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EXPERIMENTAL ARTICLES

Interrelationships between Yeast Fungi and Collembolans in Soil

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Abstract—The possibility of feeding on green and newly fallen leaves of the small-leaved lime *Tilia cordata* was studied for the collembolans *Protaphorura armata* and *Vertagopus pseudocinereus*. Young leaves grown under sterile conditions and almost free of yeast fungi were found to be toxic to the collembolan *V. pseudocinereus*: feeding on them led to the death of the animals. Leaves grown under natural conditions were nontoxic: when used by the collembolans as feed, they provided for collembolan growth and fecundity. Feeding preferences of the collembolans in relation to the yeasts attributed to different ecomorphs—epiphytes, litter saprophytes, pedobionts, and saccharobionts—were studied. Of the 24 yeast strains isolated from plant green parts, litter, and soil and assigned to eight species, no strain was revealed that was not used by the collembolans. However, certain yeast strains were preferable for the collembolans. The population of the *V. pseudocinereus* collembolans feeding on the yeast *Rhodotorula glutinis* (nss 31-4) exceeded that grown on *Cryptococcus terricola* (2044) 1.5-fold. Thus, the collembolans have feeding preferences in relation to yeast fungi, as was shown earlier with mycelial micromycetes. The possible mechanisms of the feeding preferences of the collembolans in relation to yeasts are discussed.

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Key words: yeasts, collembolans, interactions, feeding, feeding preferences.

Invertebrates are involved in the decomposition of plant material; however, they prefer decomposing litter to newly fallen leaves. Repellents contained in the leaves are considered to be a possible cause [1]. Microarthropods, collembolans in particular, are among the first to colonize plant litter. They graze on the tissues of the decomposing leaves colonized by microorganisms, thus regulating the activity and composition of the litter microbial complex [2–4]. The relationships between microorganisms and microarthropods on newly fallen leaves not yet colonized by microorganisms have not been studied so far. At the early stages of litter colonization, microarthropods encounter an epiphytic microbial population, a considerable part of which is represented by yeast fungi. It is on the surface of leaves that yeasts are most abundant and diverse [5]. Whether collembolans can feed on the phylloplane yeast fungi is unknown. However, it is known that fungi are one of the main sources of feed for microarthropods. Microarthropods show preferences in relation to certain fungi. It has been experimentally shown that, for microarthropods, the mycelium of saprophytic fungi is a more attractive feed than that of mycorrhizal fungi [6], and nitrogen-rich mycelium is preferable to mycelium with a lower nitrogen content [7, 8]. The chemical signals issuing from fungi are of great importance [9]. It is unknown whether microarthropods have preferences in relation to yeast fungi.

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The aim of this work was to clarify whether collembolans feed on newly fallen leaves, as well as to determine whether they have feeding preferences in relation to yeast fungi.

MATERIALS AND METHODS

The collembolans *Protaphorura armata* Jacobs, W, De Bruyn (collected in soil) and *Vertagopus pseudocinereus* Fjellberg, 1975 (collected on tree bark) were studied. The animals were maintained on decomposing lime leaves (*Tilia cordata* Mill.) in desiccators filled with a moistened mixture of gypsum and activated carbon (10 : 1). The feeding preference experiments were performed in Petri dishes filled with the same mixture.

The possibility of feeding of the *V. pseudocinereus* collembolans on green lime leaves was studied. Leaves almost free of fungi were grown in the laboratory. To do this, lime branches with swollen buds were gathered in the Losinyi Ostrov (Moose Island) National Park in spring, before the trees shot their leaves. Cuttings with two or three buds were washed in sterile distilled water and then grown under sterile conditions in flasks closed with cotton wool–gauze stoppers at constant illumination until the leaves shot out. Leaves grown under natural conditions were also gathered. Plating of aliquots of a 1 : 10 diluted wash-off onto wort agar acidified to pH 4.0 failed to reveal any fungi on the leaves grown in the laboratory. The leaves gathered in the forest were

