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Heterotrophic flagellates in the primary lakes and hollow-pools of mires in the European North of Russia

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Summary

Species diversity and morphology of heterotrophic flagellates from 5 primary mire lakes and 4 secondary hollow-pools in mires were studied. Samples were taken from three microbiotopes: plankton, benthos, and periphyton. Micrographs and morphological descriptions for all observed species were given. A total of 40 species and forms were found. The most common species were *Bodo saltans, Goniomonas truncata, Neobodo designis, Rhynchomonas nasuta*, and *Ancyromonas sigmoides*. The higher species richness, as well as the greater number of unique species was registered in primary mire lakes. *Bodo saltans, Neobodo designis*, and *Spumella* sp. were found in all types of the studied microbiotopes. Greater species diversity was discovered in benthos.

Key words: heterotrophic flagellates, species diversity, morphology, mires, primary mire lakes, hollow-pools

Introduction

Heterotrophic flagellates are a polyphyletic group of unicellular heterotrophic eukaryotes that have one or more flagella at least at one stage of the life cycle (Patterson, Larsen, 1991). Heterotrophic flagellates are widespread in diverse freshwater and marine biotopes and play an important role in functioning of the microbial food web since they feed on bacteria and small protists, also being food objects for ciliates and metazoa (Pomeroy, 1974; Sherr et al., 1982; Arndt et al., 2000). Most morphospecies of heterotrophic flagellates are cosmopolites (Lee, 2015; Azovsky et al., 2016). Modern studies show that the distribution of these protists depends mainly on the hydrochemical and hydrophysical characteristics of the water body, but not on the geographic location (Finlay, 1998; Finlay et al., 1998; Lee and Patterson, 1998).

Water ecosystems in mires are poorly understood both in terms of biodiversity and structural and functional organization (Philippov, 2017). In this case, only consideration of the hydrobiocenosis of mires as a set of separate types of mire water bodies makes it possible to understand the processes taking place in these ecosystems.

By the example of mires in the Pinega District, Arkhangelsk Region (Prokina et al., 2017a), we showed that each type of mires in general and mire water bodies in particular host a specific set of species of heterotrophic flagellates. In the literature, one can find information on these protists in primary mire

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lakes (Tikhonenkov and Mazei, 2007; Tikhonenkov, 2007/8; Kosolapova and Kosolapov, 2011), but there are hardly any similar data for hollow-pools (Prokina et al., 2016). Considering this gap, we studied the species composition and external morphology of heterotrophic flagellates in primary mire lakes and hollow-pools in the European North of Russia.

Material and methods

Mire lakes belong to primary mire water bodies since they arose in the depressions because of late glacial and post-glacial water bodies' degradation. They can be of different size (0.0001 to more than 10.0 square kilometers), shape (rounded, oval, irregular), and depth (which depends on morphometric features of the initial tectonic depression and rate of paludification), marginally or centrally positioned in the mire. Bottom sediments are comprised by peats, silts, and sapropels. Typically, vegetation covers less than 10 per cent of the area (Philippov, 2014; Sadokov and Philippov, 2017).

Mire hollow-pools belong to secondary mire water bodies since they emerged because of regressive processes occurring at the final stages of oligotrophic mires' evolution. Hollow-pools typically arise in central parts of large mire massifs and/or in the upper part of the slope. Hollow-pools comprise mire complexes along with ridges and hollows. In raised bogs, hollow-pools have irregular, rounded or slightly elongated shape with an area of 10 to 500 square meters, and depth of 2 to 3 meters, with peat or peat-silt bottom and sides. Vegetation is marginal, and typically covers less than 5 to 10 per cent of the bottom area (Lobunicheva and Philippov, 2011; Philippov, 2015).

Field survey was carried out in accordance with the developed methodology of hydrobiological studies of mires (Philippov et al., 2017). Samples were collected by D.A. Phillipov in 9 mire water bodies (5 primary lakes and 4 hollow-pools) in the Republic of Karelia, Saint Petersburg, Arkhangelsk and Vologda Regions in 2015 and 2017. The detailed hydrochemical and hydrophysical characteristics of the lakes are presented in Table 1.

Benthos, plankton or periphyton samples were placed in 15 ml plastic tubes and transported to laboratory at 4°C. In the laboratory, samples were enriched with a suspension of *Pseudomonas fluorescens* Migula bacteria at the ratio of 0.15 ml of suspension per 5 ml of sample and placed in Petri dishes. Samples were kept at 22° C in the dark and observed for 10 days to reveal the cryptic species diversity according to the accepted methodology (Vørs, 1992).

For observations, an AxioScope A1 light microscope (Carl Zeiss, Germany) with DIC and phase contrast and water immersion objectives (total magnification ×1120) was used. Video recording was made by an AVT HORN MC1009/S analog video camera. Electron microscope preparations were carried out according to the described method (Moestrup and Thomsen, 1980) and observed in a JEM-1011 transmission electron microscope (Jeol, Japan).

Results

We found 40 species and forms of heterotrophic flagellates from 33 genera and 3 supergroups. List of the observed heterotrophic flagellates with descriptions of sampling sites, morphological descriptions of species, and their worldwide distribution is presented below. We used the current eukaryotic macrosystem (Adl et al., 2012), in which the asterisks mark the rank of taxa. Choanoflagellate system is given in accordance with Nitsche et al. (2011). Abbreviations used are as follows: BL – cell body length, F – flagella/flagellum, AF – anterior flagellum, PF – posterior flagellum, LL – lorica length, StL – stalk length, PsL – pseudopodia length, CV – contractile vacuole, LM – light microscope, TEM – transmission electron microscope.

OPISTHOKONTA Cavalier-Smith, 1987

**Choanoflagellatea Cavalier-Smith, 1998

***Craspedida Cavalier-Smith, 1997

Codosiga botrytis (Ehrenberg, 1838) Kent, 1880 [bas.: *Epistylis botrytis* Ehrenberg, 1838] (Fig. 1a).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=7.5–10.0 μm; F=1.5–2.5×BL. Oval cell body with basal protrusion and truncated anterior end. Two CVs in the basal part of the cell body are contracted alternately. Several (3–7) cells joined by their basal protrusion at the apex of the long common stalk (3–5×BL).

Distribution. Europe (Vørs, 1992; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017b), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012), Australia (Lee et al., 2005).

Table 1. Characteristics of the studied lakes and pools and sample collection sites.

