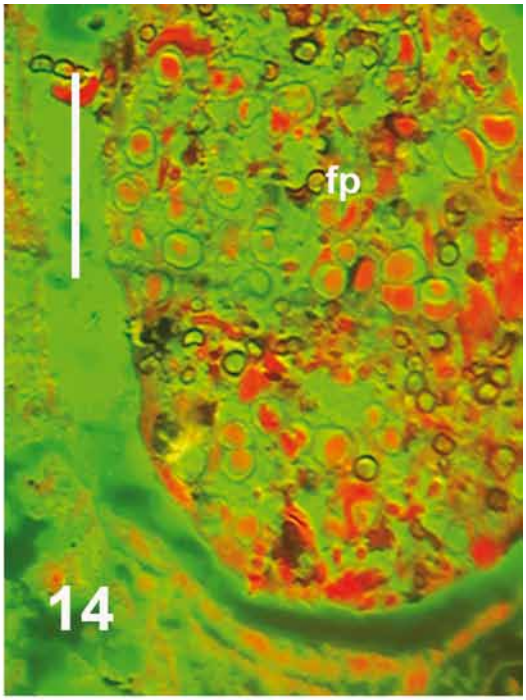
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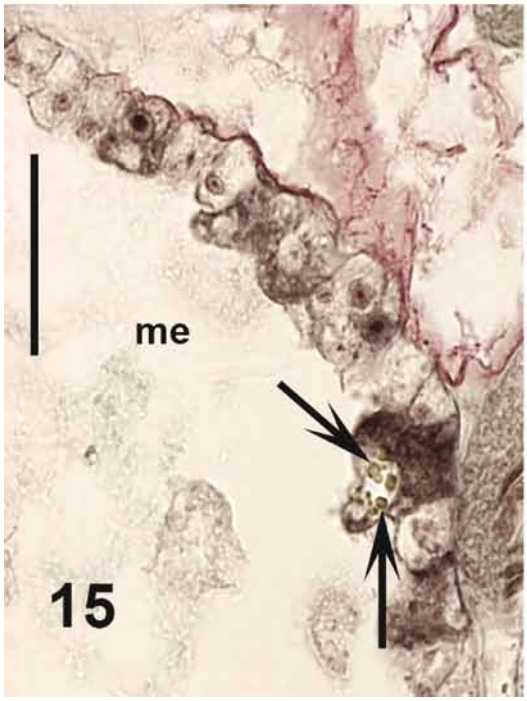
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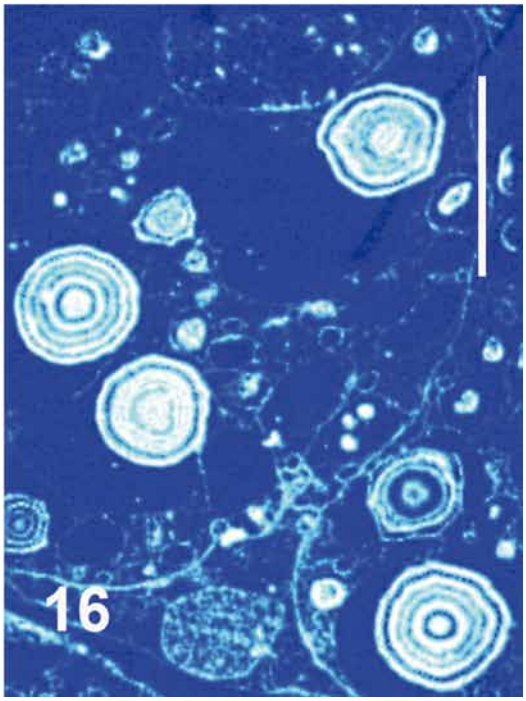
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Hemocytes usually occur in the haemolymph of arthropods (Wigglesworth 1978, Smrž 1995, Symonová & Smrž 2009). They are produced by ectodermal tissue adjacent to the epidermis and transport praecursors of enzymes, enzymes and metabolites (guanine) (Smrž 2006a). They occur mainly around the alimentary tract, mesenteron and mesenteral caeca. They are able to penetrate into the walls of mesenteral caeca where they induce the apocrine secretion of enzymes (Figs. 12, 19). Their presence confirms active digestion, especially in mycophagous mites, but also in mites with other feeding habits.

No animal is able to produce chitinolytic enzymes. Therefore, mycophagous mites, including oribatids and acaridids, depend on other organisms such as bacteria to produce these enzymes for them (Smrž & Trelová 1995, Smrž & Čatská 2010). Although actimycetes and some other fungi produce chitinolytic enzymes, only bacteria are recorded doing this in mites (Smrž & Soukalová 2008). They occur around the mesenteron and mesenteral caeca in what are referred to as *bacterial clusters* or *bodies*, which are similar to the mycetome in insects (Figs 20–21). The close contact of hemocytes with these clusters facilitates the transport by the hemocytes of bacterial chitinolytic enzymes to secretory cells in the mesenteral caeca and subsequently into the gut (Figs 12, 18). There are several mycophagous oribatid and acaridid mites (Smrž & Jungová 1989). Twelve species of chitinolytic enzyme producing bacteria have been isolated from soil saprophagous mites (Fig. 22) (Smrž & Soukalová 2008, Smrž & Čatská 2010).