Table 1. Yeasts used in the experiments

Species (strain)	Source of isolation
	Group: Basidiomycetes
	Ecomorph: Epiphytes
Sporobolomyces roseus (oduv. tsv. ottsv. 35-2)	Dandelion flowers that finished blooming (*Taraxacum officinale* Wigg.)
S. roseus (nss 25-4)	Strawberry leaves, Malinki Biological Station, Moscow oblast
S. roseus (nss 2-7)	Strawberries, Novosibirsk
Rhodotorula glutinis (listv. 61-1)	Coniferous needles of common (European) larch (*Larix decudua* Miller)
R. glutinis (nss 61-1)	Birch leaves, Malinki
R. glutinis (3238)	Plant sample, outlet of a hot spring, the shore of the Sea of Okhotsk
	Ecomorph: Litter saprobionts
Trichosporon pullulans (el' 409-1)	Coniferous needles of common (Norway) spruce (*Picea abies* (L.) Karst)
T. pullulans (dub 124-1)	English oak (*Quercus robur* L.) leaves
T. pullulans (3329)	Soil, eastern Pamirs
Cystofilobasidium capitatum (2942)	Cedar litter after a bottom fire
C. capitatum (bereza 186-2)	Common birch (*Betulla pendula* Roth.)leaves
C. capitatum (dub 89-1)	English oak (*Quercus robur* L.) leaves
	Ecomorph: Pedobionts
Cryptococcus terricola (2044)	Soil, arable horizon A, Valdai
C. terricola (zhvch 320-1)	*Ajuga reptans* L., leaves
C. terricola (zhvch 144-1)	*Ajuga reptans* L., leaves
Cryptococcus podzolicus (podor. 10-2)	Common plantain leaves (*Plantago major* L.)
C. podzolicus (3244)	Grass, river valley, tundra, Kamchatka
C. podzolicus (3576)	Worm course, horizon A, localities near Moscow
	Group: Ascomycetes
	Ecomorph: Saccharobionts
Metschnikowia pulcherrima (zeml. tsv. 3-2)	Strawberry flowers
M. pulcherrima (oduv. tsv. 41-1)	Dandelion flowers (*Taraxacum officinale* Wigg.)
M. pulcherrima (khvoshch 67-2)	Horsetail
Saccharomyces cerevisiae (bereza 209-2)	Common birch (*Betulla pendula* Roth.) leaves
S. cerevisiae (listv. 2-1)	Coniferous needles of common (European) larch (*Larix decudua* Miller)
S. cerevisiae (zhvch 204-1)	*Ajuga reptans* L., leaves

found to harbor 2×10^3 CFU/g of fungi. The leaves free of fungi and the leaves with a natural content of fungi were then offered to the collembolans as the only source of feed.

The leaves were also subjected to freezing at –18°C for 24 h and then thawing or drying at 18–20°C with subsequent moistening. It was supposed that such a treatment would change the qualitative chemical composition of the leaves. Some of the leaves were offered to the collembolans without treatment. The leaves were colonized by the collembolan *V. pseudocinereus* at a rate of 50 adult specimens per 100 mg of the leaf cut-

Table 2. The number of the *Vertagopus pseudocinereus* specimens after two weeks of maintaining them on green lime leaves grown in the laboratory and gathered in forest

Leaf origin	Freezing–thawing	Drying–moistening	Without treatment
Grown in the laboratory	14 ± 8*	12 ± 5	0
Gathered from trees	79 ± 19	73 ± 40	100 ± 13

Note: 50 animals are placed on each leaf.
* Standard deviation; $n = 3$.

