Species composition, spatial distribution and seasonal dynamics of testate amoebae community in a sphagnum bog (Middle Volga region, Russia)

Yuri A. Mazei¹ and Andrei N. Tsyganov²

¹ Department of Zoology and Ecology, Penza VG Belinsky State Pedagogical University, Penza, Russia
² Department of Hydrobiology, Moscow MV Lomonosov State University, Moscow, Russia

Summary

An ecological study of the testate amoebae community in a sphagnum bog in the Middle Volga region (Russia) during April–October 2004 revealed 63 taxa, belonging to 21 genera. Within the limits of the bog two types of community differing by species composition are formed: (1) moss dwelling testate amoebae assemblage in sphagnum quagmire and (2) detritus testate amoebae assemblage in bottom sediments of drain. In accordance with the distributional pattern, it is possible to differentiate the following groups of species. Detritophilous group (occurs in assemblages of quagmire margin and bottom sediments of drain) is represented by Arcella gibbosa, A. vulgaris, A. hemisphaerica, A. discoides, A. intermedia, A. mitrata, Centropyxis aculeata sphagnicola, Cyclopyxis kahlii, Diffugia glans, Lesquereusia spiralis, Netzelia tuberculata and Phryganella hemisphaerica. Stenotopic sphagnophilous species (inhabit typical sphagnum biotopes only) are Archerella flavum, Euglypha cristata, Diffugia juzeppienensis, Cryptodiffugia compressa, Sphenoderia fissirostris and Nebela militaris. Eurytopic sphagnophilous species (inhabit both typical sphagnum biotope and quagmire margin) are Nebela tenella, N. tincta, Euglypha ciliata, Bullinularia indicia, Assulina seminulum, A. muscorum, Hyalosphenia elegans, Diffugia globulosa, D. parva and Centropyxis aculeata. Eurytopic species (occur in all biotopes) are Arcella arenaria, Euglypha laevis, Trigonopyxis arcula, Hyalosphenia papilio and Trinema complanatum.

Within the sphagnum quagmire of the bog investigated, three types of testate amoebae communities in terms of species structure were revealed: (i) xerophilous community (in hummocks with Polytrichum strictum, Sphagnum papillosum and S. angustifolium) Assulina muscorum–A. seminulum–Cryptodiffugia compressa; (ii) hygrophilous community (in lawns with Sphagnum palustre and S. magellanicum) Hyalosphenia papilio–H. elegans–Heleopera sphagni–Nebela tenella; and (iii) hydrophilous community (in submerged Sphagnum riparium) Cyclopyxis eurystoma–Phryganella hemisphaerica–Heleopera sphagni–Hyalosphenia papilio. The main factor determining differences in community structure was depth to water table (moisture content). Community forming at the edge of quagmire was the most specific. Assemblages in moist biotopes at the centre of quagmire were quite homogenous, while in dry biotopes they were more different. Density of organisms was higher in moist habitats. Thirty-five percent of the testate amoebae fauna was alive at the moment of sampling. The share of live organisms was higher in moist habitats (36–45%) than in dry biotopes (22–27%).

We explored the patterns of testate amoebae distribution in macroscopically homogeneous Sphagnum angustifolium carpet at the scale from 1 cm to 2 m. The spatial distribution analysis of populations of different species showed that most of them combined into slightly marked
aggregations with unclear bounds. So, these aggregations probably resemble more or less expressed patches of different size smoothly passing into each other rather than a distinct spatially constrained groups. The size of agglomerations is species-specific and in some cases (*Assulina muscorum* and *A. seminulum*) has positive correlations with amoebae shell size. Some species produce aggregations of different size, the smallest patch reaching 1 cm. Degree of aggregation of species distribution rises with increase of the study scale, but at the same time community heterogeneity grows too, i.e. aggregations of different species of testate amoebae are not connected with each other in meter scale. Minimal size of testate amoebae community (minimum-areal) does not exceed several centimeters.

The presence of a well-defined vertical structure of testate amoebae community in sphagnum biotopes was shown. The species *H. papilio, A. flavum, A. muscorum, A. seminulum, H. sphagni* were characteristic of the upper parts of *Sphagnum* stem, some of them (*A. flavum, H. sphagni, H. papilio*) were mixotrophs. In the upper 0–3 cm of sphagnum layer, species number and species diversity were minimal, whereas abundance was maximal. The share of living organisms in the upper zone was significantly higher (about 75%) than in the lower one. Communities forming under drier conditions have the most heterogeneous vertical structure. The opposite tendencies in distribution of pairs species *H. papilio–H. elegans* were noted. Mixotrophic species (*H. papilio*) dwell in the upper sphagnum part while heterotrophic species (*H. elegans*) lives in the lower one.

During vegetation season, from May to September, the species richness increased, while species diversity and evenness remained at the same level with insignificant fluctuations. At the same time, species abundance could increase, decrease or vary without well-defined directed tendencies. Characteristics of seasonal dynamics of dominant species in different community variants were shown. In hygrophilous community species dominant in spring *H. papilio, N. tincta* and *H. sphagni*, and in summer-autumn, *N. tenella* and *H. elegans*. In xerophilous community the spring community was dominated by *A. muscorum, N. tincta, H. sphagni*, the summer one, by *N. tenella, A. seminulum, H. elegans, E. ciliata* and the autumn community, by *C. compressa, T. arcula, A. seminulum*. It was found that closely related species have opposite tendencies in seasonal distribution. So, in pairs of species *H. papilio–H. elegans, N. tincta–N. tenella, A. muscorum–A. seminulum* all the former species were characteristic of spring and the beginning of summer, while all the latter were mainly found at the end of summer and in early autumn. A great share of empty tests of the genus *Assulina* is accounted for, first of all, by low moisture content in biotopes where these species live (under these conditions tests are better preserved) and, secondly, by r-strategy of these small organisms, whose population abundance increases or decreases fast as a reaction to environment changes.

**Key words:** testate amoebae, sphagnum bog, community structure, Middle Volga Region, microscale spatial distribution, vertical structure, patches, seasonal dynamics.

## Introduction

Testate amoebae are free-living heterotrophic protists with a wide geographical distribution and a significant range of habitats from water to soil. They are especially abundant and diverse in sphagnum biotopes, where they play a key role in functioning of the microbial loop (Gilbert et al., 1998a, 1998b; Mitchell et al., 2003; Gilbert and Mitchell, 2006).

Present-day studies of testate amoebae concentrate on revealing the quantitative value of ecological optimum of species in relation to the basic environment factors, first of all to moisture, acidity, vegetation and organic content (Charman and Warner, 1992, 1997; Tolonen et al., 1994; Bobrov et al., 2002; Booth, 2002; Mitchell, 2004; Lamentowitcz and Mitchell, 2005; Opravilová and Hájek, 2006). More rarely attention is paid to coenotic factors determining structural features of testate amoebae communities, such as feeding (Gilbert et al., 2000, 2003; Gilbert and Mitchell, 2006), or to morphological patterns of niche space separation (Bobrov et al., 1995, 1999; Bobrov et al., 2002).

It is known that the main factors determining
horizontal distribution of testate amoebae in sphagnum are moisture content and pH (Meisterfeld, 1977, 1978; Warner, 1987; Tolonen et al., 1992, 1994; Charman and Warner, 1992; Beyens and Chardez, 1994; Charman, 2001; Mitchell et al., 1999; Booth, 2001, 2002; Bobrov et al., 2002; Lamentowicz and Mitchell, 2005; Opravilová and Hájek, 2006, etc.). For many species the presence of clear-cut environmental preferences was shown, this stenotopy making them very useful bioindicators (Meisterfeld, 1997; Foissner, 1999). In this way testate amoebae are used for reconstruction of past environmental conditions (Harnisch, 1929; Grospietsch, 1952, 1953a, 1953b; Tolonen, 1966; 1986; Laminger, 1975; Laminger et al., 1981; Warner and Charman, 1994; Woodland et al., 1998; Charman et al., 2000; Hendon et al., 2001; Mitchell et al., 2001; Charman, 2001, Schnitchen et al., 2003; Bobrov, 2003a; Bobrov et al., 2004; Davis, Wilkinson and 2004; Geary and Caseldine, 2006; Hughes et al., 2006) and for assessment of lake water pollution (Patterson et al., 1996, 2002) and peatlands regeneration after peat extraction (Buttler et al., 1996; Hendon and Charman, 2004).

Although the body of literature on peatland testate amoebae is growing and similar findings have been obtained from most locations, further investigation of unexplored regions is still necessary. First of all, such work will demonstrate universality of earlier results taking into account all variety of bogs, and, secondly, will open up possibilities to apply local features of community structure to regional environmental monitoring.

In Russia studies of sphagnobiont testate amoebae were carried out mainly in the north and northwest of the European part and partially in Siberia (Bassin, 1944; Alekseev, 1984; Bobrov et al., 1995, 1999, 2002; Bobrov, 1999, 2003a). Investigations of southern regions were exceptionally faunistic (Tarnogradsky, 1959, 1961).

Until recently testate amoebae communities in Sphagnum-dominated ecosystems of the Middle Volga Region remained poorly investigated. These bogs, located near the south border of bog distribution, are not numerous because of insufficient humidity and elevated relief with erosional surface, which in most cases exclude formation of close internal-drainage hollows. However, these bogs are very interesting for research and may yield results different from those of the better-studied regions. Several earlier investigations focused on sphagnum bogs of Middle Volga (Keller, 1903; Dokturovskiy, 1925; Chiguryaeva, 1941; Sprygin, 1986 – post mortem publication of a study from early 1940ies) was carried out in the first half of the 20th century. They revealed that all these bogs originate from overgrown lakes of flood-lands and divides. At present nearly all of them have been altered by human activity (Chistyakova and Kulikovsky, 2004; Ivanov and Chistyakova, 2005; Stoiko, Mazei, 2005; Ivanov et al., 2006).

In this connection, one of the aims of the present work was to study species composition, community species structure and pattern of testate amoebae distribution in relation to biotope heterogeneity in the bog Bezimyanoe located in the Sura river basin (Middle Volga Region, Russia).

Testate amoebae living in sphagnum biotopes provide a good possibility of investigating general patterns of community structure in space and time. Community structure analysis is mainly based on data on spatio-temporal distribution of organisms. It is well known that spatial distribution of live organisms is nonrandom (Begon et al., 1986). Such heterogeneity very often reflects irregularity of spatial distribution of environmental parameters or stems from species interaction or past process (Borcard et al., 1992). Most issues concerning patterns of community spatial distribution are still unexplored. In particular, it is not quite clear so far how the spatial scale of investigations influences the community structure patterns revealed (Schneider, 1994; Huston, 1999). However, it is known that the patterns of community spatial structure depend on size of organisms (Rusek, 1992; Burkovsky et al., 1994; Balik, 1996a, 1996b; Azovsky, 2000, 2002; Udalov et al., 2004; Azovsky et al., 2004). This question is especially important in the case of unicellular organisms, since successful investigation of minute organisms’ communities, living in another spatio-temporal scale than the person studying them, is only possible if the study is carried out at the same scale of space-time continuum in which the main processes resulting in protozoan community formation are realized. The problem is further complicated by the fact that microgradients of environmental factors, which influence the microorganisms, are invisible (Mitchell et al., 2000). It was shown on some protist groups that changes in patterns of microspatial distribution depend on the investigation scale (Burkovsky and Aksenov, 1996; Burkovsky et al., 1996 – marine littoral interstitial ciliates; Saburova et al., 1991, 1995 – marine littoral microphytobenthos).