Place, wetland	Coordinates	pH	t° C	Sample #	Microbiotopes	Date
Primary mire lakes						
Republic of Karelia, Loukhi District, near "Kartesh", lake Krugloe	66°20'29" N 33°36'07" E	5.9	16	1a	plankton	23.06.2015
				1b	benthos	
Vologda Region, Cherepovets District, mire Ulomskoe, lake Chyornoe	58°59'44" N 37°03'26" E	5.7	23	2a	plankton	16.08.2017
				2b	benthos	
Vologda Region, Cherepovets District, mire Ulomskoe, lake Kolodenskoe	59°00'16" N 37°04'06" E	5.8	23	3a	plankton	16.08.2017
				3b	benthos	
Vologda Region, Cherepovets District, mire Bol'shoj Mokh, lake Morotskoe	58°43'29" N 37°39'07" E	7.1	22	4a	plankton	16.08.2017
				4b	benthos	
Vologda Region, Syamzha District, mire Shichengskoe, lake Shichengskoe	59°56'58" N 41°19'16" E	6.2	21	5a	plankton	27.07.2015
				5b	benthos	
Secondary hollow-pools						
Saint Petersburg, mire Sestroretskoe	60°07'23" N 30°02'37" E	4.1	25	6a	plankton	28.06.2015
				6b	periphyton	
Arkhangelsk Region, Pomorskij District, mire Lajskoe	64°31'54" N 40°13'58" E	4.4	20	7a	plankton	01.08.2015
				7b	periphyton	
Arkhangelsk Region, Pinega District, mire Udebnoe	64°32'48" N 43°21'37" E	3.9	16	8a	plankton	09.08.2015
				8b	benthos	
Vologda Region, Syamzha District, mire Shichengskoe	59°57'03" N 41°19'08" E	3.8	24	9a	plankton	27.07.2015
				9b	periphyton	

Monosiga ovata Kent, 1880 (Fig. 1b).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=4.5–6.0 μm; F=1.5–3.0×BL. Cell body ovoid in shape. Cells attached to substrate by their basal parts. Swimming cells can form radial filopodia (not shown).

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Kopylov et al., 2006), Africa (Prokina et al., 2017c), South America (Lugo et al., 1990), Antarctica (Hawthorn and Ellis-Evans, 1984).

Salpingoeca clarki Stein, 1878 non Schiller, 1953 (Fig. 1c–e).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=4.5–6.5 μm; F=1.5–3.0×BL; LL=1.5×BL; StL=1.0–1.5×BL. Ovoid cell body with a small neck at the anterior end. Oval lorica attached to substrate by a short stalk.

Distribution. Europe (Auer and Arndt, 2001; Prokina et al., 2017a).

Salpingoeca minor Dangeard, 1910 (Fig. 1f–g).

Found. Primary mire lake Kolodenskoe (benthos – sample # 3b).

Description. BL=4.0–5.5 μm; F=1.5×BL; LL=1.1–1.2×BL. Round cell body occupies almost the whole lorica. There is a small neck at the anterior end of the cell body. Round lorica without stalk, attached to the substrate by its basal part.

Distribution. Europe (Mylnikov and Kosolapova, 2004), Asia (Tikhonenkov et al., 2012).

SAR

*Stramenopiles Patterson, 1989

**Bicosoecida Grassé, 1926

Bicosoeca exilis Penard, 1921 (Fig. 1h–i).

Found. Primary mire lakes Morotskoe (plankton – sample # 4a) and Shichengskoe (benthos – sample # 5b).

Description. BL=5.5–6.5 μm; AF=1.5–2.0× BL; PF=1×BL; LL=1.5×BL; StL=1.5×BL. PF directed posteriorly and lies in a longitudinal groove. Cell body attached to the bottom of lorica by PF. Ovoid lorica narrowed anteriorly and expanded posteriorly, with a stalk.

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Kopylov et al., 2006), Africa (Prokina et al., 2017c), Antarctica (Hawthorn and Ellis-Evans, 1984).

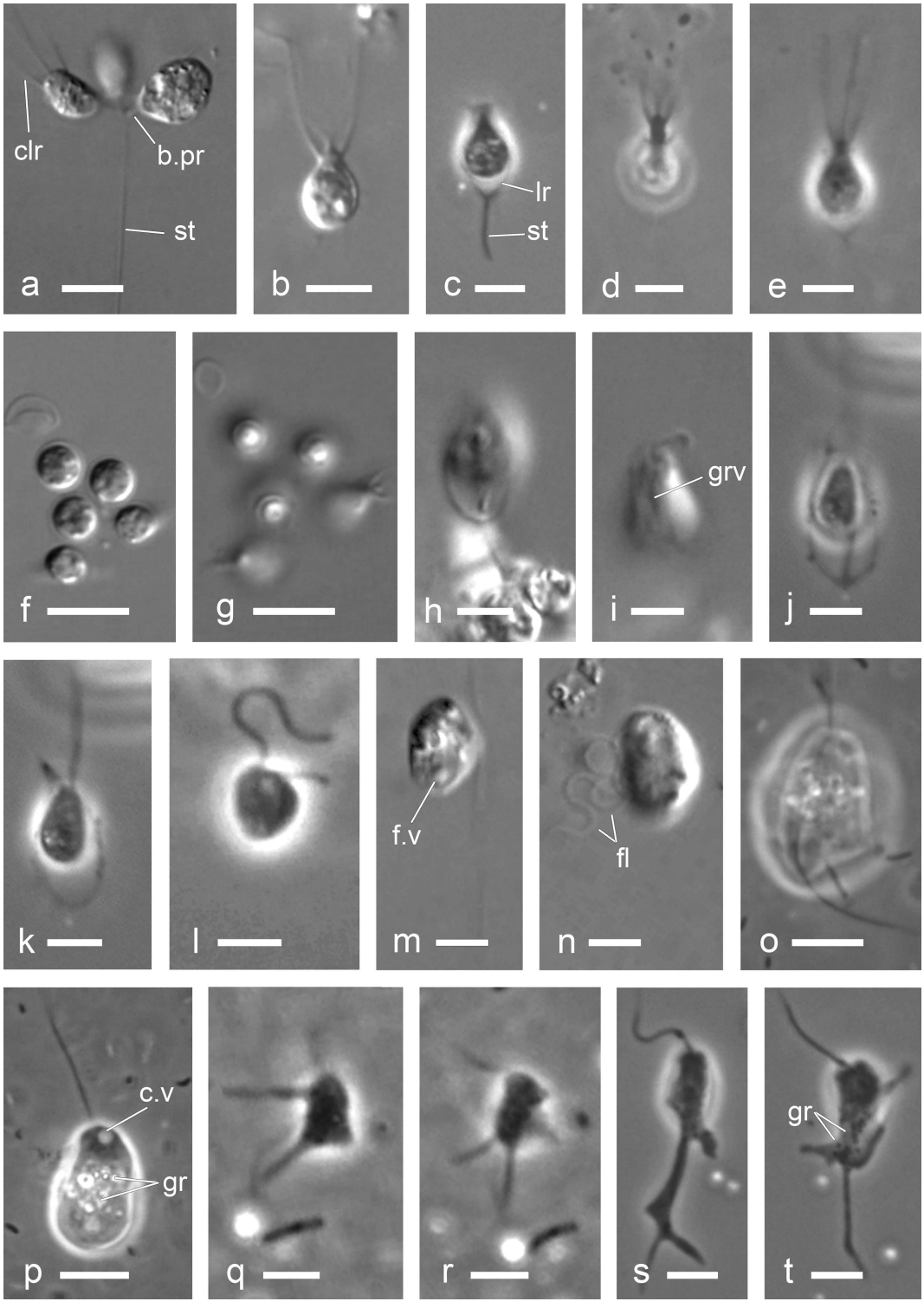

Fig. 1. Heterotrophic flagellates (DIC: a, b, f–i, m, n; PhC: c–e, j–l, o–t): a – *Codosiga botrytis*; b – *Monosiga ovata*; c–e – *Salpingoeca clarki*; f–g – *Salpingoeca minor*; h–i – *Bicosoeca exilis*; j–k – *Bicosoeca lacustris*; l – *Spumella* sp.; m–n – *Colponema* sp.; o–p – *Cercomonas granulifera*; q–r – *Cercomonas* sp.; s–t – *Metabolomonas insania*. *Abbreviations*: b.pr – basal protrusion, clr – collar, c.v – contractive vacuole, fl – flagella, f.v – food vacuole, gr – granules, grv – groove, lr – lorica, st – stalk. Scale bar: a, f–g, o–p – 10 µm; b–e, h–n, q–t – 5 µm.