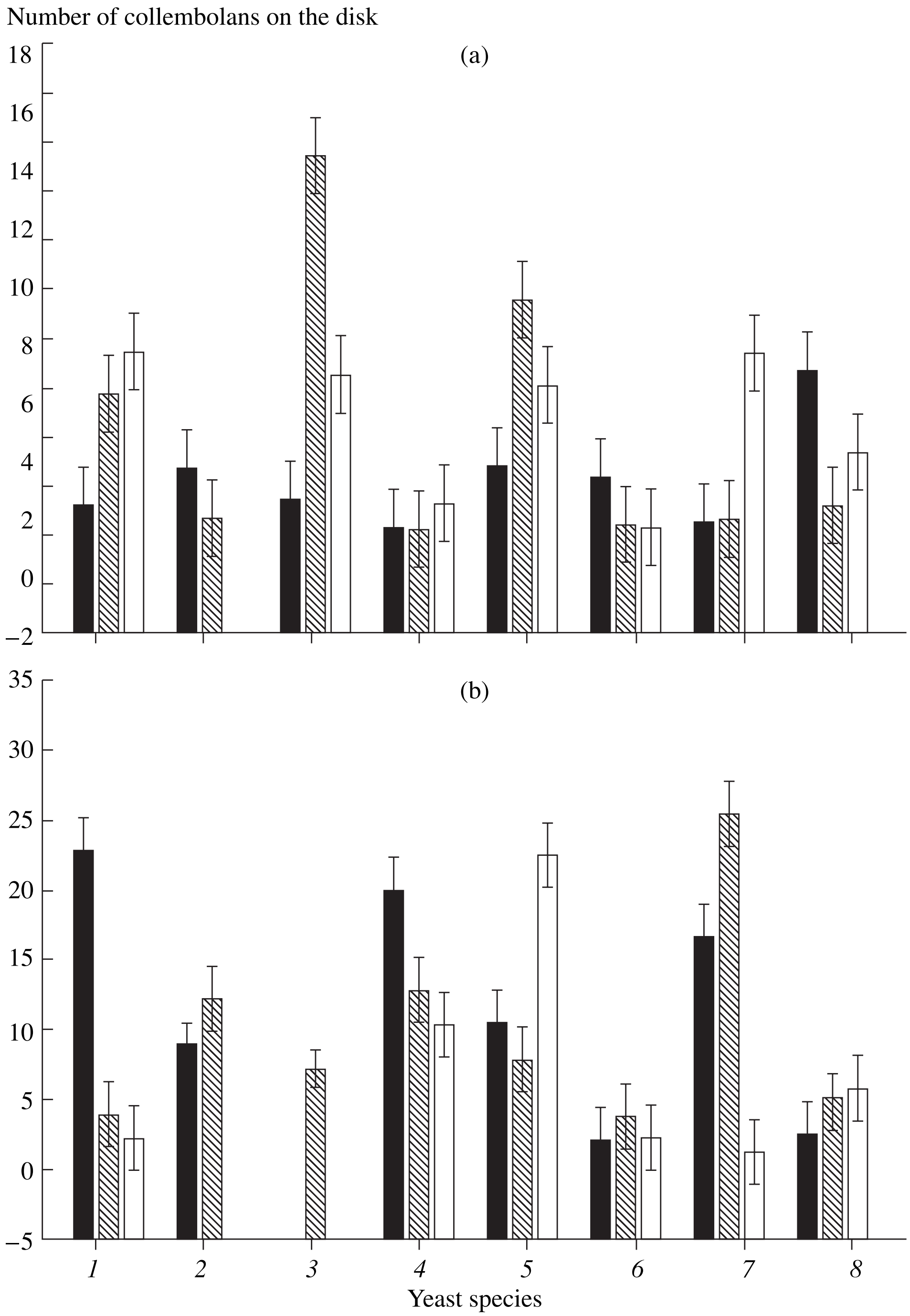

Fig. 1. Preferences in the collembolans (a) *Vertagopus pseudocinereus* and (b) *Protaphorura armata* in relation to the yeasts. The values of attendance by the collembolans of the disks inhabited by different strains of eight yeast species were averaged over 20 counts within 96 h. Different strains of the same species are indicated by different hatching. Designations: (*1*) *Cryptococcus podzolicus* (black column, strain podor. 10-2; hatched column, strain 3244; white column, strain 3576); (*2*) *Cryptococcus terricola* (black, 2044; hatched, zhvch 320-1); (*3*) *Cystofilobasidium capitatum* (black, 2942; hatched, bereza 186-2; white, dub 89-1); (*4*) *Metschnikowia pulcherrima* (black, zeml. tsv. 3-2; hatched, oduv. tsv. 41-1; white, khvoshch 67-2); (*5*) *Rhodotorula glutinis* (black, listv. 61-1; hatched, nss 31-4; white, 3238); (*6*) *Saccharomyces cerevisiae* (black, bereza 209-2; hatched, listv. 2-1; white, zhvch 204-1); (*7*) *Sporobolomyces roseus* (black, oduv. tsv. ottsv. 35-2; hatched, nss 25-4; white, nss 2-7); (*8*) *Trichosporon pullulans* (black, el' 409-1; hatched, dub 124-1; white, 3329).

tings. The collembolan feeding was assessed by the presence of nibbles on the leaves and the number of animals two weeks after they had colonized the leaves.