Our work attempts to solve some of the above-mentioned questions of protozoan ecology by studying spatial structure of testate amoebae community from Sphagnum-dominated ecosystem.

Spatial heterogeneity may also be vertical. Vertical organization of ecosystems results from direction of gravitation and light (Margalef, 1992). Primary pro-
duction forms in photic zone, where light is available for primary producer. Mineralization takes place in aphytic zone, where heterotrophs are dominant. Thus, the environment contains a great amount of organic matter, which is oxidized in the upper levels and reduced in the lower levels (of ecosystems) (Margalef, 1992). Such vertical differentiation is prominent in sphagnum biotopes (Denisenkov, 2000). Sphagnum mosses produce specific environment in the context of landscape and in the tussock (Zavarzin, 2004). Branches forming dense heads at the top cover thin and long sphagnum stem without rhizoids. Annually the lower part of sphagnum dies, and the upper one grows due to remaining buds. Dead sphagnum parts, submerged in water with low oxygen content, feebly decay producing peat. As a result, horizons with specific conditions are formed. From sphagnum surface to 3–6 cm depth upright stems of “green moss” are located, further down to 15 cm depth “white moss”, which has lost chlorophyll due to shading, appears. And at a depth of 20 cm the layer of peat-forming “brown moss” begins.

Testate amoebae community structure changes with depth according to vertical zonality of biotope (Heinis, 1945; Chacharonis, 1956; Bonnet, 1958; Heal, 1962; Schönborn, 1963; Meisterfeld, 1977; Buttlar et al., 1996; Booth, 2002; Mitchell and Gilbert, 2004). At the same time, distinct vertical differentiation of communities was marked not only for typical sphagnum biotopes but also for drier biotopes with a significant share of Polytrichum strictum in moss carper. Species diversity of testate amoebae also increased with the depth; mixotrophic species with organic shell without cover elements were shown to dominate in the upper levels of sphagnum stems, while species with heavy shells with attached particles dominated in lower zones (Bonnet, 1958; Chacharonis, 1956; Heal, 1962; Schönborn, 1963; Meisterfeld, 1977). However, in dry habitats these patterns could be feeble (Mitchell and Gilbert, 2004).

Despite the long research history, the number of studies of vertical structure of testate amoebae communities in recent Sphagnum in microscale is insufficient (Heinis, 1945; Chacharonis, 1956; Bonnet, 1958; Heal, 1962; Schönborn, 1963; Meisterfeld, 1977; Mitchell and Gilbert, 2004). Many aspects of vertical changes of testate amoebae communities remain unclear. How does community structure change along the vertical gradient in sphagnum? In which horizon do the most significant changes take place? To what extent is vertical structure stable in time? How do the characteristics of vertical structure depend on those of the biotope? Discussion of these questions is the aim of this study.

Seasonal pattern of community structure represents another general view of community organization. Seasonal changes in community structure of protists in temperate climate have a well-defined cyclical character (Wang, 1928; Burkovsky, 1971, 1978, 1984; Patterson et al., 1989; Jax, 1992; 1996; Guhl et al., 1994; Mathes and Arndt, 1995; Auer and Arndt, 2001; Mazei and Burkovsky, 2002). Dynamic processes manifest themselves in changes of species composition and integral community parameters. All these changes are characterized by variability and direction simultaneously. Directional changes are caused by regular changes of environmental conditions during vegetation season. At the same time, considerable fluctuations of environment modify and make insignificant the common tendencies, introducing the accidental element.

Studies of patterns of seasonal dynamics of testate amoebae communities are scanty. There are some investigations of soil assemblages (Smith, 1973; Schönborn, 1975, 1977, 1978, 1982, 1986; Coûteaux, 1976; Laminger, 1978; Laminger et al., 1980; Lousier, 1984, 1985), benthic and periphytic freshwater communities (Schönborn, 1981; Jax, 1992, 1996; Vikol, 1992). Heal (1964) described seasonal changes in abundance and activity of Testacea in Sphagnum, but considered only three species (Hyalosphenia papilio, Amphitrema flavum and Nebela sp.). So, the aim of this study was investigation of seasonal changes of testate amoebae community structure in Sphagnum.

Thus, in the present paper we have set five aims in order to describe testate amoebae community structure in space and time:

- to investigate species composition and species distribution,
- to reveal species structure and influence of moisture as the main factor controlling testate amoebae community structure in boggy biotopes,
- to investigate microspatial horizontal structure in homogeneous Sphagnum angustifolium carpet at a scale from 1 cm to 2 m,
- to investigate microspatial vertical structure in relation to environmental conditions,
- to describe temporal patterns according to seasonal climatic changes.

**Material and Methods**

**Study site**

The bog Bezimyanoe where this study was performed is one of the largest in Svetlaya Polyana bog complex located 15 km North-East from Penza city.
The bog is roundish, about 300 meters in diameter. The lawn vegetation of the study area is dominated by reed-grass (*Calamagrostis canescans* (Web.) Roth), cotton-grass (*Eriophorum vaginatum* L.) and bogbean (*Menyanthes trifoliata* L.). The centre of the bog became overgrown with bushy trees of white birch (*Betula pubescens* Ehrh.) and Scotch pine (*Pinus sylvestris* L.), as well as with undershrubs of wood myrtle (*Myrtus communis* L.). The moss carpet is quite flat, with predominant species *Sphagnum palustre* L., *Sphagnum magellanicum* Brid. and *Sphagnum angustifolium* (C. Jens ex Russ.) C. Jens. At the centre there are hummocks formed by different sphagnum species (manly *Sphagnum papillosum* Lindb. and *S. angustifolium*) and moss *Polytrichum strictum* Brid., on which sundew (*Drosera rotundifolia* L.) grows. Peat was excavated in the bog, there is a drain along its edge and some ditches with open water in the centre, where common bladder-wort (*Utricularia vulgaris* L.) and least bur-reed (*Sparganium minimum* Wallr.) were found. The edge of the sphagnum quagmire directed to the drain is formed by *Sphagnum riparium* Aongstr. (Ivanov and Chistyakova, 2005; Ivanov et al., 2006).

**FIELD SAMPLING**

Samples were collected between April 20 and October 23, 2004 every month with equal intervals at seven stations (Table 1). One station was represented by bottom sediments (tree waste and coarse detritus) from drain. The others were located within the sphagnum quagmire where two types of samples were taken. The first one was subsoil water with peat particles located at the depth from 5 to 30 centimeters below surface of sphagnum carpet. The second one was sphagnum stems where testate amoebae inhabit sinuses of leaves. The material obtained was placed in plastic bottles and 3% formaldehyde was added for fixation.

Sampling sites were selected in an attempt to represent the full range of microhabitats within the bog. Two stations (st.1 and st.2) were located at the centre of the bog, where microrelief (e.g. hummocks and hollows) and lignosa (birch and pine) are prominent. Two stations (st.5 and st.6) were at the edge of quagmire, the station 6 right on the border with the drain, and the station 5 at the area with well-formed and regular sphagnum carpet. Finally, two stations (st.3 and st.4) were located on the border between the peripheral and the central zone of the bog, where there were of *Betula pubescens* and first hummocks were present. The detailed description of the microhabitats investigated and a designation of the stations are presented in table 1. Three stations (st.1, st.3 and st.5) were located in different zones of the bog but in rather similar sites of moss carpet, with the predominance of large-leaved sphagnum (mainly *S. palustre*) and depth to water table from 2 to 16 cm. It is interesting that on the least moist station (st.5) one more species, *S. magellanicum*, appeared; it is characteristic of such conditions (Denisenkov, 2000). Two stations (st.2 and st.4) were located on hummocks with depth to water table from 16 to 32 cm. Hummocks in the bog centre were drier. Stations 6 and 7 were influenced by drain (station 6 was located at the edge of...
quagmire, station 7, in the bottom sediments of the drain). They were characterized by the lower values of acidity (pH 4.5–5.2 in contrast to 4.0–4.1 at other stations), electric conductivity, and temperature, because of shading bordering trees. Redox-potential at the all sites was quite high, which reflects prevalence of oxidizing processes in the ecosystem investigated.

Species composition was investigated in the bottom sediments and subsoil waters (stations 1–7). Community structure was analyzed in sphagnum stems (stations 1–6).

In order to investigate microscale horizontal distribution, samples (altogether 84) were collected on August 20, 2004, in macroscopically homogenous Sphagnum angustifolium carpet. For sampling a plot 270 × 270 cm was subdivided into 4 subplots, 135 × 135 cm in size. In each subplot, the first sample was taken at the centre (diagonal cross), the others were placed diagonally at a distance of 1 cm, 3 cm, 9 cm, 27 cm and 81 cm from the first one (Fig. 2). At the scale of the whole plot, we had another scale, 192 cm. A single stem of Sphagnum moss was carefully extracted from the carpet, the green part (upper 3 centimeters) was cut out and stored in a vial. Later 3% formaldehyde was added for fixation. Only live amoebae were identified and counted. So it was possible to compare communities forming at different distance from each other. Altogether we analyzed 6 scales: 1 cm, 3 cm, 9 cm, 27 cm, 81 cm and 192 cm.

To investigate vertical community structure, a

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Station*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Substrate (sphagnum species)</td>
<td>S. palustre</td>
</tr>
<tr>
<td>Depth of water table, cm</td>
<td></td>
</tr>
<tr>
<td>average for season</td>
<td>5</td>
</tr>
<tr>
<td>range</td>
<td>(2–7)</td>
</tr>
<tr>
<td>standard deviation</td>
<td>2.16</td>
</tr>
<tr>
<td>pH</td>
<td></td>
</tr>
<tr>
<td>average for season</td>
<td>4.0</td>
</tr>
<tr>
<td>range</td>
<td>(3.7–4.4)</td>
</tr>
<tr>
<td>standard deviation</td>
<td>0.28</td>
</tr>
<tr>
<td>Eh, mV</td>
<td></td>
</tr>
<tr>
<td>average for season</td>
<td>190</td>
</tr>
<tr>
<td>standard deviation</td>
<td>55.81</td>
</tr>
<tr>
<td>Electro-conductivity, mkSim/cm</td>
<td></td>
</tr>
<tr>
<td>average for season</td>
<td>56</td>
</tr>
<tr>
<td>standard deviation</td>
<td>25.87</td>
</tr>
<tr>
<td>Water temperature, °C</td>
<td></td>
</tr>
<tr>
<td>average for season</td>
<td>18.2</td>
</tr>
<tr>
<td>range</td>
<td>(8.5–27.7)</td>
</tr>
<tr>
<td>standard deviation</td>
<td>6.97</td>
</tr>
</tbody>
</table>

*st.1 — centre of the bog, flat sphagnum, st.2 — centre of the bog, hummock, st.3 — middle part of the bog, flat sphagnum, st.4 — middle part of the bog, hummock, st.5 — peripheral part of the bog, flat sphagnum, st.6 — peripheral part of the bog, edge of quagmire directed to drain, st.7 — bottom sediments of drain.