Bicosoeca lacustris James-Clark, 1867 (Fig. 1j–k).

Found. Primary mire lakes Krugloe and Morotskoe (benthos – samples ## 1b, 4b).

Description. BL=5.5–7.5 μm; AF=1.5–2.0×BL; PF=1×BL; LL=1.5–2.0×BL. Morphology is the same as of *B. exilis*, except for the absence of a stalk.

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012), Africa (Tikhonenkov, 2009; Prokina et al., 2017c), Australia (Tong, 1997).

**Chrysophyceae Pascher, 1914

Spumella sp. (Fig. 1l).

Found. Primary mire lake Krugloe (benthos – sample # 1b) and secondary hollow-pools in Sestroretskoe mire (periphyton – sample # 6b) and Shichengskoe mire (plankton – sample # 9a).

Description. BL=4.5–5.5 μm; Long F=1.5–2.0×BL; Short F=1×BL. Round or triangular cell body attached to substrate by a small basal protrusion. Species of this genus are difficult to distinguish since they all have approximately the same morphology in both LM and TEM.

*Alveolata Cavalier-Smith, 1991

**Incertae sedis Alveolata

Colponema sp. (Fig. 1m–n).

Found. Primary mire lake Morotskoe (plankton and benthos – samples ## 4b, 4b).

Description. BL=9.5–12.5 μm; AF=1.2–1.8×BL; PF=3×BL. Oval cell body with prominent short groove at the ventral side. Flagella insert subapically from the ventral side and straight along the longitudinal axis of the body. Large food vacuole located in the posterior part of the cell body. Cells swim fast and straight, but sometimes can stop moving and exhaust its flagella (fig. 1n).

*Rhizaria Cavalier-Smith, 2002

**Cercozoa Cavalier-Smith, 1998

***Cercomonadidae Kent, 1880 emend. Mylnikov et Karpov, 2004

Cercomonas granulifera (Hollande, 1942) Mylnikov et Karpov, 2004 [bas.: *Cercobodo granulifera* Hollande, 1942] (Fig. 1o–p).

Found. Primary mire lake Krugloe (benthos – sample # 1b) and secondary hollow-pools in Lajskoe mire (periphyton – sample # 7b).

Description. BL=17–20 μm; AF=1×BL; PF=1.5–2.0×BL. Oval cell body with strong metaboly, one or two CV located anteriorly. Finger-shaped pseudopodia formed from the lateral and posterior sides of the cell body. Cytoplasm contains a large number of granules.

Distribution. Europe (Mylnikov and Kosolapova, 2004), Asia (Tikhonenkov et al., 2012).

Cercomonas sp. (Fig. 1q–r).

Found. Secondary hollow-pools in Shichengskoe mire (periphyton – samples # 9b).

Description. BL=3.5–5.5 μm; AF=1×BL; PF=2×BL. Round to oval cell body with strong metaboly. A large number of long branched pseudopodia formed from the whole surface of the cell body. AF moves rapidly from side to side.

Metabolomonas insania Kiss et al. in Brabender et al., 2012 (Fig. 1s–t).

Found. Secondary hollow-pools in Lajskoe mire (plankton and periphyton – samples ## 7a, 7b).

Description. BL=8.0–12 μm; AF=1×BL; PF=1.5–2.0×BL. Elongate-oval cell body with a large number of pseudopodia variable in shape. Cytoplasm contains numerous dark granules. Cells with strong metaboly, move fast and change their shape quickly.

Distribution. Europe (Brabender et al., 2012; Prokina and Mylnikov, 2017), Africa (Prokina et al., 2017c).

***Glissomonadida Howe et Cavalier-Smith, 2009

Allantion tachyploon Sandon, 1924 (Fig. 2a).

Found. Primary mire lakes Kolodenskoe (benthos – sample # 3b) and Morotskoe (plankton and benthos – samples ## 4a, 4b) and secondary hollow-pools in Shichengskoe mire (plankton – sample # 9a).

Description. BL=7.5–8.5 μm; AF=0.2×BL; PF=2.5–3.5×BL. Oval rigid and not flattened cell body. AF too short and seen more often only in EM (Mylnikov et al., 2006). PF directed posteriorly and trailing. Posterior part of cells raised above substrate.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Mylnikov and Kosolapova, 2004), Asia (Tikhonenkov et al., 2012), Antarctica (Hawthorn and Ellis-Evans, 1984; Butler et al., 2000).

Bodomorpha sp. (Fig. 2b).

Found. Primary mire lake Krugloe (benthos – sample # 1b) and secondary hollow-pools in Lajskoe mire (periphyton – sample # 7b).