The interactions between the collembolans and 24 yeast strains affiliated to 8 species belonging to four different ecomorphs were studied (Table 1). The most typical species of the ecomorphs were chosen. The yeasts were grown in liquid wort for 48 h. The cells were washed with sterile tap water by two times repeated centrifugation. The cell suspension (50 μl) was transferred onto a caprone filter (pore diameter, 0.2 μm), and the filters were placed on the surface of wort agar for the yeasts to grow for 48 to 72 h. In another experimental variant, filters with 50 μl of the cell suspension were immediately placed on the gypsum without additional cultivation of yeasts. To study the feeding preferences of the collembolans, 25-mm caprone disks with the yeasts applied onto them were placed in a dish with a gypsum mixture. One hundred and sixty collembolans were put at the center of each dish. The preference of collembolans for one or another yeast as a source of feed was determined by calculating the number of the animals on each filter each hour from 12:00 to 5:00 p.m. over four days. The experiment was carried out in three replicates. The conditions for cultivation of the yeasts and feeding of the collembolans were constant throughout the experiment.

The feeding value of the yeasts *Rhodotorula glutinis* (nss 31-4) and *Cryptococcus terricola* (2044) was determined for the collembolan *V. pseudocinereus.* For this purpose, five experimental series were set. Five caprone disks with one of the yeast strains were put into each dish, and 50 collembolans were allowed to colonize the dish. At the beginning of the experiment, the yeast mass in the air-dry state (after drying the disks at 105°C) was determined. Every week, the disks of one of the series were weighed on an analytical balance, and the number of collembolans was counted. Disks that bore yeasts applied onto them but which were not colonized by collembolans served as controls. The experiments were set in three replicates.

RESULTS

The possibility of collembolan feeding on fresh leaves. All the leaf samples offered to the collembolans were eaten by them. This was judged from the presence of nibbles at the distal parts of the leaves. Reproduction of collembolans occurred when they fed on the lime leaves grown under natural conditions. No significant differences were observed in the number of animals feeding on untreated green leaves and leaves treated by freezing–thawing or drying. On the contrary, when feeding on the leaves grown under the laboratory conditions, the collembolans died, and their number decreased to zero after two weeks (Table 2).

Feeding preferences of the collembolans in relation to the yeasts. Statistically significant differences were observed in the attractiveness of different yeast strains and species for the collembolans. Figure 1 shows the average attendance by the collembolans of the disks inhabited by different strains of eight yeast