Table 1. Description of the biotopes investigated

- Substrate (sphagnum species)
  - S. palustre
  - S. angustifolium, P. strictum
  - S. palustre
  - S. papillosum
  - S. palustre, S. magellanicum
  - S. riparium
  - Detritus

- Depth of water table, cm
  - average for season: 5, 27, 7, 23, 12, 1
  - range: (2–7), (22–32), (2–13), (16–27), (10–16), (0–3)
  - standard deviation: 2.16, 4.57, 61.2, 18.2, 2.61, 1.41

- pH
  - average for season: 4.0, 4.0, 4.0, 4.2, 4.1, 4.5, 5.2
  - range: (3.7–4.4), (3.7–4.4), (3.7–4.4), (3.6–4.6), (4.1–4.9), (4.9–5.4)
  - standard deviation: 0.28, 0.3, 0.43, 0.28, 0.35, 0.28, 0.19

- Eh, mV
  - range: (110–270), (200–270), (90–170), (90–260), (90–170), (90–240), (120–230)
  - standard deviation: 55.81, 32.4, 57.49, 64.22, 71.22, 50.53, 37.36

- Electro-conductivity, mkSim/cm
  - average for season: 56, 58, 44, 44, 48, 25, 31
  - range: (48–94), (48–94), (26–75), (26–75), (36–77), (19–36), (23–40)
  - standard deviation: 25.87, 25.96, 18.93, 21.16, 18.81, 5.98, 6.68

- Water temperature, °C
  - average for season: 18.2, 17.9, 17.1, 17.1, 17.2, 16.4, 15.5
  - range: (8.5–27.7), (8.5–26.1), (8.8–24.1), (8.8–24.1), (5.2–26.0), (5.5–22.7), (5.5–22.8)
  - standard deviation: 6.97, 5.46, 6.09, 5.97, 7.14, 6.38, 6.48

*st.1 — centre of the bog, flat sphagnum, st.2 — centre of the bog, hummock, st.3 — middle part of the bog, flat sphagnum, st.4 — middle part of the bog, hummock, st.5 — peripheral part of the bog, flat sphagnum, st.6 — peripheral part of the bog, edge of quagmire directed to drain, st.7 — bottom sediments of drain.
part of sphagnum was taken from sward and 10 separate plants were picked out from it. Then they were cut up according to vertical differentiation of the biotope. At the station within the main part of the bog (stations 1–4), five zones 0–3, 3–6, 6–9, 9–12 and 12–20 cm were distinguished. Samples taken from the bog edge, where peat layer were feebly-marked and the drain influence was significant, were divided into six parts: 0–3, 3–6, 6–9, 9–12, 12–20 and 20–30 cm at station 5 and 0–3, 3–6, 6–9, 9–12, 12–15 and 15–35 cm at station 6.

**COUNTING OF AMOEBAE**

During sampling a part of sphagnum was taken from quagmire and 10 separate plants were picked out. To extract testate amoebae from the moss, samples were thoroughly shaken and stirred for 10 min in some distilled water. The suspension without sphagnum stems was poured off to a Petri dish; live amoebae and empty tests were distinguished and counted separately in one-tenth field of vision of stereomicroscope MBS–9 (Russia) at a magnification of ×60. The amounts of cells obtained were evaluated to 1 gram of absolute dry sphagnum weight. If necessary, the tests were transferred, with the help of a thin pipette, to an object-plate, placed in a drop of glycerin and investigated at a magnification of ×150 or ×300 with the use of BIOMED–2 microscope (Russia).

Active diversity was estimated on the basis of live testate amoebae numbers. For assessment of total diversity, empty tests were also counted. Always present in testate amoebae assemblages because of their resistance to decay, empty tests reflect the integral pool of species living in a biotope (Bobrov, 2003a).

Separate counting of live organisms and empty tests allows a twofold description of communities. Taking into account only live organisms, we can estimate the characteristics of community structure at the moment of sampling. Calculation of total testate amoebae abundance (including empty tests) gives an adequate representation of full species composition of habitat (total diversity). Involvement of the “passive” part of the assemblage allows one to avoid laborious seasonal studies aimed at revealing rare species and to obtain exact data from a single sampling (Rakhleeva and Korganova, 2005).

Data on the abundance of live organisms were used only for analysis of seasonal changes.

**DATA ANALYSIS**

Investigation of species composition and distribution of species. For estimation of reliability of distinctions between species richness in different assemblages, Mann-Whitney test with Bonferroni correction was used. A hierarchical cluster analysis, based on the average distance between all members in two groups with the Raup-Crick index as a similarity measure for presence-absence data, and principal components analysis (PCA) were used for community classification. PCA was also performed to reveal a pattern of species distribution.

Investigation of community structure. For community classification a principal component analysis was performed separately for relative species abundance data (which allows one to take into account only structural differences) and for species abundance data transformed on average (which allows one to consider only trends of changing species abundance in different communities). To explain possible relationships between the moss dwelling testate amoebae fauna and the measured environmental variables (moisture, pH and habitat type), Spearman correlation coefficient was calculated between values of environmental variables and factor scores.

Investigation of microspatial horizontal distribution. Aggregation degree of the organisms’ spatial distribution was estimated with the help of Casy index:

\[ C = \left( S^2 - M \right) / M^2, \]

where \( M \) is average abundance of a given species in all the samples in the scale, \( S^2 \) is dispersion. Use of this index allows one to reveal the character of the organisms’ spatial distribution: if \( C = 0 \), distribution is random, if \( C < 0 \), distribution is regular, if \( C > 0 \), distribution is aggregated.

To estimate the homogeneity level of the species
Table 2. List and occurrence of testate amoebae species in Bezimyanoe sphagnum bog.
Occurrence higher than 0.5 is in bold type

<table>
<thead>
<tr>
<th>Testate amoebae taxon</th>
<th>Stations</th>
<th>Occurrence in base of leaves</th>
<th>Occurrence in bottom and peat sediments</th>
</tr>
</thead>
<tbody>
<tr>
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<td><em>D. juzepehiniensis</em> Dekhtyar, 1993</td>
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<td><em>D. urceolata</em> Carter, 1864</td>
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<td><em>H. papillo</em> Leidy, 1879</td>
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<td><em>Nebelidae</em> Taranek, 1882</td>
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<td><em>E. seminulum</em> Ehrenberg, 1848</td>
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<td><em>E. e. decorata</em> Jung, 1942</td>
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<td><em>E. filifera</em> Penard, 1890</td>
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<td><em>E. laevis</em> Perty, 1849</td>
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<td><em>E. s. heterospermo</em> Walles, 1912</td>
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structure in the community, average Pianka similarity index was calculated between all pairs of samples separately for each scale. To reveal the level of species connectedness between all pairs of samples, we computed average Pianka similarity index between all species pairs according to their spatial distribution.

Investigation of vertical structure. For community ordination and classification we used the principal component analysis of relative abundance data, which allows one to take into account only structural differences, and the hierarchical cluster analysis, which is based on the average distance between all members in two groups with the Morisita as a similarity measure. Principal component analysis for species abundance data transformed to average (which allows one to consider only trends of changing species abundance in different sphagnum zones) was performed for revealing species groups with a similar character of vertical distribution. To compare integral parameters of local communities, we applied Mann-Whitney test with Bonferroni correction.

Investigation of seasonal dynamics. Ordination of local community variants by means of correspondence analysis of data on relative species abundance (which allows one to take into account only the structural aspect of community differences) was used for description of species structure changes. Indices of significance of temporal gradient presence (P), degree of structural heterogeneity of seasonal changes of species structure (S), degree of gradient of seasonal changes of species structure (B), degree of discreteness of seasonal changes of species structure \((D/D_r)\), which characterize structure of similarity matrices ordered along time gradient (Pielou, 1983; Azovsky, 1993), were calculated for description of the seasonal changes of community structure. The methods of calculating these indices are described in more detail in the Results section, alongside with the corresponding data, and in works of Pielou (1983) and Azovsky (1993).

Statistical analysis was carried out using software package PAST1.18 (Hammer et al., 2001), ECOS 1.3 (Azovsky, 1993) and STATISTICA 5.5A (StatSoft, 1999). In the present paper the system of eukaryotes offered by the international committee (Adl et al., 2005) is accepted.

Results

Species composition and distribution of testate amoebae

The microscopic analysis of 46 samples (the first kind of samples from detritus and subsoil water) from the bog investigated revealed 63 testate amoebae taxa (species, varieties and forms), belonging to 21 genera and 13 families (Table 2). The highest species diversity was in the genera *Arcella* (14 species), *Difflugia* (8), *Euglypha* (7), *Centropyxis* (6). The most common species were *Centropyxis aculeata* (occurred in 80% of samples), *Hyalosphenia elegans* (78%), *Trinema lineare* (76%), *Nebela tenella* (74%), *Hyalosphenia papilio* (74%), *Euglypha laevis* (72%) and *Assulina muscorum* (70%).

The average number of taxa per sample varied from 8 to 24 species, detritus samples contained on the average fewer species (Fig. 3) than sphagnum ones (the differences are statistically significant, Mann-Whitney test with Bonferroni correction; \(P < 0.05\)). The maximal number of species revealed during the vegetation season was at the station 6 (39 species). The species richness on other stations varied from 24 to 29 species (Fig. 4). The margin of
the quagmire seems to be, to a certain extent, an ecotone including both detritophilous and sphagnumophilous species.

In fact, the classification of testate amoebae assemblages based on species composition indicates the presence of three community variants: sphagnumophilous assemblage (forming at stations 1–5), detritophilous assemblage (station 7) and transitional assemblage (station 6) (Fig. 5). It is interesting that the same procedure based on species abundance (Fig. 6) showed, besides the above-mentioned results, some differences among sphagnumophilous communities. On the one hand, there were assemblages forming at the centre of the bog and in the middle zone in hummocks (stations 1, 2 and 4), on the other hand, there were assemblages forming at the periphery of the quagmire and in the middle zone in the hollow (stations 3 and 5).

Reliability of distinctions between the four distinguished variants of communities was estimated with the aid of the discriminant analysis (Table 3). Significant distinctions are noted only between station 7 and all the others. All other variants represent, as a matter of fact, a single community type.

PCA confirmed the classification revealed by the cluster analysis (Fig. 7). It was found that 70% of the total community variance was determined by differences between pair communities forming at stations 6 and 7 and the communities at other stations. Along
the second PCA-axis (which accounted for only 11% of variance), communities of moist sphagnum (stations 3 and 5), communities of dry sphagnum (stations 1, 2 and 4) and communities influenced by drain (stations 1 and 3) are distinguished.