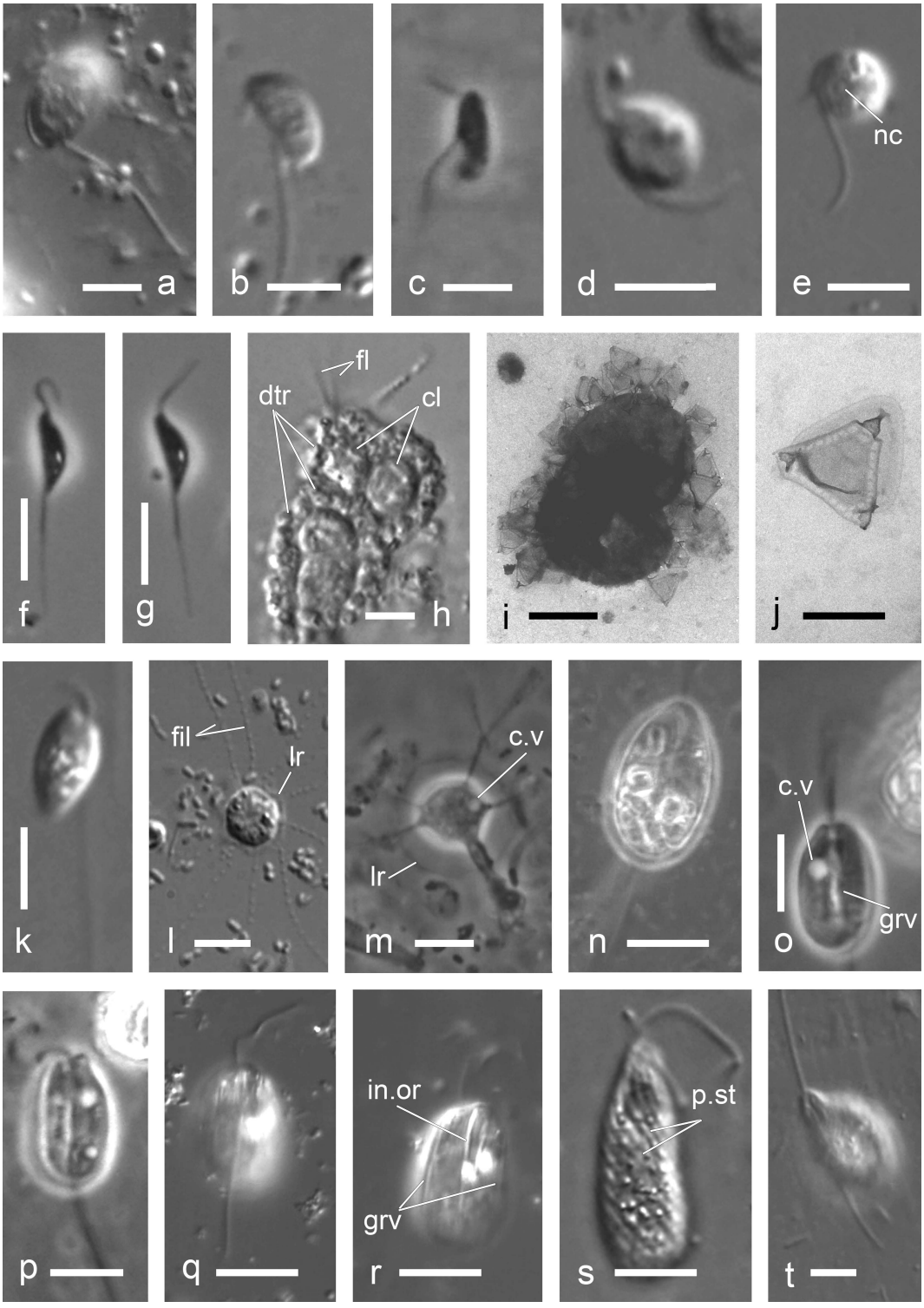

Fig. 2. Heterotrophic flagellates (DIC: a, b, d, e, k, l, n, q–t; PhC: c, f–h, m, o, p; TEM: I, j): a – *Allantion tachyploon*; b – *Bodomorpha* sp.; c – *Neoheteromita* sp.; d – *Sandona* sp.; e – *Teretomonas rotunda*; f–g – *Agitata* aff. *agilis*; h – *Spongomonas uvella*; i–j– *Thaumatomonas seravini* (i – total preparat in TEM; j – single scale in TEM); k – *Protaspa simplex*; l–m – *Microcometes paludosa*; n – *Anisonema acinus*; o–p – *Anisonema ovale*; q–r – *Entosiphon sulcatum*; s–t – *Heteronema globulifera*. *Abbreviations*: cl – cell, dtr – detritus, fil – filopodia, in.or – ingestion organelle, nc – nucleus, p.st – pellicular striation. Other abbreviations as in Fig. 1. Scale bar: n–r – 10 μm; a–h, k–m, s–t – 5 μm; i – 1 μm; j – 0.5 μm.

Description. BL=5–6 μm; AF=0.5×BL; PF=1.5–2.2×BL. Bean-shaped rigid cell body with an anterior rostrum. AF directed posteriorly and flapping weakly. Trailing PF with acronema. Distinguished from other glissomonad genera by visible rostrum and AF directed posteriorly.

Neoheteromita sp. (Fig. 2c).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=5.5–6.0 μm; AF=1×BL; PF=1.5×BL. Elongated bean-shaped cell body with high metaboly. Posterior end of the cell forms pseudopodial tail used for the cell rotation. AF almost always directed anteriorly. Distinguished from other glissomonad genera by metabolic and elongate cell body and a protoplasmic tail.

Sandona sp. (Fig. 2d).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b) and secondary hollow-pools in Sestroretskoe mire (periphyton – sample # 6b).

Description. BL=3.0–3.5 μm; AF=0.5×BL; PF=1.5×BL. Oval rigid cell body without metaboly. AF flapping from posterior to anterior directions. Distinguished from other glissomonad genera by oval rigid cells with jerky moving and flapping AF for 180º (Howe et al., 2009).

Teretomonas rotunda Howe et al., 2009 (Fig. 2e).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=3.5–4.5 μm; AF=0.2–0.3×BL; PF=2.5×BL. Round rigid cell body without metaboly. AF usually perpendicular to PF, which is trailed and directed posteriorly. Distinguished from other glissomonad species by round rigid cells, short and almost not moving AF directed perpendicularly to PF, and more smooth gliding.

Distribution. Europe (Prokina and Mylnikov, 2017; Prokina et al., 2017a), North America (Howe et al., 2009).

***Pansomonadida Vickerman, 2005

Agitata* aff. *agilis (Moroff, 1904) Cavalier-Smith in Howe et al., 2011 [bas.: *Dimastigamoeba agilis* Moroff, 1904; syn.: *Cercobodo agilis* (Moroff, 1904) Lemmermann, 1910; *Cercomonas agilis* (Moroff, 1904) Mylnikov et Karpov, 2004] (Fig. 2f–g).

Found. Primary mire lake Krugloe (benthos – sample # 1b) and secondary hollow-pools in Sestroretskoe mire (plankton – sample # 6a).

Description. BL=4–5 μm; AF=1×BL; PF=2.5×BL. Elongate amoeboid cell body. AF flapping from side to side actively, trailing PF with an acronema. Differs from *A. agilis* by smaller body size and longer PF.

****Spongomonadida Hibberd, 1983

Spongomonas uvella Stein, 1878 (Fig. 2h).

Found. Primary mire lake Kolodenskoe (benthos – sample # 3b) and secondary hollow-pools in Lajskoe mire (periphyton – sample # 7b) and Udebnoe mire (benthos – sample # 8b).

Description. BL=5.0–6.5 μm; F=2.5–3.5×BL. Oval cell body attached to substrate by its basal part. Two to seven cells connected in a colony and covered by particles. Two equal flagella insert apically and flicker.

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Tikhonenkov et al., 2012).

****Silicofilosea Adl et al., 2005

*****Thaumatomonadida Shirkina, 1987

******Thaumatomonadidae Hollande, 1952

Thaumatomonas seravini Mylnikov et Karpov, 1993 (Fig. 2i–j).

Found. Primary mire lakes Krugloe (plankton and benthos – samples ## 1a, 1b) and Shichengskoe (benthos – sample # 5b).

Description. We observed only on TEM. Cells covered by siliceous scales. Scales consist of 2 triangular plates, connected with 3 columns at each corner. Plate side is 0.5–0.7 μm. A row of holes located along each side of the upper plate.

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012).

***Thecofilosea Cavalier-Smith, 2003

****Cryomonadida Cavalier-Smith, 1993

Protaspa simplex (Vørs, 1992) Cavalier-Smith in Howe et al., 2011 [bas.: *Protaspis simplex* Vørs, 1992] (Fig. 2k).

Found. Primary mire lakes Krugloe (benthos – sample # 1b) and Morotskoe (plankton – sample # 4a) and secondary hollow-pools in Sestroretskoe mire (plankton – sample # 6a).

Description. BL=5.5–6.0 μm; AF=1×BL; PF=2–3×BL. Oval cell body, posterior part is raised above substrate. AF directed anteriorly, slightly elevated and flapping from side to side. PF is trailing.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Mylnikov and Kosolapova, 2004), Asia (Tikhonenkov et al., 2012), Australia (Lee et al., 2005).

**Incertae sedis Cercozoa

Microcometes paludosa Cienkowsky, 1876 (Fig. 2l–m).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=6.5–7.0 μm; LL=7.0–8.0 μm; PsL=15–21 μm; F=2–3 μm. Round cell body lies on substrate inside a lorica. Lorica with 3–5 apertures through which branched filopodia with extrusomes insert. Two equal short flagella usually not visible, 3–5 CVs located laterally.

Distribution. Europe (Prokina et al., 2017a), Australia (Lee et al., 2005).