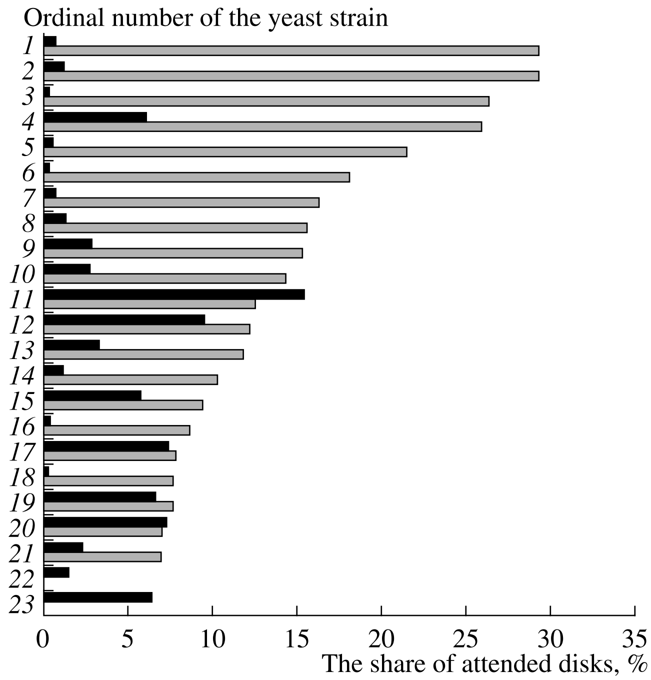

Fig. 2. Comparison of the attendance of different yeast strains by the collembolans *Vertagopus pseudocinereus* (black columns) and *Protaphorura armata* (cross-hatched columns). The same yeast strains are paired. Designations: (*1*) *Sporobolomyces roseus* (nss 2-7), (*2*) *Cryptococcus podzolicus* (podor. 10-2); (*3*) *Metschnikowia pulcherrima* (zeml. tsv. 3-2); (*4*) *Rhodotorula glutinis* (3238); (*5*) *Sporobolomyces roseus* (nss 25-4); (*6*) *Metschnikowia pulcherrima* (oduv. tsv. 41-1); (*7*) *Cryptococcus terricola* (2044); (*8*) *Metschnikowia pulcherrima* (khvoshch 67-2); (*9*) *Rhodotorula glutinis* (listv. 61-1); (*10*) *Cryptococcus terricola* (zhvch 320-1); (*11*) *Cystofilobasidium capitatum* (dub 89-1); (*12*) *Rhodotorula glutinis* (nss 31-4); (*13*) *Trichosporon pullulans* (3329); (*14*) *Trichosporon pullulans* (el' 409-1); (*15*) *Cryptococcus podzolicus* (3244); (*16*) *Saccharomyces cerevisiae* (zhvch 204-1); (*17*) *Cryptococcus podzolicus* (3576); (*18*) *Saccharomyces cerevisiae* (listv. 2-1); (*19*) *Trichosporon pullulans* (dub 124-1); (*20*) *Sporobolomyces roseus* (oduv. tsv. ottsv. 35-2); (*21*) *Saccharomyces cerevisiae* (bereza 209-2); (*22*) *Cystofilobasidium capitatum* (bereza 186-2); (*23*) *Cystofilobasidium capitatum* (zhvch 1 55-2).

species (20 counts over 4 days were performed). Different collembolans had their own preferences. For example, for *V. pseudocinereus* (Fig. 1a), these were two strains of *C. capitatum*, two strains of *C. podzolicus*, two strains of *R. glutinis*, one strain of *S. roseus*, and one strain of *T. pullulans* each. The list of yeasts preferred by the collembolan *P. armata* (Fig. 1b) is quite different. These animals were more often attracted by the disks with *S. roseus* (nss 2-7), while *C. capitatum* (bereza 186-2) and *R. glutinis* (nss 31-4), preferred by *V. pseudocinereus*, were eaten by *P. armata* to a lesser degree (Fig. 2).

We also observed a change in the attendance by the collembolans of different yeast strains over time. The