On the basis of the PCA results (Fig. 7) it is possible to differentiate the following groups of species. Detritophilous group (occurs in assemblage of sward margin and bottom sediments of drain – stations 6 and 7) is represented by Arcella gibbosa, A. vulgaris, A. hemisphaerica, A. discoides, A. intermedia, A. mirata, Centropyxis aculeata sphagnicola, Cyclopyxis kahlil, Diffugia glans, Lesquereusia spiralis, Netzelia tuberculata, Phryganella hemisphaerica. Stenotopic sphagnophilous species (inhabiting typical sphagnum biotope only, stations 1–5) are Archerella flavum, Euglypha cristata, Diffugia juzepehiniensis, Cryptodifflugia compressa, Sphenoderia fissirostris, Nebela militaris. Eurytopic sphagnophilous species (inhabiting both typical sphagnum biotope and quagmire margin, stations 1–6) are Nebela tenella, N. tincta, Euglypha ciliata, Bullinularia indica, Assulina seminulum, A. muscorum, Hyalosphenia elegans, Diffugia globulosa, D. parva, Centropyxis aculeata. Eurytopic species (occurring in all biotopes, stations 1–7) are Arcella arenaria, Euglypha laevis, Trigonopyxis arcula, Hyalosphenia papilio, Trinema complanatum.

PCA of species from sphagnum biotopes only (Fig. 8) revealed the following groups of species: (i) typical sphagnobiont species with high occurrence within the quagmire (Hyalosphenia elegans, H. papilio, Assulina muscorum, A. seminulum, Nebela tenella, N. tincta, Euglypha laevis, E. ciliata, Trinema complanatum).
lineare, T. complanatum, Bullinularia indica, Centropyxis aculeata, Diffugia globulosa, D. parva), (ii) species characteristic of moist peripheral parts of the quagmire (Archerella flavum, Euglypha cristata, Arcella artocea pseudocatinus, Diffugia juzepehiniensis, Heleopera sphagni), (iii) species characteristic of dry parts at the centre of the quagmire (Arcella arenaria, Cryptodifflugia compressa, Corythion dubium, Nebela militaris) and (iv) rare species. It is interesting that only 14% of all the variance in the community composition was associated with differences of communities from moist peripheral biotopes and from the dry central ones. More than 70% of variance resulted from the features of distribution of the most frequently revealed species and rare species with accidental distribution within the bog. Thus, on the whole, the testate amoebae assemblage from typical sphagnum biotopes appears rather homogeneous on species composition.

The degree of heterogeneity of species composition at the scale of the whole bog was unequal during the vegetation season. The maximal homogeneity of the community was noted during the moistest period in spring; the minimal one, during the driest period in August (Fig. 9). The following patterns of species composition were revealed. In May communities of dry habitats (stations 1, 2 and 4) were most similar among themselves and in moist biotopes three different variants of communities formed (Fig. 10, A). In August (Fig. 10, B), communities of the bog margin (stations 6 and 7) had clear-cut distinctions, communities from sphagnum hummock (stations 2 and

Fig. 8. PCA-ordination scatterplot based on species abundance (only sphagnum stations 1–5). PC 1 – first principal component accounting for 77.2 % of the total community variance, PC 2 – second principal component accounting for 14.0 % of the total community variance.
in moist biotopes some differences in species composition were present. On the contrary, in dry period the communities from the moist habitat were characterized by common species composition, while in dry biotopes it was specific.

**Mesoscale horizontal distribution**

The microscopic analysis of 134 samples (the second kind of samples from sphagnum stems) from the biotopes investigated revealed 55 testate amoebae taxa (species, varieties and forms), though only 46 taxa were alive at the moment of sampling.

**Total diversity of community.** Twelve species were structure-formative, with abundance more than 2% at least at one station on the average for a season (Table 4). The ordination of local community variants forming at different stations (Fig. 11) revealed that 55% of the total community structure variance was accounted for by differences of assemblages from hummocks (stations 2 and 4) and the other assemblages. Factor scores along 1 PC are positively correlated with the depth of water table (DWT) (Spearman correlation coefficient, P<0.1). The correlation is prominent if we use for calculation minimal DWT values at a station for season than if we use average or maximal ones. The second PC (accounting for 24% of the total community structure variance) resulted from differences of assemblage from the edge of the quagmire (station 6) and corresponded to pH of the samples (Spearman correlation coefficient, P<0.1). The third PC related to 17% of the total variance in the testate amoebae data and reflected differences of assemblages forming at hummock stations 2 and 4.

Basing on the data from Table 4 and the results of ordination (Fig. 11) it is possible to distinguish three types of testate amoebae communities within the sphagnum quagmire: (i) xerophilous assemblage *Assulina muscorum*–*A. seminulum*–*Cryptodifflugia compressa*; (ii) hygrophilous assemblage *Hyalosphenia papilio*–*Heleopera sphagni*–*Nebela tenella*; and (iii) hydrophilous assemblage *Cyclopyxis eurystoma*–*Phryganella hemisphaerica*–*Heleopera sphagni*–*Hyalosphenia papilio*.

The ordination of species abundance data transformed on average (which allows one to consider only trends of changing of abundances and not their absolute value) revealed that more than 60% of differences of total variance was accounted for by the features of distribution of hydrophilous species on the one hand (*Arcella gibbos, A. arenaria, A. intermedia, Cyclopyxis eurystoma, Phryganella hemisphaerica*) and xero- and hygrophilous species
on the other hand. More than 20% of the total variance related to distribution of xerophilous species (*Cryptodiffugia compressa*, *Centropyxis aerophila sphagnicola*) and hygrophilous species (*Heleopera sphagni*, *Hyalosphenia papilio*, *H. elegans*, *Nebela tenella*, *N. tincta*, *Euglypha ciliata*, *Centropyxis aculeata*, *Archerella flavum*). Ten percent of the total variance was caused by the domination of different xerophilous species in various hummocks. Thus, testate amoebae communities in moist sphagnum biotopes were quite homogenous, while in dry habitats (hummock) they were more differentiated. The most specific assemblage formed at the edge of the sphagnum quagmire.

The maximal number of testate amoebae taxa per season was revealed in submerged sphagnum from station 6, while the minimal one was in hummocks from stations 2 and 4 (Table 4). The mean number of taxa per sample in communities within moist biotopes (stations 1, 3, 5 and 6) was approximately at the same level. It is an evidence of great seasonal variability of species composition in the assemblage at the edge of the sphagnum quagmire. Abundance of testate amoebae was higher in moist biotopes (sta-


Active diversity of community. If we take into account only live individuals, 16 species were structure-formative (Table 5). The share of live organisms was minimal in dry biotopes (22–27%), while in moist habitats it was noticeably higher and reached 36–46% (Table 5).

The ordination of local community variants at different stations with the use of active diversity revealed the same types of communities as those obtained by total diversity analysis (Fig. 12). However, more than 60% of the total community structure variance was caused by differences between the community forming at the edge of the sphagnum quagmire (station 6) and the communities at sphagnum lawn (stations 1, 3, 5) and hummocks (stations 2, 4). Factor scores along 1 PC are positively correlated with DWT (Spearman correlation coefficient, P<0.1). The second PC (accounting for 30% of the total community structure variance) resulted from differences of the sphagnum lawn assemblages from the others. The third PC related to 15% of the total community variance in the testate amoebae data and reflected differences between assemblages forming at hummock stations 2 and 4.

Basing on the data from Table 2 and ordination results (Fig. 13), it is possible to differentiate the following types of sphagnum testate amoebae communities: (i) xerophilous assemblage with two variants a) Assulina muscorum–A. seminulum and b) Cryptodifflugia compressa; (ii) hygrophilous assemblage Heleopera sphagni–Nebela tenella–

Fig. 11. PCA-ordination diagram for communities based on relative species abundance (total diversity). 1 PC – 55.7%, 2 PC – 24.2%, 3PC – 16.7%.

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Table 5. Relative abundances (%) of dominant species of testate amoebae from sphagnum stems and integral community parameters (active diversity). Relative abundances higher than 10% are in bold

<table>
<thead>
<tr>
<th>Species</th>
<th>Stations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Arcella arenaria</td>
<td>0.1</td>
</tr>
<tr>
<td>A. intermedia</td>
<td>0.0</td>
</tr>
<tr>
<td>Archerella flavum</td>
<td>1.2</td>
</tr>
<tr>
<td>Assulina muscorum</td>
<td>0.8</td>
</tr>
<tr>
<td>A. seminulum</td>
<td>5.9</td>
</tr>
<tr>
<td>Centropyxis aerophila sphagnicola</td>
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<tr>
<td>Cryptodifflugia compressa</td>
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<tr>
<td>Cyclopyxis eurystoma</td>
<td>0.0</td>
</tr>
<tr>
<td>Euglypha ciliata</td>
<td>3.3</td>
</tr>
<tr>
<td>Heleopera sphagni</td>
<td>18.8</td>
</tr>
<tr>
<td>Hyalosphenia elegans</td>
<td>18.1</td>
</tr>
<tr>
<td>H. papilio</td>
<td>12.5</td>
</tr>
<tr>
<td>Nebela tenella</td>
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</tr>
<tr>
<td>N. tincta</td>
<td>5.9</td>
</tr>
<tr>
<td>Phryganella acropodia</td>
<td>0.0</td>
</tr>
<tr>
<td>Trigonopyxis arcula</td>
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<tr>
<td>Share of live organisms, %</td>
<td>46.3±18.9</td>
</tr>
<tr>
<td>Total species number</td>
<td>18</td>
</tr>
<tr>
<td>Average species number per sample</td>
<td>13.8±0.8</td>
</tr>
<tr>
<td>Average abundance per sample, thousand individuals per gram</td>
<td>29.1±7.5</td>
</tr>
<tr>
<td>Average Shannon-Wiever diversity index per sample</td>
<td>1.37±0.14</td>
</tr>
<tr>
<td>Average Pielou evenness measure per sample</td>
<td>0.59±0.04</td>
</tr>
</tbody>
</table>

**Hyalosphenia papilio–H. elegans; and (iii) hydrophilous assemblage Cyclopyxis eurystoma–Hyalosphenia papilio–Phryganella hemisphaerica.**

Ordination of abundance data of live organisms transformed on average (allowing one to consider only trends of changing of abundances and not their absolute value) gave the same results (Fig. 14) as in the case of total diversity (Fig. 12).

Distribution of integral community parameters, calculated from the active diversity, revealed some differences with those obtained from total diversity. Minimal species number per season was revealed in lawn (station 1) and in hummock (station 4). Maximal species diversity estimated by Shannon-Weaver diversity index was measured at the edge of the quagmire (station 6) and in hummock (station 4). Trends of abundance changing remained as in the case of total diversity.