There are three ways of feeding on fungi:

(1) they pierce fungal cells and extract their contents, (2) they cut off and eat pieces of mycelium or spores, the cellular contents of which are exracted and digested by a process called "drinking". These two groups, however, only feed on the contents of cells, hence, on simple sacharids including trehalose (Wigglesworth 1978, Almeida et al. 2007) and other simple substances in the contents of cells. The chitinous cell wall remains intact.

(3) *The mycophagous mites consume and digest fungi including the cell walls.* Hence, these species have evolved a close association with chitinolytic producing bacteria. By plating homogenized mites and isolating the bacteria it is possible to identify the chitinolytic bacteria (Smrž et al. 1991, Smrž & Soukalová 2008, Smrž 2009, Smrž & Čatská 2010). These bacteria were purified and identified by CCM Brno (Czech Collection of Microorganisms, Masaryk University Brno) an internationally certified laboratory for the identification of microorganisms. Their chitinolytic effect on fungi was demonstrated using purified isolates of bacteria obtained from homogenates of mites (Figs 23–24).

Some species of mites can feed on bacteria but most feed on either fungi or litter. Erban & Hubert (2008) and Erban et al. (2007) studied this phenomenon and record the very important role of the various enzymes, especially lysozyme, which is a very effective enzyme. Although it is not classified as a digestive enzyme it has an important role in the digestion of bacteria.

The great bulk of the food of mites is rich in cellulose. The digestion of polysaccharides presents a similar problem to the digestion of chitin. The structure of chitin is similar to that of cellulose. Only snails can produce celullolytic enzymes. Other animals depend on a close association with organism that can produce these enzymes, of which bacteria are the most important. Some fungi