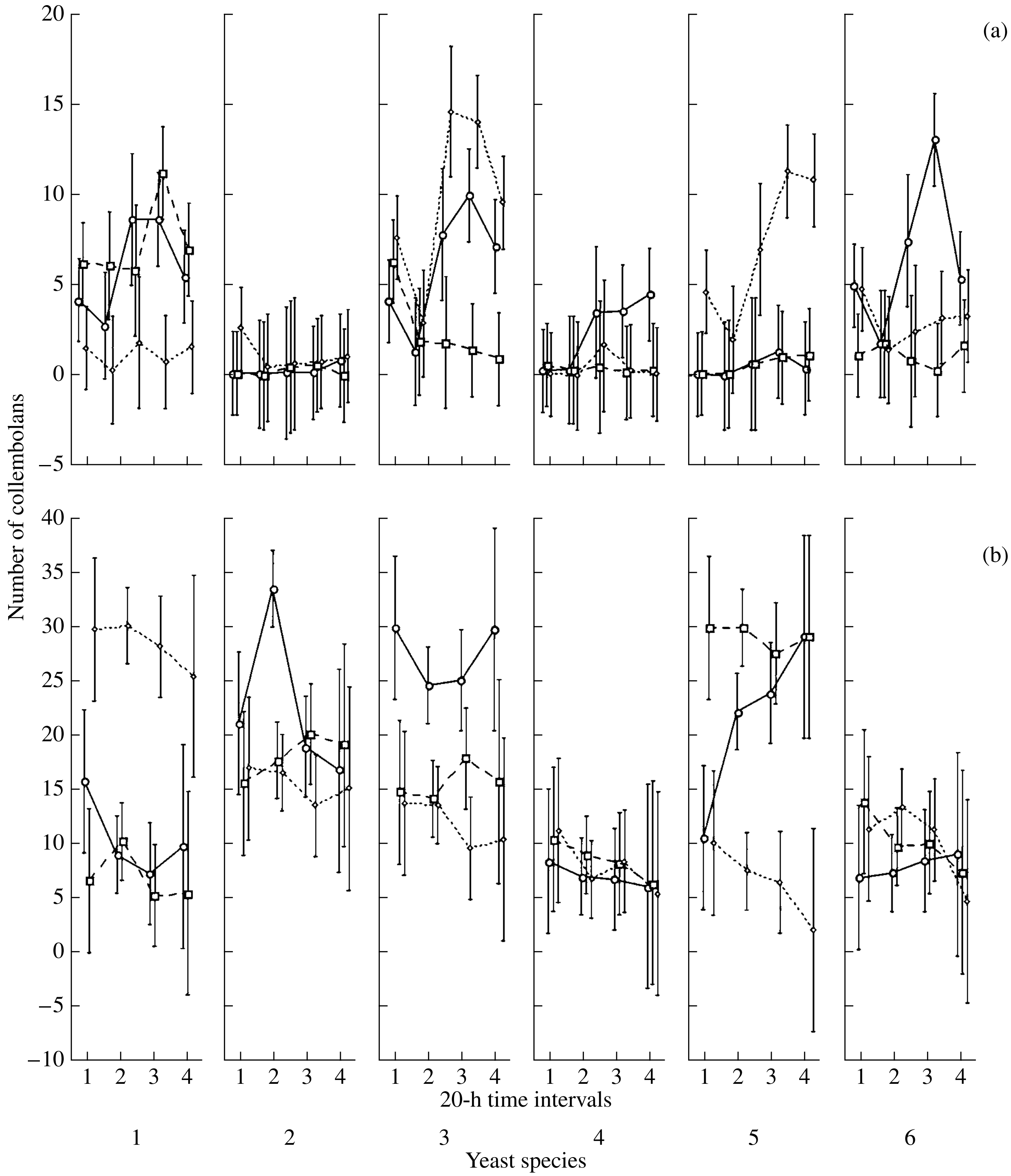

Fig. 3. Dynamics of the number of the collembolans (a) *Vertagopus pseudocinereus* and (b) *Protaphorura armata* attending disks inhabited by different yeasts. Each point represents the average number of specimens over 20 h with 5-h counts every day for each yeast species. Different yeast strains of the same species are designated by different line types. (1) *Cryptococcus podzolicus* (solid line, podor. 10-2; broken line, 3244; points, 3576); (2) *Metschnikowia pulcherrima* (solid line, zeml. tsv.s 3-2; broken line, oduv. tsv. 41-1; points, khvoshch 67-2); (3) *Rhodotorula glutinis* (solid line, listv. 61-1; broken line, nss 31-4; points, 3238); (4) *Saccharomyces cerevisiae* (solid line, bereza 209-2; broken line, listv. 2-1; points, zhvch 204-1); (5) *Sporobolomyces roseus* (solid line, oduv. tsv. ottsv. 35-2; broken line, nss 25-4; points, nss 2-7); (6) *Trichosporon pollulans* (solid line, el' 409-1; broken line, dub 124-1; points, 3329).

collembolans' choice recorded during the first hours of the investigation was not single and definitive. Throughout the experiment, the collembolans changed their preferences. Whereas the attendance of the disks with one yeast strain may sharply increase, the number of collembolans on the other disks is unchanged or even decreases. Although these fluctuations in the number of the collembolans may be considerable (Fig. 3), the