**Microscale horizontal distribution**

General characteristics of testate amoebae community. A total of 13 testate amoebae species were identified in the course of investigation of microscale testate amoebae distribution within the macroscopically homogeneous Sphagnum angustifolium carpet (Table 6). At all stations Heleopera petricola dominated in the community, with Hyalosphenia papilio being subdominant. Other species were rare. Species abundance distribution was described by a geometrical model. It means that species diverged significant-
for one or more niche parameters, which decreased competition for resources in the local community (Burkovsky, 1992). Thus, the community analyzed at the sample scale (a single Sphagnum stem) could be considered as minimal, and the sample size as a minimum-area of the community (Bobrov, 2003b).

**Analysis of species aggregations.** Calculation of the aggregation index (Table 6) showed that the dominant species (*Heleopera petricola* and *Hyalosphenia papilio*) formed a feebly marked agglomeration. Degree of aggregation was quite low (Casy index did not exceed 1.0). On the whole, the aggregation index of different species did not exceed 3.3 (on the average, 0.92). All these facts point to an unvarying community structure at the scale investigated, corresponding to the physical homogeneity of the territory. Some species with low abundance had random distribution at some scale (*Euglypha ciliata* and *Bullinularia indica* at a scale of 192 cm, *Hyalosphenia elegans* at the scale of 3 and 9 cm). For some rare species regular distribution was noted (*E. ciliata* at a scale 9 cm, *B. indica* at a scale 1 cm, *H. elegans* at a scale 1 cm and 81 cm). Distribution of *Nebela tenella* was the most aggregated, whereas that of *Hyalosphenia elegans* was close to random.

Spatial distribution patterns changed according to the investigation scale. Observing changes in aggregation index for separate species with increasing scale, it is possible to estimate the size and intensity of the corresponding agglomerations (Fig. 15). Their size appears to be species-specific. For instance, for two dominate species the opposite dynamic was revealed (Fig. 15). Distribution of *H. petricola* at a scale up to 81 cm was close to random, but at a maximal scale it became aggregated; the situation was *vice versa* for subdominant *H. papilio*. The opposite tendencies were also noted for the two congeners *Assulina muscorum* and *A. seminulum*. At the same time, these

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**Fig. 12.** PCA-ordination diagram for species, data transformed on average species abundance (total diversity). 1 PC – 62.2 %, 2 PC – 21.4 %, 3 PC – 10.7 %.
species, like some others, formed agglomerations of different size: *A. muscorum* at a scale of 1 cm and 81 cm, *A. seminulum*, 9 cm and 192 cm. It is interesting that the size of agglomerations of these species correlated positively with shell size: the smaller species *A. muscorum* (shell length 35–55 µm) had smaller agglomerations than the bigger species *A. seminulum* (shell length 70–95 µm).

On the average, in most species the aggregation level of distribution grew with increasing of the investigation scale (Fig. 16). At the same time, dispersion of species’ aggregation level in the community was maximal at the maximal scale (Fig. 17). In other words, the community at the maximal scale is formed by species with different level of patchiness. Minimal dispersion of aggregation level of different species was registered at the middle scale (27 cm).

**Changes of integral community characteristics.**

Heterogeneity of testate amoebae populations was revealed not only at the species level but also at the level of integral community parameters. So, the average species number in the community and the degree of its variability changed according to the investigation scales (Fig. 18). The species number, however, changed slightly. It is well known that the number of species revealed increases with increasing investigation area (Hillebrandt et al., 2001). Hence we could expect a greater species number at a scale of 192 cm than at a smaller one. However, no distinctions in species number at different investigations scales were revealed. At each investigation scale, 10–12 species were identified.

The average similarity of spatial distribution of species remained the same at different scales (Fig. 19). Average Pianka similarity index changed slightly, decreasing a little at a greater scale, but all the differences were not significant. Maximal homogeneity of the
Fig. 14. PCA-ordination diagram for species, data transformed on average species abundance (active diversity). 1 PC – 64.7 %, 2 PC – 19.0 %, 3 PC – 9.9 %.

Table 6. Species composition, relative species abundances (%) and character of microspatial distribution of species in community

<table>
<thead>
<tr>
<th>Species</th>
<th>%</th>
<th>Average for all scales Casy aggregation index</th>
<th>Variation coefficient for Casy index, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arcella arenaria sphagnicola</td>
<td>0.19</td>
<td>1.56</td>
<td>69.7</td>
</tr>
<tr>
<td>Arcella artoorea</td>
<td>0.38</td>
<td>1.48</td>
<td>68.9</td>
</tr>
<tr>
<td>Assulina muscorum</td>
<td>1.24</td>
<td>0.79</td>
<td>49.0</td>
</tr>
<tr>
<td>A. seminulum</td>
<td>1.37</td>
<td>0.68</td>
<td>55.7</td>
</tr>
<tr>
<td>Bullinularia indica</td>
<td>0.06</td>
<td>0.24</td>
<td>258.2</td>
</tr>
<tr>
<td>Euglypha ciliata</td>
<td>0.55</td>
<td>0.75</td>
<td>140.9</td>
</tr>
<tr>
<td>E. laevis</td>
<td>0.02</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Heleopera petricola</td>
<td>86.46</td>
<td>0.37</td>
<td>65.6</td>
</tr>
<tr>
<td>Hyalosphenia elegans</td>
<td>0.07</td>
<td>0.05</td>
<td>1809.4</td>
</tr>
<tr>
<td>H. papilio</td>
<td>9.51</td>
<td>0.68</td>
<td>36.4</td>
</tr>
<tr>
<td>Nebela tenella</td>
<td>0.15</td>
<td>2.48</td>
<td>37.3</td>
</tr>
<tr>
<td>N. tincta</td>
<td>0.01</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Zivkovicia compressa</td>
<td>0.002</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Fig. 15. Change in Casy aggregation index with increasing distance between samples for dominant species. Whiskers are error of mean.

Fig. 16. Change in average Casy aggregation index for all species with increasing distance between samples. Whiskers are error of mean.

Fig. 17. Change in variation coefficient of Casy aggregation index for different species with increasing distance between samples.

Fig. 18. Change in average organisms' density at various investigation scales. Whiskers are error of mean.

Fig. 19. Change in average Pianka similarity index between all pairs of species based on their distribution according to investigation scales. Whiskers are error of mean.
Changes in species structure of alive amoebae. On the basis of the species structure, three community variants were distinguished in the moistest biotope (submerged Sphagnum riparium at station 6) (Fig. 21). More than 80% of the total variance in the testate amoebae data was associated with differences between the lowest zone (15–35 cm with domination of Arcella intermedia, A. gibbosa, A. hemisphaerica) and the upper ones. A little more than 10% of the total community structure variance is accounted for by variations in the structure of upper layers. Hyalosphenia papilio and Phryganella hemisphaerica dominated in the top 0–3 cm, H. papilio and Cyclopyxis eurystoma at a depth of 3–6 cm, H. papilio, C. eurystoma, Hyalosphenia elegans at 6–15 cm. Ordination of the abundance data transformed on average for live organisms (allowing one to consider only trends of changing of abundances and not their absolute value) gave the same results (Fig. 22). In spite of the fact that most species occurred at all levels, they had more or less pronounced preferences. For instance, Ph. hemisphaerica preferred the upper three centimeters of sphagnum, A. gibbosa, A. intermedia, A. megastoma the lower 15–35 cm, and H. sphagni 6–15 cm down the sphagnum plant.

In the community at station 5 located in flat sphagnum quagmire with domination of Sphagnum magellanicum and S. palustre, four variants were found (Fig. 23). More than 80% of the total community structure variance resulted from differences between the upper zone (0–3 cm, dominant complex contained Hyalosphenia papilio and Heleopera sphagni) and the underlying zones. H. sphagni, H. elegans, Nebela tenella dominated at 3–6 cm, N. tenella and H. elegans at 6–20 cm, N. tenella and Difflugia juzephiniensis at 20–30 cm. The results of species ordination (Fig. 24) indicate that Archerella flavum, H. papilio, H. sphagni prefer the upper layer, D. juzephiniensis, the deepest part, H. elegans and N. tincta, section 3–20 cm, and N. tenella, 6–30 cm below the surface.

In the community at station 3 located in Sphagnum palustre lawn in the middle of the bog three variants are revealed (Fig. 25). The community of the upper zone (0–3 cm), with domination of H. sphagni and H. papilio, differed from the underlying one (3–6 cm), where H. papilio and N. tenella prevailed. In the lower layer (6–20 cm) N. tenella dominated (over 50% of total abundance). The results of species ordination (Fig. 26) show the presence of well-defined preferences of the dominant species to certain layers. H. sphagni was strongly associated with 0–3 cm, H. papilio with 0–6 cm, N. tincta and H. elegans with 6–9 cm, N. tenella with 6–20 cm, D. juzephiniensis with 12–20 cm horizon.

In the community at station 1 located in the centre part of the bog in Sphagnum palustre lawn, three variants were found (Fig. 27). H. sphagni and H. papilio dominated in the 0–3 cm zone, H. elegans and N. tenella in 3–9 cm, N. tenella in 9–20 cm zone. The results of species ordination (Fig. 28) evidence that H. papilio and H. sphagni prefer the upper 0–3 cm, N. tincta the 6–12 cm layer and N. tenella the 9–20 cm layer.

In the community at station 4 (hummock formed by Sphagnum papillosum) two variants could be distinguished (Fig. 29). One of them was confined to the upper 0–9 cm horizon, where Assulina muscorum and A. seminulum dominated. The other was confined to the lower 9–20 cm level with domination of N. tenella. Besides these local communities, there was a transitional one with a specific complex of subdominant species (N. tincta, Bullinularia indica, Centropyxis aerophila sphagnicola, Cyclopyxis eurystoma) in the 3–6 cm and 6–9 cm zones. The results of species ordination (Fig. 30) indicate that A. muscorum and A. seminulum prefer the 0–9 cm zone, C. eurystoma 3–6 cm, B. indica and C. a. sphagnicola 6–9 cm, N. tenella, H. elegans, E. ciliata 9–20 cm zone.

In the hummock community formed by Sphagnum angustifolium and Polytrichum strictum (station 2) three variants were revealed (Fig. 31). In the top 0–3 cm H. papilio, Archerella flavum, Euglypha laevis dominated. In the lower part Cryptodifflugia compressa prevailed, and in 6–9 cm H. elegans joined it. The results of species ordination (Fig. 32) show that H. papilio, A. flavum, E. laevis, H. sphagni prefer the top 0–3 cm, N. tincta, E. ciliata, A. seminulum 3–6 cm and decreased at the maximal scale (Fig. 20).

**Microscale vertical distribution**

Fig. 20. Change in average Pianka similarity index between all pairs of local communities (homogeneity of community structure) according to investigation scale. Whiskers are error of mean.
Fig. 21. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species (more than 5% of total abundance at least at one horizon). 1 PC – 82.5 %, 2 PC – 11.3 %. Station 6.
cm, *H. elegans* 6–9 cm, *N. tenella* and *C. compressa* 9–20 cm below the surface.