EXCAVATA Cavalier-Smith, 2002

*Discoba Simpson in Hampl et al., 2009

**Discicristata Cavalier-Smith, 1998

***Euglenozoa Cavalier-Smith, 1981

****Euglenida Bütschli, 1884

*****Heteronematina Leedale, 1967

Anisonema acinus Dujardin, 1841 (Fig. 2n).

Found. Primary mire lake Morotskoe (benthos – sample # 4b).

Description. BL=15.5–17 μm; AF=1.5×BL; PF=3.5×BL. Oval rigid cell body is dorsoventrally flattened. Ingestion organelle not visible. Pellicular striations with 8–10 poorly visible grooves (not shown).

Distribution. Europe (Prokina and Mylnikov, 2017; Prokina et al., 2017b), Asia (Duangjan et al., 2017), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000; Lee et al., 2005).

Anisonema ovale Klebs, 1893 (Fig. 2o–p).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=15–16 μm; AF=1.0–1.2×BL; PF=1.5–2.0×BL. Oval rigid cell body with apical excavation at the anterior end. One groove at the ventral side.

Distribution. Asia (Duangjan et al., 2017), South America (Lugo et al., 1990).

Entosiphon sulcatum (Dujardin, 1841) Stein, 1878 [bas.: *Anisonema sulcata* Dujardin, 1841] (Fig. 2q–r).

Found. Primary mire lakes Krugloe, Chyornoe, Morotskoe and Shichengskoe (benthos – samples ## 1b, 2b, 4b, 5b).

Description. BL=11–13 μm; AF=1×BL; PF=1.5×BL. Oval rigid cell body is flattened dorsoventrally, with 3 dorsal and 3 ventral grooves. Well-marked ingestion organelle protrusion from anterior end of the cell body.

Distribution. Europe (Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017), Asia (Tikhonenkov et al., 2012; Duangjan et al., 2017), Australia (Lee et al., 2005).

Heteronema globulifera (Ehrenberg, 1838) Stein, 1878 [bas.: *Trachelius globulifer* Ehrenberg, 1838] (Fig. 2s–t).

Found. Primary mire lake Shichengskoe (benthos – sample # 5b).

Description. BL=13–16 μm; AF=2×BL; PF=1.2–1.5×BL. Elongate-oval to round cell body with high metaboly. Ingestion organelle is visible. AF straight and almost without motion, only its apex vibrates. Well-marked spiraled pellicular striations.

Distribution. Australia (Lee and Patterson, 2000; Lee et al., 2005), South America (Larsen and Patterson, 1990).

Jenningsia fusiforme (Larsen, 1987) Lee et al., 1999 [bas.: *Peranema fusiforme* Larsen, 1987; syn.: *Pseudoperanema fusiforme* (Larsen, 1987) Larsen et Patterson, 1990] (Fig. 3a).

Found. Primary mire lake Morotskoe (plankton – sample # 4a).

Description. BL=17–22 μm; F=1.5×BL. Sack-shaped high metabolic cell body with delicate pellicular striation. Ingestion organelle clearly visible. One emergent flagellum.

Distribution. Europe (Mylnikov and Kosolapova, 2004), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000), South America (Larsen and Patterson, 1990).

Jenningsia sp. (Fig. 3b–d).

Found. Primary mire lake Morotskoe (plankton – sample # 4a).

Description. BL=22–25 μm; F=1.2×BL. Similar to *J. fusiforme* by flexible sack-shaped cell body, delicate pellicular striation and presence of one emergent flagellum. Differs by spiraled twisting of its body during metaboly (Fig. 3c–d).

Notosolenus apocamptus Stokes, 1884 (Fig. 3e).

Found. Primary mire lakes Krugloe and Kolo-

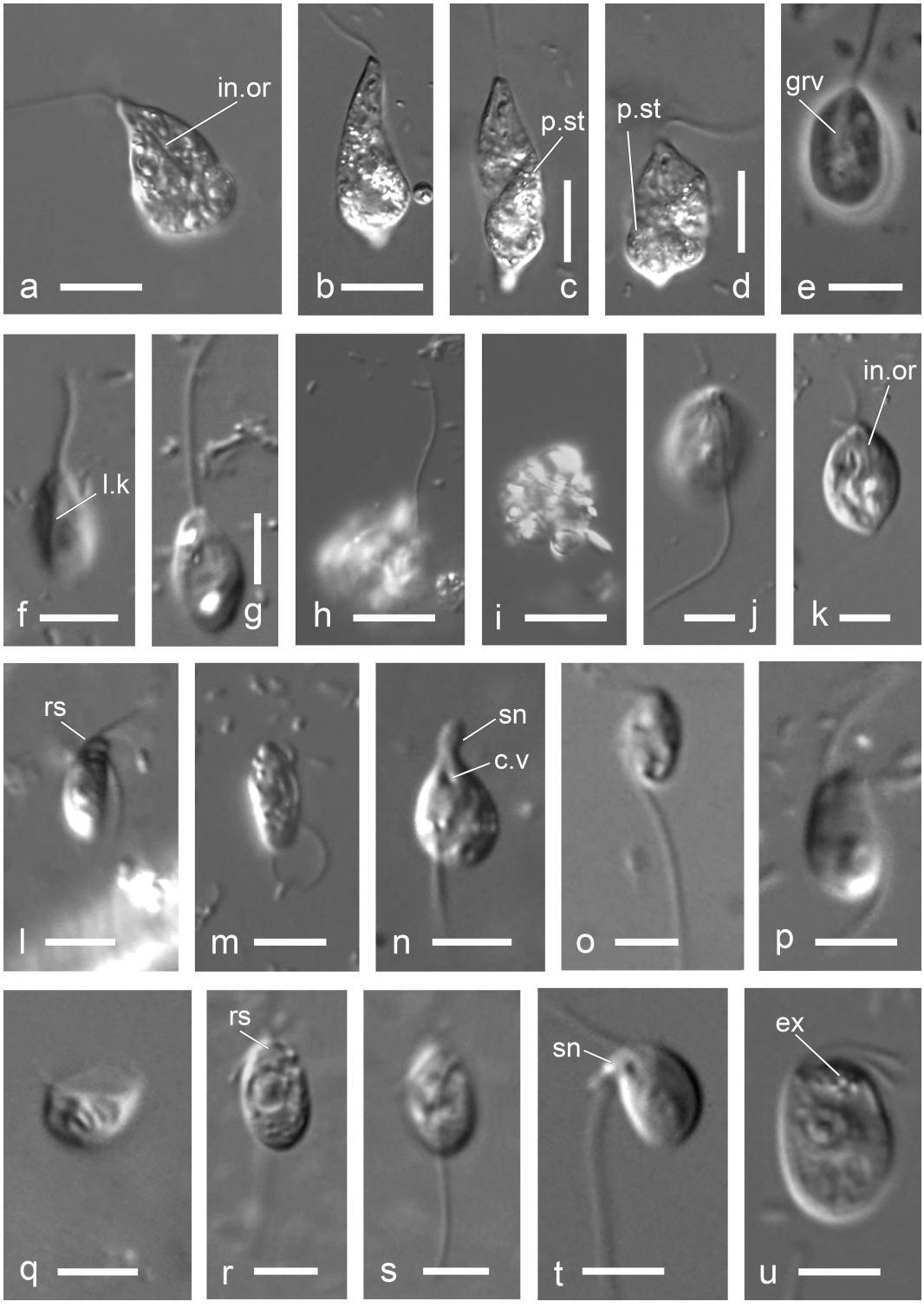

Fig. 3. Heterotrophic flagellates flagellates (DIC: a–d, f–u; PhC: e): a – *Jenningsia fusiforme*; b–d – *Jenningsia* sp.; e – *Notosolenus apocamptus*; f – *Petalomonas minor*; g – *Petalomonas poosilla*; h–i – *Petalomonas* sp.; j–k – *Ploeotia obliqua*; l–m – *Neobodo designis*; n – *Rhynchomonas nasuta*; o – *Bodo saltans*; p – *Bordnamonas tropicana*; q – *Reclinomonas americana*; r–s – *Pseudophyllomitus apiculatus*; t – *Ancyromonas sigmoides*; u – *Goniomonas truncata*. *Abbreviations*: ex – extrusomes, l.k – longitudinal keel, rs – rostrum, sn – snout. Other abbreviations as in Fig. 1, 2. Scale bar: a–d, h–i – 10 μm; e–g, j–q – 5 μm.

denskoe (benthos – samples ## 1b, 3b).