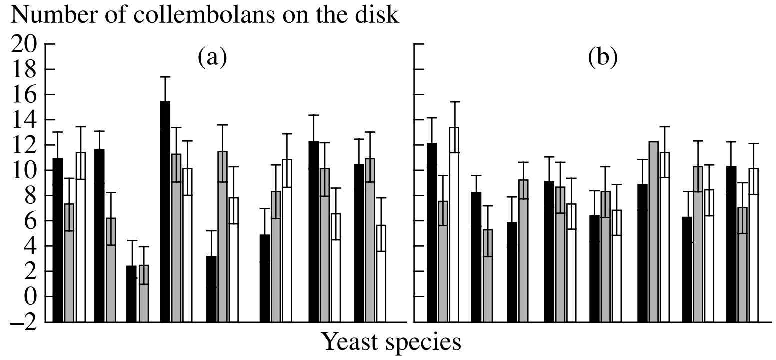

Fig. 4. Preferences of *Protaphorura armata* in relation to the yeasts recorded in two different experiments, (a) and (b). The values of attendance by the collembolans of the disks inhabited by different strains of eight yeast species were averaged over 20 counts within 96 h (see Fig. 1 for designations).

value of the attendance of the yeasts by the collembolans averaged over four days gives evidence of the existence of feeding preferences (see Fig. 1). Comparison of the data obtained in two independent experiments confirmed the existence of yeast preferences by the collembolans (Figs. 4a, 4b).

To make sure that the choice of the yeasts was not accidental, the collembolan *P. armata* was offered eight disks inhabited only by the readily grazed culture of *M. pulcherrima* oduv. tsv. 41-1. The attendance dynamics over 50 h (12 observations, eight disks) appeared to be of a very similar character. The values of attendance by the collembolans of the eight identical feeders, averaged over 50 h of observations, did not differ significantly (Fig. 5).

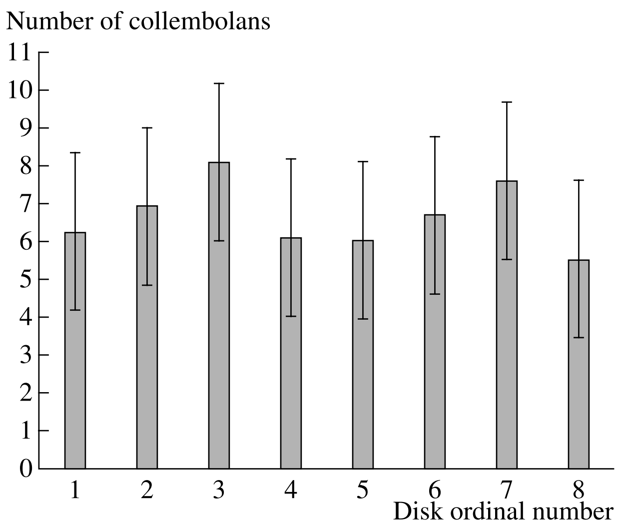

Fig. 5. Attendance by the collembolan *Protaphorura armata* of the disks inhabited by *Metschnikowia pulcherrima* (oduv. tsv. 41-1). The average value is given for 50 h; the collembolans were counted for an hour four to five times daily.

In addition to revealing feeding preferences, the feeding value of the yeasts for the collembolans was determined. For this purpose, we studied the dynamics of the *V. pseudocinereus* population when the animals were fed with *R. glutinis* or *C. terricola*. Different dynamics of population growth were revealed. The number of collembolans peaked after four weeks when the animals were fed on either of the yeast strains, but it constituted about 800 specimens in the case of feeding on *C. terricola* and more than 1200 specimens in the case of feeding on *R. glutinis* (Table 3). The biomass of the yeasts that the collembolans fed on decreased significantly (Table 4).

DISCUSSION

Microarthropods are among the first to inhabit leaf litter. It is not clear whether they feed on the leaf substances per se or on the microorganisms colonizing the leaves. It is also unknown whether the collembolans are able to feed on newly fallen leaves or whether it is necessary that biochemical changes accompanying aging occur in them [10]. This investigation showed that, of all the leaves offered to the collembolans, only the green leaves grown in the laboratory were unsuitable for feeding (Table 2). Since the collembolans ate them but died as a result, it may be considered that the green leaves are toxic for the animals. Freezing–thawing and drying–moistening of the green leaves gathered under natural conditions did not change the reaction of the collembolan *V. pseudocinereus* to them. At the same time, treatment of the leaves grown in the laboratory and not colonized by fungi made them suitable for the collembolans. Evidently, the phylloplane microorganisms (bacteria and fungi), which prepare the leaves to be used by the collembolans, are of great importance. They may be the only source of feed for these