**Changes in integral community parameters.** Integral community parameters changed along the vertical gradient in the sphagnum carpet (Fig. 33). In the upper zones species number and species diversity were lower, but the abundance of organisms was higher than in the others. However, only the differences between species number and species diversity at 0–3 cm and 6–20 cm layers were significant (Mann-Whitney test).

Ratio live organisms to empty tests changed with depth (Fig. 33). In the upper zone the share of live organisms was much higher than in the lower one. In the moistest biotopes (stations 1, 3, 5 and 6) the share of live organisms in the top layer was 65–75%, whereas in dry hummocks (stations 2 and 4) it was 30–40%.

The degree of total heterogeneity varied in communities at different stations (Fig. 34). The most heterogeneous communities in terms of vertical structure are formed in dry conditions, but the differences were not significant in all the cases. It is interesting that the degree of heterogeneity of local communities forming under various conditions (different stations) within the bog was more different in comparison with those in various vertical zones (Fig. 35). The community was the most homogenous when the upper and the low horizons were compared, and each variant was the most specific when the middle layers (3–9 cm) were compared. However, the differences were not statistically significant in this case, too.

**Seasonal dynamics**

**Seasonal changes in environmental variables.** During the study period the temperature and acidity changed cyclically (maximal values in July and
Fig. 23. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species. 1 PC – 85.5 %, 2 PC – 11.8 %. Station 5.
August) and the redox-potential and electro-conductivity had directional changes (Fig. 36). Redox-potential (Eh) decreased towards the end of season, while electro-conductivity grew at the same time, which might have been caused by accumulation of mineral ions and organic matter. The depth to water table remained at the same level, with the exception of stations 2 and 4 (hummocks), where this parameter was minimal at the end of summer.

Changes in integral community parameters during the study season. Species number increased during the vegetation season, while species diversity and evenness remained at the same level with insignificant fluctuations (Fig. 37). Changes in the average organisms’ abundance in the community at all stations did not show any directional tendencies, but had fluctuations (Fig. 38). Analyses of seasonal changes in species abundance in the communities at different stations revealed three types of dynamics (Fig. 38), which were not associated with the community type (community of hydro-, hygro- and xerophilous species). The first type (stations 2 and 3) was characterized by low values of species abundance in May–June and high values in July–September. The second type was distinguished by high numbers in the beginning of the season (May–June at stations 1, 5 and May at station 6). The third type was defined by the absence of clear tendencies in abundance dynamics at station 4.

Spatial differentiation of the community at the scale of the bog also changed during the season. The average value of similarity index between all pairs of local communities can give a general idea about the heterogeneity level (Fig. 39). Heterogeneity remained at the same level during all the season. The least value of heterogeneity was marked in August when tem-

![PCA-ordination diagram for dominant species based on data transformed on average species abundance. 1 PC – 68.8%, 2 PC – 24.8%. Station 5.](image-url)
Fig. 25. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species. 1 PC = 87.1 %, 2 PC = 9.8 %. Station 3.
temperature was maximal and moisture was minimal. The highest heterogeneity value was in September. However, all distinctions were statistically insignificant.

Correspondence analyses revealed the following features of community heterogeneity at the scale of the whole bog in different months (Fig. 40). In May the most specific structure was formed in hummocks (Assulina muscorum dominated at station 4 and Heleopera sphagni at station 2), while Hyalosphenia papilio prevailed at all other stations. In June four structural variants of communities formed: A. muscorum, Euglypha ciliata, Nebela tenella dominated at station 4, Nebela tincta at station 2, H. papilio, Arcella arenaria, Archerella flavum at station 6, H. sphagni and H. papilio at stations 1, 3, and 5. In July and August an identical situation was recorded, communities were revealed at station 6 (with the characteristic species complex of Phryganella hemisphaerica and Arcella intermedia), at station 4 (Assulina seminulum and A. muscorum were leaders) and at station 1, 2, 3, 4, 5 (with species N. tenella, N. tincta, H. sphagni, Hyalosphenia elegans). In September the dominant species were Arcella arenaria, Centrocyxis aculeata, C. platystoma at station 6, Cryptodifflugia compressa at station 2, C. compressa, A. muscorum, A. seminulum, Trigonopyxis arcula at station 4, N. tenella, H. sphagni, H. elegans at station 1, 3 and 5.

Changes in species structure of community during the season studied at different stations. Seasonal changes in testate amoebae community at different stations had some particular characteristics. Integral community parameters are represented in Table 7. The presence of directional changes in community structure was noted at stations located at the edge of Sphagnum sward only (stations 5 and

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Sp. 26. PCA-ordination diagram for dominant species based on data transformed on average species abundance. 1 PC – 65.0%, 2 PC – 27.0%. Station 3.
Fig. 27. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species. 1 PC – 87.6 %, 2 PC – 10.8 %. Station 1.
6). Total value of seasonal changes (the degree of structural heterogeneity of community S) could be estimated as the average Pianka similarity index between all pairs of seasonal states of community. The less this parameter, the higher structural heterogeneity of seasonal changes. It turned out that heterogeneity level was almost equal in communities at all stations (with the exception of station 2, where it was high). Figure 28. PCA-ordination diagram for dominant species based on data transformed on average species abundance. 1 PC – 88.0 %, 2 PC – 8.1 %. Station 1.

<table>
<thead>
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<td></td>
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<td>6</td>
</tr>
<tr>
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<td>-0.42</td>
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<td>D_1/D_2</td>
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<td>1.74</td>
<td>1.23</td>
<td>0.18</td>
<td>0.55</td>
<td>1.49</td>
</tr>
</tbody>
</table>

Fig. 29. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species. 1 PC – 86.2 %, 2 PC – 9.6 %. Station 4.
Changes in community structure in time could be divided into two components. The first is the heterogeneity associated with the background patchiness of species distribution (average differences between contiguous seasonal states of communities). The second one is the heterogeneity revealed in directed changes in community structure. The greater the contribution of the last component, the more different are the communities separated by increasing time intervals. The quantitative measure of this component is the coefficient of linear regression "similarity index vs. distance between samples" taken with the opposite sign. This value (degree of gradient) shows how much the similarity between seasonal states of community decreases with the increasing time interval between them. Significant directed seasonal changes were noted at station 5 and an unimportant one in the community at station 1. The maximal level of gradient in the community at station 5 indicated that the species composition changed completely during the study season. Seasonal changes in communities at other stations are more likely to reflect the fact of recombination of constant species composition. Finally, an important indicator of seasonal changes' character is the measure of discreetness of changes. It could be estimated by comparing dispersion of similarity indices between contiguous seasonal states of the community ($D_1$) with the total dispersion of all the possible values of pairwise similarity ($D_2$). Ratio $D_1/D_2$, close to zero indicates continuous transitions between community states, that close to one is a sign of presence of some positions which are strongly different in species structure, and if this parameter is greater than 1 then succession consists of numerous states with distinct differences from each other. It turned out that the most continuous changes were in the communities at stations 4 and 5. In the communities...
Fig. 31. Results of community classification and ordination by cluster and principal component analyses (PCA) based on relative abundance of dominant species. 1 PC – 71.9 %, 2 PC – 17.0 %. Station 2.
at other stations a high level of seasonal changes was revealed.

The results of correspondence analyses of seasonal variants of the community at different stations are represented in Fig. 41. In the hydrophilous community at station 6 (Fig. 41, A) nine species were structure-formative (i.e. formed more than 10% of the total abundance at least in one of the seasonal community states); at the same time, from two to four species only dominated in each seasonal structure. *H. papilio* and *Arcella catinus* prevailed in May, *H. papilio* and *Archerella flavum* in June, *Phryganella hemisphaerica* and *Arcella intermedia* in July and August, *Centropyxis platystoma*, *C. aculeata*, *Arcella gibbosa* in September.

In the hydrophilous community at station 5 (Fig. 41, B) only four species were structure-formative. *H. papilio* dominated in May, *Heleopera sphagni* and *Hyalosphenia elegans* in June and July, *Nebela tenella* in August and September.

In the hydrophilous community at station 3 (Fig. 41, C) six species were structure-formative. *H. papilio* and *Arcella catinus* prevailed in May, *H. papilio* and *H. sphagni* in June, *N. tincta*, *H. sphagni*, *N. tenella* and *H. elegans* in the other months.

In the hydrophilous community at station 1 (Fig. 41, D) six species were structure-formative, too. *H. sphagni*, *H. papilio* and *N. tincta* dominated in June, *N. tenella* and *Assulina seminulum* in July and August, *N. tenella* and *H. elegans* in September.

In the xerophilous community at station 4 (Fig. 41, E) ten species were structure-formative. *N. tenella*, *Assulina muscorum*, *A. seminulum* and *Euglypha ciliata* dominated during all season. Specific character of the seasonal states was determined mainly by subdominants. *C. eurystoma* and *N. tincta* formed
subdominant complex in May, *H. elegans* in June, *Trinema lineare* in July. In September specific species composition was organized by *Cryptodifflugia compressa* as a leader and *Trigonopyxis arcula* as a subdominant.

In the xerophilous community at station 2 (Fig. 41, F) nine species formed the community structure. *H. papilio, H. sphagni, N. tincta, A. flavum, E. ciliate* prevailed in May and June, *N. tenella, H. elegans, A. seminulum* in July, *C. compressa* formed more than 80% of total abundance in September.

**Abundance dynamics of dominant species.** Seasonal dynamics of the characteristics of abundance of live organisms and empty tests of some dominant species is represented in Fig. 42. Abundance of live *H. papilio* individuals was maximal in May and significantly decreased to the middle of summer, remaining at a low level until
autumn. At the same time, the share of empty tests increased in the second part of summer. The opposite tendencies were revealed in abundance dynamics of a closely related species *H. elegans*: minimal numbers of live individuals were observed in May, then the numbers increased in June and remained at the same level until September. However, the share of empty tests increased in the second half of summer, too. These opposite tendencies were especially prominent when relative abundances in the community were counted (Fig. 43). *H. papilio* prevailed in the community in May, while *H. elegans* from July to September.

Abundance of live organisms of *N. tincta* remained at the same level during all summer, while the numbers of a closely related species *N. tenella* increased in the second half of the study period (Fig. 42). The share of empty tests of the latter species was lower than that of the former. The opposite tendencies in these closely related species are revealed even more clearly when only relative abundances are taken into account (Fig. 43). The role of *N. tincta* was significant in spring and early summer, but after that *N. tenella* dominated.