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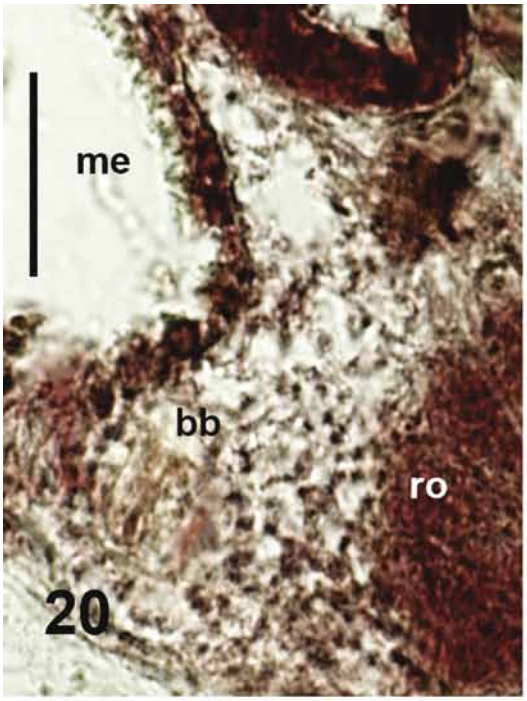
Figs 17–20. Alimentary tract and its surroundings: 17 – *Archegozetes longisetosus*, apocrine secretion in mesenteron (arowheads); 18 – *Hermannia gibba*, hemocytes (arrows), microvilli in rectum (arrowheads); 19 – *Hermannia gibba*, hemocytes penetrating into the walls of mesenteral caeca, some with empty vacuoles (white arrowheads) and others with full vacuoles (arrows); 20 – *Damaeus onustus* (Koch,1841), cluster of associated bacteria. Stained with Masson's trichrome (17, 19), viewed through a Nomarski prism (18, 20). Abbreviations used: bb – associated bacteria; co – colon; he – hemocytes; me – mesenteron; mec – mesenteral caeca; ro – glycogen rosette. Scale bars: 0.1 mm (17), 0.05 mm (18, 20), 0.02 mm (19).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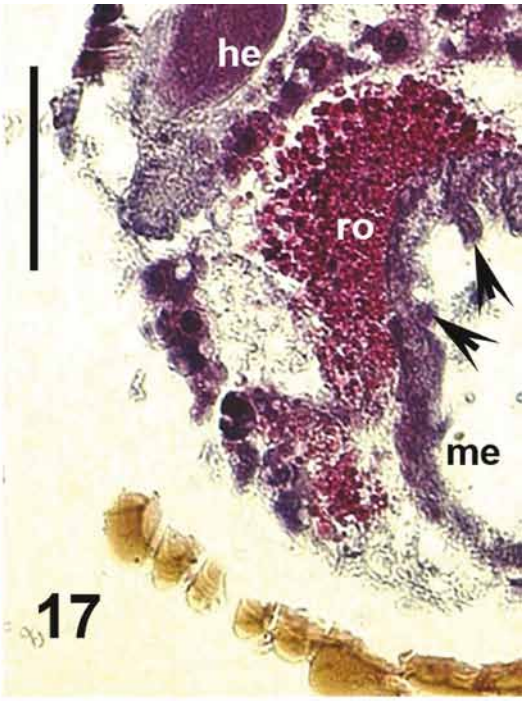
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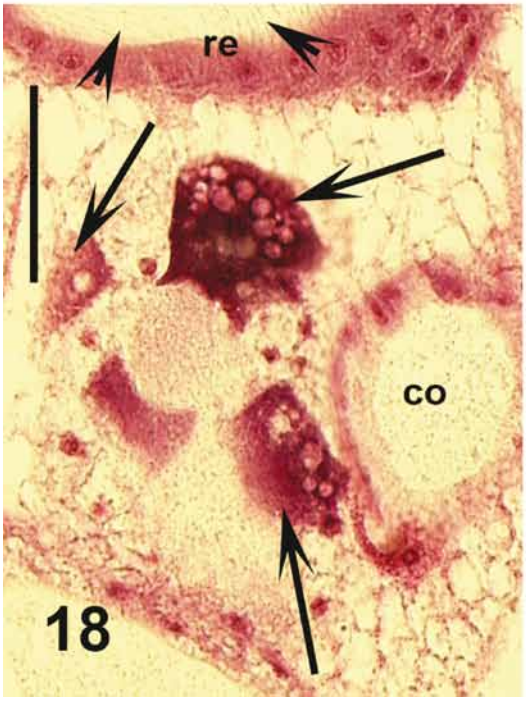
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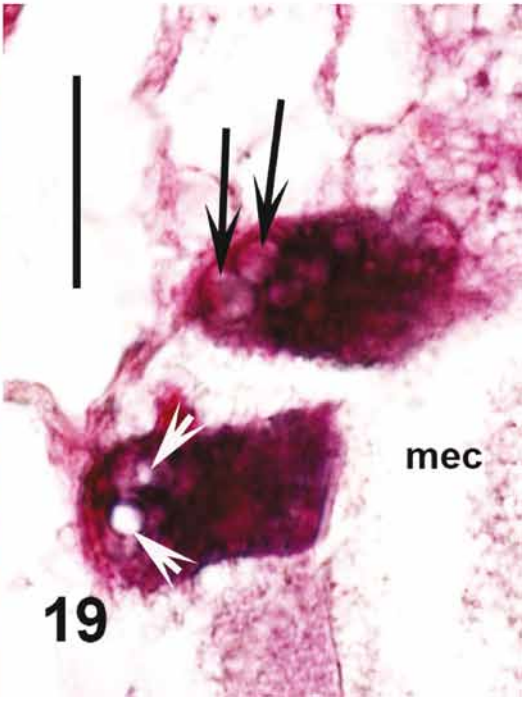
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are also classified as cellulolytic (*Stachybothrys*, *Bothrytis*: Hudson 1986). A few experiments have either indicated or rather insinuated that mites are capable of decomposing cellulose material. The destruction of plant litter can be mainly attributed to fungi that feed on plant litter (cf. Hudson 1986, Schneider & Maraun 2005). Mites, probably, search for leaves that have been partially consumed by fungi. This is possibly true for other substances that take longer to decompose, e.g. lignin. The nature of the food combined with feeding habits of soil animals seems to be a very important ecological factor. It influences the migration, settlement and colonization of microhabitats. While localities are affected by abiotic factors (moisture, temperature, orography, soil structure and characterization) at a large scale, the availability of various foods and its palatability for soil animals including mites are regulated at smaller "island" scales – microhabitats (cf. Anderson 1977, Mitchell 1978, Smrž 2007). This phenomenon is conspicuous especially in extreme microhabitats such as the moss cover on rocks, trees or buildings (Travé 1953, Smrž & Kocourková 1999, Smrž 2006b) or in reclamation plots (Dunger et al. 2001, Frouz 2008), or agroecosystems (Seibert 1993, Žilová 1999, Hajmová & Smrž 2001).

CONCLUSIONS

A multi-method approach for studying the nutritional biology of mites is presented in this paper. A histological study was supplemented by an analysis of faeces using fluorescence and confocal microscopy, recording the activity of enzymes and presence of chitinolytic bacteria in their gut contents. The latter is essential when assessing whether the mites are mycophagous, which can confirmed by offering them soil fungi. These methods should be used along with stable isotopes analyses, molecular methods for assessing the presence of bacteria in mites and fatty acid analyses in the future. In this way we shall obtain a better understanding of the nutritional relations of soil dwelling organisms.