Description. BL=7–9 μm; AF=1.2×BL; PF=0.5×BL. Flattened oval cell body with slightly narrowed anterior end. A deep longitudinal groove at the dorsal side of the cell body.

Distribution. Europe (Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Tikhonenkov et al., 2012), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000; Lee et al., 2005), North America (Lugo et al., 1990), South America (Larsen and Patterson, 1990).

Petalomonas minor Larsen et Patterson, 1990 (Fig. 3f).

Found. Primary mire lake Morotskoe (plankton – sample # 4a).

Description. BL=4.5–7μm; F=1×BL. Rhomboid cell body flattened ventrally and with a longitudinal keel at the dorsal side.

Distribution. Europe (Prokina et al., 2017a, 2017b), Asia (Lee, 2002; Tikhonenkov et al., 2012), Africa (Tikhonenkov, 2009), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000).

Petalomonas poosilla (Skuja, 1948) Larsen et Patterson, 1990 [bas.: *P. pusilla* Skuja, 1948] (Fig. 3g).

Found. Primary mire lake Morotskoe (benthos and plankton – samples ## 4a, 4b).

Description. BL=6–9 μm; F=1.5×BL. Elongated oval cell body with a slightly narrowed anterior end.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017, Prokina et al., 2017a, 2017b), Asia (Lee, 2002; Kopylov et al., 2006; Tikhonenkov et al., 2012), Africa (Tikhonenkov, 2009; Prokina et al., 2017c), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000; Lee et al., 2005), South America (Larsen and Patterson, 1990).

Petalomonas sp. (Fig. 3h–i).

Found. Primary mire lakes Morotskoe (plankton – sample # 4a) and Shichengskoe (benthos – sample # 5b).

Description. BL=11.5 μm; F=1.5×BL. Round to pear-shaped cell body densely covered with sticky particles, so that the cell surface is hard to observe.

Ploeotia obliqua (Klebs, 1893) Schroeckh et al., 2003 [bas.: Entosiphon obliquum Klebs, 1893] (Fig. 3j–k).

Found. Primary mire lakes Krugloe and Shichengskoe (benthos – samples ## 1b, 5b).

Description. BL=12–13 μm; AF=1×BL; PF=2.0–2.5×BL. Oval flattened cell body with prominent ingestion organelle from anterior and posterior ends, reminds a lemon in outline.

Distribution. Europe (Prokina and Mylnikov, 2017; Prokina et al., 2017a), Asia (Duangjan et al., 2017), Australia (Lee et al., 2005).

****Kinetoplastea Honigberg, 1963

*****Metakinetoplastina Vickerman in Moreira et al., 2004

******Neobodonida Vickerman in Moreira et al., 2004

Neobodo designis (Skuja, 1948) Moreira et al., 2004 [bas.: *Bodo designis* Skuja, 1948] (Fig. 3l–m).

Found. Primary mire lakes Kolodenskoe (plankton and benthos – samples ## 3a, 3b), Krugloe and Chyornoe (plankton – samples ## 1a, 2a) and Shichengskoe (benthos – sample # 5b) and secondary hollow-pools in Lajskoe mire (periphyton – sample # 7b) and Shichengskoe mire (plankton – sample # 9a).

Description. BL=8.0–9.5 μm; AF=1×BL; PF=2.0–2.5×BL. Elliptical, not flattened cell body with a rostrum at the anterior end. AF twisted around the cell body during feeding. Acronematic PF temporarily attached to substrate by its tip. Cells gliding on substrate with return movements or swim with rotations.

Distribution. Europe (Larsen and Patterson, 1990; Vørs, 1992; Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a, 2017b), Asia (Lee, 2002; Tikhonenkov et al., 2012), Africa (Tikhonenkov, 2009; Prokina et al., 2017c), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000; Lee et al., 2005), South America (Larsen and Patterson, 1990), Antarctica (Butler et al., 2000).

Rhynchomonas nasuta (Stokes, 1888) Klebs, 1893 [bas.: *Heteromita nasuta* Stokes, 1888] (Fig. 3n).

Found. Primary mire lakes Krugloe (plankton and benthos – samples ## 1a, 1b), Kolodenskoe (plankton and benthos – samples ## 3a, 3b) and Shichengskoe (benthos – sample # 5b) and secondary hollow-pools in Shichengskoe mire (plankton – sample # 9a).

Description. BL=4.5–6.5 μm; PF=2.5–3.0×BL; snout=0.5×BL. Oval flattened and flexible cell body

with high metaboly. AF located in the anterior snout, which is flapping slowly. A large CV located near the snout.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a, 2017b), Asia (Lee, 2002; Kopylov et al., 2006; Tikhonenkov et al., 2012), Africa (Prokina et al., 2017c), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000; Lee et al., 2005), North America (Lugo et al., 1990), South America (Larsen and Patterson, 1990), Antarctica (Hawthorn and Ellis-Evans, 1984; Butler et al., 2000).

******Eubodonida Vickerman in Moreira et al., 2004

Bodo saltans Ehrenberg, 1838 [syn.: *Pleuromonas jaculans* Perty, 1852] (Fig. 3o).

Found. Primary mire lakes Kolodenskoe (plankton and benthos – samples ## 3a, 3b), Morotskoe (plankton – sample #4a), Chyornoe and Shichengskoe (benthos – samples ## 2b, 5b) and secondary hollow-pools in Sestroretskoe mire (plankton – sample # 6a), Lajskoe mire (periphyton – sample # 7b) and Shichengskoe mire (plankton and periphyton – samples ## 9a, 9b).

Description. BL= 6.5–8.0 μm; AF=1×BL; PF= 2.5–3.5×BL. Oval cell body attached to substrate by PF, quickly changes its position on substrate.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a, 2017b), Africa (Prokina et al., 2017c), Australia (Lee et al., 2005), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012), North America (Lugo et al., 1990), Antarctica (Hawthorn and Ellis-Evans, 1984; Butler et al., 2000).

*****Incertae sedis Kinetoplastea

Bordnamonas tropicana Larsen et Patterson, 1990 (Fig. 3p).

Found. Primary mire lake Krugloe (benthos – sample # 1a).

Description. BL=5–8 μm; AF=1×BL; PF= 2×BL. Oval flattened and relatively rigid cell body with broad posterior and narrow anterior end. Thick non-acronematic flagella almost not moving and holding the arc position.