Abundance of live organisms of *A. muscorum* remained approximately at the same level and the numbers of *A. seminulum* increased slightly in July and August (Fig. 42). It is interesting that these xerophilous species, which dominate in communities in sphagnum hummocks, had a higher share of empty tests than hydro- and hygrophilous species. These two species, similarly to the previous pairs of closely related species, obviously showed the opposite tendencies in seasonal dynamics. Only in one of the communities where these species were represented in significant numbers *A. muscorum* dominated in spring and the beginning of summer and *A. seminulum* prevailed in the end of summer and in autumn.
Species composition and distribution of testate amoebae

Most of the species typical of the bog investigated were common in other sphagnum bogs, too (Gilbert and Mitchell, 2006): Assulina muscorum, A. seminulum, Nebela tincta, N. militaris, Corythion dubium, Hyalosphenia papilio, H. elegans, Euglypha laevis, E. ciliata, Archerella flavum, Bullinularia indica, Arcella arenaria, Heleopera sphagni, Trigonopyxis arcula, Trinema lineare, Difflugia juzephiensis. At the same time, some species common in other bogs (Phryganella acropodia, Euglypha compressa, E. strigosa, Physochila griseola, Heleopera petricola, H. rosea) were absent or very rare in Bezimyanoe bog. However, some species not typical of sphagnum bogs were characteristic of the bog investigated (Centropyxis aculeata, Difflugia globulosa, D. parva, Sphenoderia fissirostris).

The clearest distinctions in species composition of testate amoebae community, which permit one to distinguish two types of assemblages in one bog, are accounted for by two different biotopes, the bottom sediments in drain and the peat deposits in quagmire. These distinctions are explained by the presence of poor-rich gradient, which was mentioned in earlier works (Schönborn, 1966; Chardez, 1967) and whose importance for formation of testate amoebae community structure was recently emphasized (Opravilová and Hájek, 2006). The differences in taxonomical composition are apparent already at the family level (Fig. 44). So, species of the families Arcellidae, Phryganellidae and Lesquereusiidae were characteristic of the quagmire margin, species of the family Cryptodifflugiidae

Discussion

Species composition and distribution of testate amoebae

Most of the species typical of the bog investigated were common in other sphagnum bogs, too (Gilbert and Mitchell, 2006): Assulina muscorum, A. seminulum, Nebela tincta, N. militaris, Corythion dubium, Hyalosphenia papilio, H. elegans, Euglypha

Fig. 38. Changes in abundance of the individuals in the communities during the study period. Whiskers are error of mean.

Fig. 39. Changes in heterogeneity of communities at the scale of whole bog during the study season. Whiskers are error of mean.
Fig. 40. Spatial structure of testate amoebae community at the scale of whole bog in different months. May: axis 1 – 47.8%, axis 2 – 29.9%. June: 44.7%, 18.5%. July: 36.1%, 23.1%. August: 43.1%, 30.0%. September: 20.0%, 10.0%.
Fig. 41. Results of ordination of seasonal stages of community at different stations. A – station 6 axis 1 – 60.7%, axis 2 – 14.2%; B – station 5: 56.9%, 32.3%; C – station 3: 41.8%, 31.2%; D – station 1: 61.1%, 43.7%; E – station 4: 47.1%, 18.2%; F – station 2: 62.4%, 24.6%
had high abundance in dry sphagnum biotopes, species of the families Heleoperidae and Amphitremidae were frequently revealed in moist sphagnum habitats and species of the families Difflugiidae, Hyalospheniidae, Nebelidae, Euglyphidae, Plagiopyxidae (Bullimalaria) were found in all biotopes within the bog investigated. On the whole, the results obtained confirm the earlier one (Opravilová and Hájek, 2006), with the exception of domination within the quagmire of species from the family Difflugiidae, which are in general characteristic of detritus biotopes (Mazei and Tsyganov, 2006a, 2006b).

The above features (domination of Centropyxis aculeata and Difflugiidae species) reflect some characteristics of the ecosystem investigated, associated with intensive restoration processes in sphagnum carpet. Thus, the presence of significant amount of the above listed testate amoebae taxa could indicate the disturbed state of the sphagnum bog ecosystem.

It is interesting that the influence of moisture of
sphagnum biotopes, which is the main determinant factor of species structure of testate amoebae communities (Charman and Warner, 1992, 1997; Bobrov et al., 2002; Booth, 2002; Mitchell, 2004; Lamentowitcz and Mitchell, 2005), in our case was less important. So, only 14% of all differences in the species distribution were accounted for by the depth to water table (Fig. 7). The distinctions in species composition of assemblages formed in biotopes with the highest moisture were revealed during the damp periods, and in dry biotopes, in droughty periods.

**Mesoscale horizontal distribution**

This investigation has shown that the patterns of species distribution in a bog in the Middle Volga Region are the same as in other parts of the world. The main factor influencing community structure was substrate moisture, and environmental acidity came second (Meisterfeld, 1977, 1978; Warner, 1987; Tolonen et al., 1994; Charman, Warner and, 1992; Charman, 2001; Mitchell et al., 1999; Booth, 2001; Bobrov et al., 2002; Lamentowicz and Mitchell, 2005). The great role of moisture in community structure was pointed out by the first researchers of testate amoebae in sphagnum bogs (Harnisch, 1924; Bassin, 1944). These authors revealed species characteristic of dry biotopes (Assulina seminulum, A. muscorum, Nebela collaris, N. militaris, etc.) and moist habitats (Archerella flavum, Amphitrema wrightianum, etc.). In the latter, Hyalosphenia papilio, Arcella disoides, Diffugia bacillifera, Nebela carinata, N. marginata, etc. reach the maximum abundance with appearance of free water and Hyalosphenia elegans, Nebela militaris do the same at the average level of moisture. Later these conclusions have been expanded and specified on the basis of diverse material (Heal,
Fig. 45. Vertical distribution of *Hyalosphenia* species.

Fig. 46. Vertical distribution of *Assulina* species.

Fig. 47. Vertical distribution of *Arcella* species.
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1962; Schönborn, 1962, 1963; Meisterfeld, 1977; Tolonen et al., 1992; Charman and Warner, 1992; Bobrov et al., 2002; Booth, 2002; Lamentowicz and Mitchell, 2005). At the same time, exact quantitative results appear a little bit different in different works, which is associated with the specificity of concrete bogs studied. Local features of Sphagnum-dominated ecosystems (vegetation, climate, humidity level, chemical composition, etc.) result in some specific features of testate amoebae communities (Mitchell et al., 2000; Booth and Zygmunt, 2005).

The results obtained in the course of our investigation reflect an "average" pattern of structural differentiation of bog communities (Bobrov et al., 2002). It illustrates the relationships between the species structure of the community and the habitat type (mainly determined by moisture) and allows one to distinguish several types of local communities on the basis of dominant species. Indicator species of dry conditions Assulina muscorum, A. seminulum, Cryptodifflugia compressa dominated at hummock formed by Sphagnum angustifolium, S. papillosum, Polytrichum strictum. Species characteristic of moist biotopes, Nebela tenella, Hyalosphenia papilio, H. elegans, Heleopera petricola, dwelled in lawns formed by Sphagnum palustre and S. magellanicum. At the edge of the quagmire, besides typical sphagnophilous species like Hyalosphenia papilio and Heleopera sphagni, which were abundant in other parts of bog, also Cyclopyxis eurystoma, Phryganella hemisphaerica, Arcella arenaria, A. hemisphaerica, A. intermedia dominated. It is interesting that species like Nebela tenella, Hyalosphenia elegans and Euglypha ciliata did not occur in the assemblage at the edge of the quagmire, but were widely represented elsewhere in the bog, both at hummocks and lawns, which made the community quite continual.

Direct comparison of absolute values of testate amoebae abundance in sphagnum is difficult because of methodical differences between the studies, but it is possible to compare general trends of changes in integral community parameters. It was shown in the previous works that on the average the organisms’ density and species diversity decrease from dry to moist biotopes, the decrease in species diversity being mainly caused by decrease in evenness (Meisterfeld, 1978; Warner, 1987). However, these conclusions are not confirmed by our results. In this work the minimal organisms’ densities were noted in the driest habitats, the species diversity being equal in all local assemblages. It may be explained by differences reflecting the specificity of the bog investigated, which is restoring after peat extraction and is located in continental climate. Incompleteness of restoration processes of the Sphagnum-dominated ecosystem is reflected in insufficient development of bog microrelief, which probably increases the “mixture” of different community types and results in continual transitions between the local community variants and in smoothing of changes in values of integral community parameters (for example, evenness). The continental climate results in “over drying” of hummocks, which prevents the abundance of organisms from reaching high values.

The results obtained confirm the possibility of using testate amoebae as bioindicators in monitoring of Sphagnum-dominated ecosystems. It is especially important because of the greater species diversity of testate amoebae in comparison with mosses and higher plants. Moreover, most testate amoebae are cosmopolite (Mitchell et al., 2000; Mitchell, 2005), which allows application of unified biomonitoring methods in different parts of the world. However, to verify universality of the patterns revealed, further investigations in unexplored regions are needed.

**Microscale horizontal distribution**

Smaller organisms are known to perceive finer environmental heterogeneity (Burkovsky et al., 1994; Azovsly, 2000, 2002). Local protozoan agglomerations with a size of about 1 cm and less have been revealed (Burkovsky, 1984, 1992; Balik, 1996b). The smallest agglomeration was determined by population factors (reproduction processes) and coenotic factors (competition, resource-consumer relationships); with the increase in investigation territory the main role in forming the communities heterogeneity shifted to abiotic factors (Burkovsky et al., 1996). All these conclusions were made on the basis of data obtained from rather heterogeneous biotopes, such as marine sand littoral, characterized by numerous spatial gradients (Burkovsky, 1992) or spruce or beech litter transiting to soil covered by mosses (Balik, 1996b).

At the same time, the moss carpet in sphagnum bogs seems to be rather homogeneous in terms of environmental conditions if it is dominated by one moss species and lacks clear micro-topography (Andrus, 1986). However, inferring ecological conditions from the vegetation or the micro-topography can be misleading (Bridgham et al., 1996). Therefore, the macroscopic vegetation pattern is only a rough indication of micro-environmental conditions and is not a priori a good indicator of testate amoebae community requirements (Mitchell et al., 2000).

In recent investigation (Mitchell et al., 2000) it was shown that within macroscopically homogeneous 40 cm x 60 cm size Sphagnum magellanicum
carpet the testate amoebae community was heterogeneous. Heterogeneity was not revealed in biomass but was distinct in species structure. The existence of patches of different size was also shown, which resulted from external environmental factors (such as food availability or the distribution of the water film) or biotic processes such as intra- or interspecific relationships.

In the course of our investigation heterogeneity was revealed in community species structure within macroscopically homogenous Sphagnum angustifolium carpet, although it was significantly lower than that forming in abiotic microgradients (Charman and Warner, 1992, 1997; Mitchell et al., 1999). Besides, we found that patterns of spatial distribution depended on investigation scale. Aggregation size is species-specific, and in some cases (Assulina muscorum and A. seminulum) is positively correlated with amoebae shell size. It is interesting that some species form aggregations of different size and the smallest patches are about 1 cm large. To sum up, spatial heterogeneity of the population, resulting in patches of several levels, forms under the influence of a complex of biotic and abiotic factors. So, these aggregations are more or less expressed patches of different size smoothly passing to each other rather than a distinct spatially constrained group.