Table 3. The number of the *Vertagopus pseudocinereus* species maintained on disks with the yeasts *Rhodotorula glutinis* and *Cryptococcus terricola*

Time (weeks)	Number of collembolans on disks with the yeas	
	R. glutinis	*C. terricola*
1	51 ± 2	59 ± 7
2	328 ± 21	206 ± 6
3	698 ± 33	525 ± 43
4	1197 ± 81	760 ± 45
5	318 ± 14	492 ± 112

Table 4. The masses of the disks with the yeasts *Rhodotorula glutinis* and *Cryptococcus terricola* used to maintain *Vertagopus pseudocinereus* collembolans

Time (weeks);	Disk mass (g)	
	R. glutinis	*C. terricola*
1	$0.024 \pm 1.23 \times 10^{-3}$	$0.026 \pm 2.5 \times 10^{-3}$
2	$0.024 \pm 1.24 \times 10^{-3}$	$0.025 \pm 1.6 \times 10^{-3}$
3	$0.022 \pm 0.97 \times 10^{-3}$	$0.023 \pm 2.26 \times 10^{-3}$
4	$0.021 \pm 1.47 \times 10^{-3}$	$0.022 \pm 0.11 \times 10^{-3}$

animals during the early stages of leaf-litter colonization.

It was shown earlier that the collembolans prefer to use certain species of mycelial fungi. The selectivity was revealed not only in relation to the species of fungi [11–13] but also to their structural elements [2, 14, 15]. The choice may be based on the perception and recognition of fungal odors. For example, the collembolan *Orchesella cincta* preferred the fungus *Cladosporium herbarum*, and *Tomocerus flavescens* preferred the fungus *Mortierella isabellina.* The analysis of the electroantennograms of the collembolans recorded in response to nine different gaseous substances that enter into the composition of the odors of these fungi revealed differences between the antenna responses to 2-methyl-1-propane, dipeptane, 1-octane, and camphor. The substances responsible for attracting *O. cincta* to *C. herbarum* and *T. flavescens* to *M. isabellina* have not been identified; however, these results indicate that the feeding preferences in the collembolans are of a physiological nature [12]. It should be mentioned that, among mycelial fungi, there are species toxic to collembolans [13].

The experiments carried out by us did not reveal any yeast strain that was not consumed by the collembolans. However, there existed collembolan preferences for yeasts; the collembolans were not equally attracted by them. These differences showed up at the strain but not at the species level. Interestingly, the first choice made by the collembolans was not definitive. When such experiments are conducted, it is a usual practice to limit oneself to noting the presence of the animals on the feed substrate virtually as soon as it is offered to the collembolans [16]. As our experiments show, the collembolans change their preferences with time (Figs. 4, 5).

The comparison of the data obtained as a result of repeating the experiments showed the absence of constant feeding preferences in the collembolans in relation to yeast strains. The strains virtually unattended throughout one experiment became the most preferable when the experiment was repeated (Figs. 4a, 4b). Nevertheless, when *P. armata* collembolans were offered eight disks with one yeast strain, no preference for any particular disk was observed (Fig. 5). Hence, the choice of feed by the collembolans is not accidental. This is also evidenced by the fact that the feed value of various yeasts is different for the collembolans (Tables 3, 4). In all probability, this means that the choice of fungi by the collembolans is determined by both physiological mechanisms and specific features of feeding behavior of these animals [17].

Thus, this work proved that collembolans depend on microorganisms at the early stage of colonization of newly fallen leaves. In addition, they show selectivity in the choice of microbial feed. The existence of feeding preferences, shown earlier in collembolans in relation to mycelial fungi, was also revealed in relation to the yeasts. However, among the micromycetes, there are those that are not consumed by collembolans, and, among the yeasts studied, there were none that were toxic or not consumed.

The fact that the attendance of the disks with particular yeasts by the collembolans changes with time is indicative of variations in feeding preferences. The preferences of the collembolans for yeasts cannot be explained by the trophic mechanism only, i.e., by the feeding value of the yeasts. The choice of the yeasts as a feed source is rather linked to both the physiology and the population behavior of the collembolans, and the motivation for preferences may be the odor issued by the yeast colony or some other stimulus.

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