Distribution. Europe (Larsen and Patterson, 1990; Vørs, 1992; Prokina and Mylnikov, 2017; Prokina et al., 2017b), Asia (Lee, 2002), Australia (Larsen and Patterson, 1990; Lee and Patterson, 2000), South America (Larsen and Patterson, 1990).

**Jakobida Cavalier-Smith, 1993

***Histionidae Flavin et Nerad, 1993

Reclinomonas americana Flavin et Nerad, 1993 (Fig. 3q).

Found. Primary mire lake Krugloe (benthos – sample # 1a) and secondary hollow-pools of mire Lajskoe (plankton – sample # 7a).

Description. BL=4.5–5.0 μm; F=1.0–1.5×BL; StL=1×BL. Cell body occupies almost the whole cup-shaped lorica and oriented perpendicular to it. One flagellum is free, another lies in a ventral groove and undulates. Lorica attached to substrate by a short thin stalk.

Distribution. Europe (Prokina and Mylnikov, 2017; Prokina et al., 2017a), Australia (Lee et al., 2005).

Incertae sedis EUKARYOTA

Pseudophyllomitus apiculatus (Skuja, 1948) Lee, 2002 [bas.: *Phyllomitus apiculatus* Skuja, 1948] (Fig. 3r–s).

Found. Primary mire lakes Morotskoe (plankton – sample # 4a), Chyornoe and Shichengskoe (benthos – sample ## 2b, 5b).

Description. BL=8–9 μm; AF=1×BL; PF=1.5–2.0 ×BL. Oval not flattened rigid cell body oblique, truncated anteriorly, forming a rostrum. Cells swim fast with rotation or attached to substrate by its anterior end. Flagella twisted around the cell body when cells stop.

Distribution. Europe (Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina et al., 2017a), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012).

*Ancyromonadida Cavalier-Smith, 1998

Ancyromonas sigmoides Kent, 1880 [syn.: *Planomonas mylnikovi* Cavalier-Smith in Cavalier-Smith et al., 2008] (fig. 3t).

Found. Primary mire lakes Morotskoe (plankton and benthos – samples ## 4a, 4b), Krugloe and Shichengskoe (benthos – samples ## 1b, 5b) and secondary hollow-pools in Shichengskoe mire (plankton – sample # 9a).

Description. BL=3.5–5.5 μm; AF=1×BL; PF=2.5–3.0×BL. Round flattened cell body with a snout at the anterior end. AF insert from base of a snout, very thin and sometimes not visible. Snout contains a row of extrusomes.

Distribution. Europe (Vørs, 1992; Auer et al., 2003; Mylnikov and Kosolapova, 2004; Prokina

and Mylnikov, 2017; Prokina et al., 2017a, 2017b), Asia (Lee, 2002; Kopylov et al., 2006; Tikhonenkov et al., 2012), Africa (Tikhonenkov, 2009; Prokina et al., 2017c), Australia (Lee and Patterson, 2000; Lee et al., 2005), Antarctica (Butler et al., 2000).

*Cryptophyceae Pascher, 1913

**Goniomonas Stein, 1878

Goniomonas truncata (Fresenius, 1858) Stein, 1878 [bas.: *Monas truncata* Fresenius, 1858] (Fig. 3u).

Found. Primary mire lakes Krugloe, Shichengskoe (benthos – samples ## 1b, 3b, 5b), Kolodenskoe (plankton and benthos – samples ## 3a, 3b), Chyornoe and Morotskoe (plankton – samples ## 2a, 4a) and secondary hollow-pools in Shichengskoe mire (plankton– sample # 9a).

Description. BL=7.5–10.0 μm; F=0.5×BL. Round to oval flattened cell body with truncated anterior and rounded posterior end. Two equal short flagella insert subapically, oriented laterally and located near to each other. Two rows of extrusomes located near the anterior end of the cell body.

Distribution. Europe (Vørs, 1992; Auer and Arndt, 2001; Mylnikov and Kosolapova, 2004; Prokina and Mylnikov, 2017; Prokina et al., 2017a, 2017b), Asia (Kopylov et al., 2006; Tikhonenkov et al., 2012), Africa (Prokina et al., 2017c), Australia (Lee et al., 2005).

Discussion

In the studied mire water bodies, a total of 40 species and forms of heterotrophic flagellates were observed, from 32 genera and 3 supergroups (Opisthokonta, SAR, Excavata), as well as from groups of uncertain systematic position. The most common species were *Bodo saltans* (found in 9 samples), *Goniomonas truncata* and *Neobodo designis* (7 samples), *Rhynchomonas nasuta* (6 samples), and *Ancyromonas sigmoides* (5 samples). Fourteen rare species were found only in 1 sample: *Bordnamonas tropicana, Cercomonas* sp., *Codosiga botrytis, Heteronema globulifera, Jenningsia fusiforme, Jenningsia* sp., *Monosiga ovata, Neoheteromita* sp., *Petalomonas minor, Petalomonas* sp., *Reclinomonas americana, Salpingoeca clarki, S. minor*, and *Teretomonas rotunda.*

High species richness (19 species) was registered in the mire lake Shichengskoe. Among them, 8 species were unique (found only in this lake): *Anisonema ovale, Codosiga botrytis, Heteronema globulifera, Microcometes paludosa, Monosiga ovata, Neoheteromita* sp., *Salpingoeca clarki*, and *Teretomonas rotunda*. High species richness (17 species) was observed also in the mire lake Krugloe; two of them were unique: *Bordnamonas tropicana* and *Reclinomonas americana*. In the mire lake Morotskoe, 16 species were found (unique – *Anisonema acinus, Colponema* sp., *Jenningsia fusiforme, Jenningsia* sp., *Petalomonas minor, P. poosilla*, and *Petalomonas* sp.); 8 species were registered in the mire lake Kolodenskoe (unique – *Salpingoeca minor*). A hollow-pool in the Shichengskoe mire was inhabited by 8 species (unique – *Cercomonas* sp.). Low species richness was observed in a hollow-pool in the Lajskoe mire (6 species, unique – *Metobolomonas insania*), the mire lake Chyornoe (5 species, none unique), a hollow-pool in the Sestroretskoe mire (5 species, none unique), a hollow-pool in the Udebnoe mire (1 species, not unique).

In all investigated primary mire lakes, 37 species of heterotrophic flagellates were identified: *Agitata* aff. *agilis*, *Allantion tachyploon, Ancyromonas sigmoides*, ***Anisonema acinus, A. ovale, Bicosoeca exilis, B. lacustris***, *Bodomorpha* sp., *Bodo saltans*, ***Bordnamonas tropicana***, *Cercomonas granulifera*, ***Codosiga botrytis, Colponema* sp., *Entosiphon sulcatum***, *Goniomonas truncata*, ***Heteronema globulifera, Jenningsia fusiforme, Jenningsia sp., Microcometes paludosa, Monosiga ovata***, *Neobodo designis*, ***Neoheteromita*** sp., ***Notosolenus apocamptus, Petalomonas minor, P. poosilla, Petalomonas* sp., *Ploeotia obliqua***, *Protaspa simplex*, ***Pseudophyllomitus apiculatus, Reclinomonas americana***, *Rhynchomonas nasuta*, ***Salpingoeca clarki, S. minor***, *Sandona* sp., *Spongomonas uvella, Spumella* sp., ***Teretomonas rotunda***, and ***Thaumatomonas seravini***. Among them, 24 species were unique (in bold), found only in one water body. The average number of species in each mire lake was 13.