With an increasing investigation territory, integral community parameters change too. So, connectedness of species slightly decreased and heterogeneity of community rose up. The most likely explanation of this fact is an increase in total environmental heterogeneity, which involves species divergence in space. The aggregation degree grows with increasing of investigation area. Thus, aggregation of testate amoebae distribution is not associated with formation of joint species agglomerations. It means that in the maximal investigated scale (1–2 m) species do not combine in local communities with more or less expressed spatial borders. The size of minimal testate amoebae community is measured by 1-2 centimeters.

**Microscale vertical distribution**

This investigation has shown that in the sphagnum bog studied in the Middle Volga Region, similarly to other ecosystems (Heinis, 1945; Chacharonis, 1954; Bonnet, 1958; Heal, 1962; Schönborn, 1963; Meisterfeld, 1977; Butller et al., 1996; Booth, 2002; Mitchell and Gilbert, 2004), vertical differentiation of testate amoebae community is prominent. The most characteristic species of the top 0–3 cm is H. papilio. It was dominant at all six stations except one (station 4). In the hydrophilous community Ph. hemisphaerica and C. eurystoma joined this species, in the hygrophilous community it was H. sphagni, in the xerophilous one, A. muscorum, A. seminulum, A. flavum, E. laevis. In the hydrophilous community H. papilio and C. eurystoma dominated in the middle horizon and Arcella species preferred the lowest one. In the middle and the lowest zone H. elegans and N. tenella dominated in the hygrophilous community, and C. compressa and E. ciliata joined them in the xerophilous community. Moreover, in the lowest layers of the hygrophilous community D. juzepchiniensis individuals were abundant.

The results obtained agree well with those of the previous investigations, summed up in the work of Mitchell and Gilbert (2004). H. papilio, A. flavum, A. muscorum, A. seminulum, H. sphagni are characteristic inhabitant of the upper parts of sphagnum (Heal, 1962). Some of these species (A. flavum, H. sphagni, H. papilio) are mixotrophic, i.e. contain zoochlorellae in the cytoplasm and partly consume them (Schönborn, 1965). At the same time, species without zoochlorellae (A. muscorum, A. seminulum) are common in the xerophilous community.

On the other hand, Heal (1962) noted that species with shells covered by xenosomes usually occur in low sphagnum zone, where the material necessary for shell construction is present, and species with both symbiotic zoochlorellae in the cytoplasm and xenosomes on the shell (H. sphagni) prefer the middle part, where there is a balance between the light requirements and the need for suitable materials for the shell construction (Heal, 1962; Buttler et al., 1996; Booth, 2002). Our study confirms this hypothesis, especially since we took into account distribution of live organisms only. The importance of this approach was emphasized in the work of Mitchell and Gilbert (2004). Otherwise the patterns observed may be partly due to the inclusion of empty shells in the counts, which would artificially increase the numbers of mixotrophic species in the lower parts of the mosses. Concerning the assumption about the increase in abundance of species with shell constructed with xenosomes in the lower layers, it should be noted that vertical distribution is strongly related with biotope conditions. So, in our study in submerged Sphagnum riparium at the sward edge species with xenosomes (Ph. hemisphaerica, C. eurystoma) dominated in upper zone, while species with organic shell (Arcella individuals) dominated in the lower part. On the other hand, species with shells constructed with idiosomes (N. tenella, E. ciliata) or with organic shell dominated in the low zone within sphagnum sward (C. compressa, H. elegans), and D.
It is interesting that under various conditions different structures of vertical distribution formed. This aspect has not been specially considered before. We found that in submerged *Sphagnum riparium* (hydrophilous community) well-defined changes in community structure were present at 15 cm down the top, where a characteristic sphagophilous community (*H. papilio, Ph. hemisphaerica, C. euryforma, H. sphagni*) turned into a complex of different *Arcella* species. Within sphagnum lawns with *Sphagnum palustre* and *S. magellanicum* as dominant species (hygrophilous community) we observed two turning points in community structure. The first one was located at a depth of 3 cm, where mixotrophic community (*H. papilio, H. sphagni*) transformed to transitional community (*H. elegans, N. tenella, H. papilio, H. sphagni*), and at a depth of 6 cm (the second point) the latter changes into a community with domination of *N. tenella*. In hummocks (xerophilous community) two variants of vertical structure formed depending on environmental conditions. In the first case there was one turning point at a depth of 9 cm, where the upper community (*A. muscorum, A. seminulum*) changed to the lower one (*N. tenella, H. elegans, E. ciliata*). In the second case there were two turning points: the first one was at a depth of 3 cm, where the upper community (*H. papilio, A. flavum, E. laevis, A. seminulum*) transformed into the middle one (*N. tincta, A. seminulum*), and at a depth of 6 cm the lower community formed (*C. compressa, N. tenella, H. elegans*).

The abundance of live organisms only allows revealing changes in integral community parameters along the vertical gradient. In the top 0–3 cm of sphagnum layer species number and diversity were minimal and the abundance of organisms was maximal. In other words, specific conditions promote development of a limited number of species with characteristic adaptations, such as zoochlorellae in the cytoplasm (*H. papilio, A. flavum, H. sphagni*) or resistance to insufficient moisture (*A. muscorum, A. seminulum*).

Another interesting aspect to be discussed in connection with vertical structure of the community is niche separation among congenic species (Mitchell and Gilbert, 2004). Patterns of vertical micro-distributions of closely related species may indicate the existence of a competitive exclusion. Species considered before in this respect (Mitchell and Gilbert, 2004) are *A. flavum*–*A. wrightitana*/*A. stenostoma*, *A. muscorum*–*A. seminulum*, *H. papilio*–*H. elegans*.

Seasonal dynamics

Our investigation showed some common features of changes in community structure from the end of spring to the beginning of autumn. The number of species increased during this period, while species diversity and evenness remained at the same level. Moreover, different changes in species abundance in various communities were recorded: it could increase, fall or vary without well-defined directed tendencies. Significant and undirected fluctuations in testate amoeba abundance were noted before (Schönborn, 1982, 1986), but in individual species dynamics more or less expressed peaks were found (Lousier, 1984, 1985). Interestingly, the abundance peaks of some species can occur not only in late autumn (November) but also in winter (Lousier, 1984, 1985). Seasonal changes in abundance of benthic testate amoebae in freshwater have different trends. So, maximal values of the organisms’ abundance were marked in spring and autumn, in summer it decreased, though in some types of biotopes the numbers of testate amoebae increased from spring to summer and then fell drastically in autumn (Vikol, 1992). Hence, there is no single trend of seasonal changes in testate amoeba abundance in different biotopes.

A characteristic feature of seasonal changes is replacement of species composition. However, changing of species complexes of testate amoebae during the season is rarely discussed in the literature. A study of benthic communities in reservoirs of the Dniester river basin revealed the following species complexes (Vikol, 1992). *Centropyxis cassis*, *C. acrosonia*, *C. minuta*, *C. spinosa*, *Diffugia bacilliarum*, *D. bacillifera*, *D. difficilis*, *D. brevicolla*, *Pontigulasia incisa*, *Euglypha aspersa* were characteristic of spring, *Trigonopyxis arcula*, *Diffugia varians*, *D. elongata*, *D. glans*, *D. lebes*, *D. mica*, *D. rubescens*, *D. scalpellum* of summer, *Centropyxis hirsuta*, *C. platystoma*, *juzepheiniensis*, a species with xenosomes, was abundant in the same zone of moist biotope.
Diffugia linearis, D. muriculata, D. compressa, D. ivorenensis, Lesquereusia spiralis of autumn. Our investigation also showed seasonal changes in the dominant species complex, species complexes being connected with habitat conditions. In the hydrophilous community from submerged Sphagnum riparium the spring species complex was represented by H. papilio, C. eurystoma, A. flavum, the summer complex by Ph. hemisphaerica, H. papilio, A. intermedia, the autumn complex by C. platystoma, C. aculeata, A. gibbosa, A. arenaria. In the hydrophilous community from sphagnum lawn formed by Sphagnum palustre and Sphagnum magellanicum the spring species were H. papilio, N. tincta and H. sphagni, and the summer-autumn species N. tenella and H. elegans. In xerophilous community from hummocks formed by Sphagnum angustifolium, Sphagnum papillosum and Polytrichum strictum the spring community was dominated by A. muscorum, N. tincta, H. sphagni, the summer one by N. tenella, A. seminulum, H. elegans, E. ciliata and the autumn community by C. compressa, T. arcula, A. seminulum.

Nevertheless, the changes registered in the composition of dominant species are reduced to a great extent by independent patterns of abundance changes of single species, which on the whole resulted in considerable discreetness of the changing processes. The intensity of directed changes for the most part of community structure dynamics was different in various stations.

We described the character of seasonal dynamics of abundance of some species, common for Sphagnum-dominated ecosystems, that were abundant in the bog studied, too. Species closely related taxonomically diverged along the temporal axis of niche space, which could be an indirect evidence of competitive relationships between them (Burkovsky, 1987). So, in the pair of closely related species H. papilio – H. elegans the former could be consider as a spring species, and the latter as a summer-autumn one. Our data on the decrease in H. papilio abundance in the end of summer are slightly at variance with the previous idea about its high numbers during all this period (Heal, 1964). These results may be the evidence of flexibility of this species, a common inhabitant of sphagnum bogs (Gilbert and Mitchell, 2006). The characteristics of seasonal dynamics are probably defined not only by biotope features but also by interspecific interactions in the community. In another pair of closely related species, N. tincta – N. tenella, the former was characteristic of spring and early summer and the latter in the end of summer and in autumn. In the species pair A. muscorum – A. seminulum no such regularities were quite clear, but still one might say that A. muscorum preferred the first part of summer and A. seminulum the second one.

Interestingly, the share of Assulina empty tests was very high in comparison with that of live organisms. This fact could be explained by two reasons. Firstly, dryness of biotopes where these species live could promote better conservation of tests because of the reduced microbial activity. Secondly, in dry habitats organisms probably react to favorable conditions (for example, biotope moistening during rains) by a fast increase in abundance. A considerable part of the population dies after reestablishment of dry conditions. In other words, populations under consideration are obviously r-strategists. This is explained not only by their physiological features, but also by their smaller size as compared to larger organisms from the genera Hyalosphenia, Nebela, Heleopera. The results obtained in the present study on abundance dynamics of live organisms and empty tests of A. seminulum are an indirect evidence in favour of the second reason. From June to July the number of empty tests increased quickly, while the abundance of live organisms remained at the same level. This fact can only be explained by a drastic increase in the live organisms’ numbers between sampling and a subsequent mass mortality of active amoebae.

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References


Meisterfeld R. 1977. Die horizontale und vertikale


Opravilová V. and Hájek M. 2006. The variation of testacean assemblages (Rhizopoda) along the complete base-richness gradient in fens: a case study from the Western Carpathians. Acta Protozool. 45, 191–204.


Address for correspondence: Yuri A. Mazei. Department of Zoology and Ecology, Penza State Pedagogical University, Lermontova str., 37, 440026 Penza, Russia. E-mail: yurimazei@mail.ru

Editorial responsibility: Sergey Karpov