A c k n o w l e d g e m e n t s

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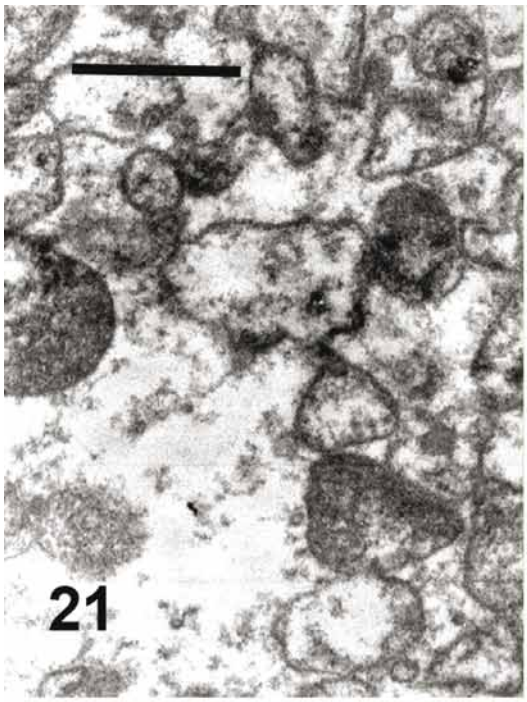
Figs 21–24. Alimentary tract and its surroundings, effect of asociated bacteria isolated from mite homogenate: 21 –*Tyrophagus putrescentiae*, TEM – associated bacteria in bacterial cluster; 22 –*Hypodamaeus riparius* (Nicolet,1855), with cluster of *Bacillus* sp. as associated bacteria; 23 – effect of *Serratia liquaefaciens* isolated from *Tyrophagus putrescentiae* on *Alternaria alternata*; 24 – effect of *Serratia marcescens* isolated from *Tyrophagus putrescentiae* on *Mucor* sp. (arrows), the arrowheads point to drop of control distilled water. TEM (21), Stained with Pianese (22), dishes with fungi (23, 24). Scales bars: 0.002 mm (21), 0.05 mm (22).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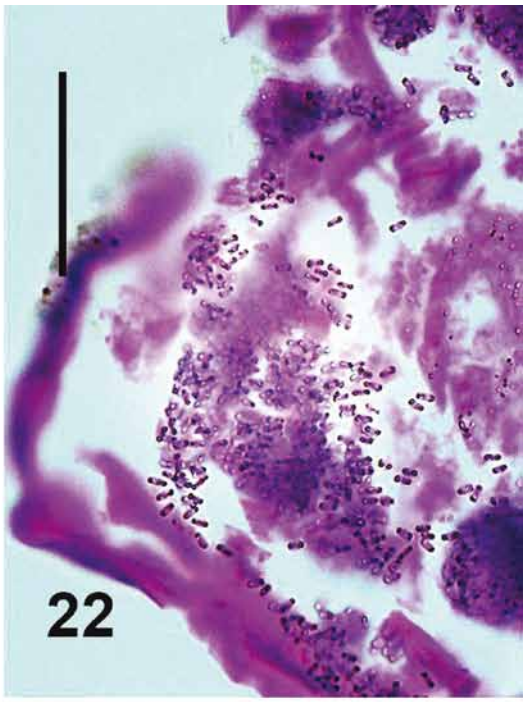
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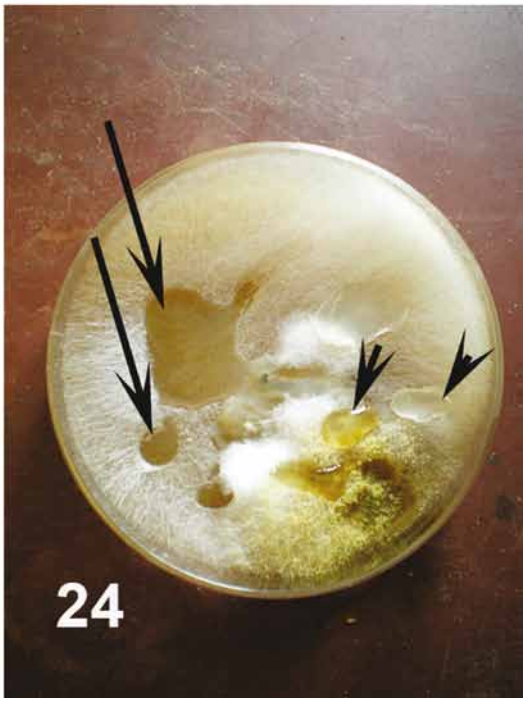
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