The data obtained in this study are in agreement with the data on species composition of heterotrophic flagellates of 14 mire lakes available in the literature. In Rdeysky Reserve, Novgorod region, 11 lakes were investigated: Russkoe (8 species were founded), Mezhnitskoe (16 species), Domchinskoe (31 species), Poddomshinskoe (17 species), Kornilovskoe (29 species), Ostrovistoe (42 species), Maloe Goretskoe (11 species), Bolshoe Goretskoe (17 species), Rogovskoe (12 species), Rdeiskoe (27 species), and Chudskoe (31 species) (Tikhonenkov,

2007/8). In Penza region, mire lake Svetloe was investigated, and 30 species were founded (Tikhonenkov and Mazei, 2007). In the Republic of Karelia, 2 mire lakes were studied: Vegarusyarvi (9 species) and Chuchyarvi (3 species) (Kosolapova and Kosolapov, 2011). A total of 104 species were identified in these lakes, among which 19 species were also found in mire lakes investigated in the present study: *Agitata* aff. *agilis, Allantion thchyploon, Ancyromonas sigmoides, Bicosoeca exilis, Bodo saltans, Cercomonas granulifera, Codosiga botrytis, Goniomonas truncata, Jenningsia fusiforme, Monosiga ovata, Neobodo designis, Notosolenus apocamptus, Petalomonas minor, P. poosilla, Reclinomonas americana, Protaspa simplex, Pseudophyllomitus apiculatus, Rhynchomonas nasuta*, and *Spongomonas uvella*. The average number of species in each of those lakes, similarly to our study, was high (21.2).

In the investigated hollow-pools, we found 15 species of heterotrophic flagellates: *Agitata* aff. *agilis*, *Allantion tachyploon, Ancyromonas sigmoides, Bodomorpha sp., Bodo saltans, Goniomonas truncata, Neobodo designis*, ***Metabolomonas insania***, *Cercomonas ranulifera*, ***Cercomonas* sp.**, *Protaspa simplex, Rhynchomonas nasuta, Sandona sp., Spongomonas uvella*, and *Spumella* sp. Only in these hollow-pools, 2 species marked in bold were found. The average number of species in each hollow-pool was 5.

Thus, in hollow-pools we observed lower species diversity in comparison with mire lakes. It can be explained by the more extreme pH values in hollow-pools (4.05 on average). In their evolution, hollow-pools were closely related to the hollows, and hence influenced by *Sphagnum* vegetation. While in mire lakes pH values were closer to normal (6.14 on average). Moderate positive correlation between pH values and species richness of heterotrophic flagellates was also shown previously in the other studies (Mazei et al., 2005; Prokina and Mylnikov, 2017; Prokina et al., 2017a). At the same time, water temperature in the sampled regions had no influence on the species diversity.

We did not find the information on species composition of heterotrophic flagellates in hollow-pools in the literature. However, there are data on the species composition of heterotrophic flagellates in hollows which, basically, are very similar to hollow-pools. In hollows of the same mires in the European North of Russia 37 species were registered earlier (Prokina et al., 2016). Among them, 6 species were common with hollow-pools, investigated in the present study: *Ancyromonas sigmoides, Bodo saltans, Cercomonas granulifera, Neobodo designis, Protaspa simplex*, and *Rhynchomonas nasuta*. The average number of species in each hollow, as well as in hollow-pools in the present study, was low: 7.4.

In each lake, samples were taken from the two microbiotopes, plankton and benthos or periphyton. In the benthos samples (## 1b, 2b, 3b, 4b, 5b, and 8b), 34 species (85% of the total number of species) were found: *Agitata* aff. *agilis*, *Allantion tachyploon, Ancyromonas sigmoides*, ***Anisonema acinus, A. ovale***, *Bicosoeca exilis*, ***B. lacustris***, *Bodo saltans, Bodomorpha* sp., ***Bordnamonas tropicana***, ***Cercomonas granulifera***, ***Codosiga botrytis***, *Colponema* sp., ***Entosiphon sulcatum***, *Goniomonas truncata*, ***Heteronema globulifera, Microcometes paludosa, Monosiga ovata***, *Neobodo designis,* ***Neoheteromita* sp.**, ***Notosolenus apocamptus***, *Petalomonas poosilla*, ***Ploeotia obliqua***, *Protaspa simplex, Pseudophyllomitus apiculatus*, ***Reclinomonas americana***, *Rhynchomonas nasuta*, ***Salpingoeca clarki, S. minor***, *Sandona* sp., *Spongomonas uvella, Spumella* sp., ***Teretomonas rotunda***, and *Thaumatomonas seravini*. Among them, 47 per cent (16 species) were unique (in bold). Average number of species in the sample was 9.

In the plankton samples (## 1a, 2a, 3a, 4a, 5a, 6a, 7a, 8a, and 9a), 19 species (47.5% of the total number of species) were found: *Aditata* aff. *agilis, Allantion tachyploon, Ancyromonas sigmoides, Bicosoeca exilis, Bodo saltans, Colponema sp., Goniomonas truncata*, ***Jenningsia fusiforme, Jenningsia* sp.**, *Metabolomonas insania, Neobodo designis*, ***Petalomons minor***, *P. poosilla*, ***Petalomons* sp.**, *Protaspa simplex, Pseudphyllomitus apiculatus, Rhynchomonas nasuta, Spumella* sp., and *Thaumatomonas seravini*. Out of them, 21 per cent (4 species) were unique (in bold). Average number of species in the sample was 4.7.

In the periphyton samples (## 6b, 7b, and 9b), 9 species (22.5% of the total number of species) were found: *Spumella* sp., *Cercomonas granulifera*, ***Cercomonas* sp.**, *Metabolomonas insania, Sandona sp., Bodomorpha sp., Spongomonas uvella, Neobodo designis*, and *Bodo saltans*. Only 1 species (11.1 per cent) was unique. Average number of species in the sample was 3.3.

Common species for plankton and benthos were *Agitata* aff. *agilis, Allantion tachyploon, Ancyromonas sigmoides, Bicosoeca exilis, Colponema sp., Goniomonas truncata, Petalomonas poosilla, Protaspa simplex, Pseudophyllomitus apiculatus, Rhynchomonas nasuta, Thaumatomonas seravini*

(11 species). Common species for plankton and periphyton was *Metabolomonas insania*. Common species for benthos and periphyton were *Bodomorpha* sp., *Cercomonas granulifera, Sandona* sp., *Spongomonas uvella* (4 species). Three species, *Bodo saltans, Neobodo designis, Spumella* sp., were common for all types of microbiotopes.

Thus, the higher species richness, greater number of unique species, as well as greater average number of species in each sample were recorded in benthos. This result can be explained by the fact that bottom sediments are rich in food items, especially bacteria (because most of heterotrophic flagellates are bacterivorous), detritus (for detritophages) as well as flagellates and other small protozoa (for predators). Moreover, the surface area of substrate is larger due to a great number of small particles of bottom sediments. This is important, because most species of heterotrophic flagellates are temporarily or permanently attached to substrate (choanoflagellates, bicosoecids, bodonids, histionids, etc.) or glide on its surface (glissomonads, cercomonads, euglenids, thaumatomonads, etc.). There is a considerably large number of species in plankton, and many heterotrophic flagellates have swimming forms, which can be registered in the plankton as well. However, the number of unique species therein is relatively low since the same species that were found in plankton were also found in benthos or periphyton.

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