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Free-living nematodes (Nematoda) of the Rokytská Slať and the Chalupská Slať peat bogs in the Bohemian Forest (Czech Republic)

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Abstract. Free-living nematodes were surveyed in the Rokytská Slať and the Chalupská Slať peat bogs in the Šumava Mts. in the eastern part of the Bohemian Forest, the Czech Republic. A total of 90 species were identified, 69 of which occurred in the Rokytská Slať and 66 in the Chalupská Slať. The majority of these nematodes belonged to the orders Dorylaimida (32%, mostly omnivorous *Eudorylaimus*), Araeolaimida (25%, mostly bacterivorous *Plectus*) and Tylenchida (20%, mostly root-fungal feeders *Filenchus*). Multivariate analyses revealed that the composition of nematode assemblages was more influenced by local conditions in individual patches of peaty soil than by the peat bog as a whole. Nevertheless, a certain effect of the peat bog on the nature of the nematode faunas was detected. Abundant populations of *Jensenonchus sphagni* indicated top-down control of nematode assemblages in the ombrotrophic Rokytská Slať peat bog. High values of the ΣMI and MI indices and low values of the PPI/MI ratio generally indicated that the peat bogs studied were in terms of habitats for free-living nematodes undisturbed or only slightly disturbed. Peat bogs thus can play an important role in the preservation of nematode diversity in the Šumava Mts. A significant change in the composition of the nematode assemblages can be used an indicator of the degradation of the peat bogs in the Šumava Mts.

Key words. Soil zoology, ecology, Nematoda, diversity, maturity, peatland, nature preservation, Šumava Mts., Bohemian Forest, Czech Republic.

INTRODUCTION

There are peat-forming wetlands (raised bogs, transition mires and fens) in a great variety of ecosystems in temperate regions. According to Franzén et al. (1996) almost all of the world's existing peat resources were formed during the Holocene. The main peatland areas of ca. $4.5 \times 10^6 \times km^2$ in extent are in the cold temperate zones north of 45°. It is also suggested that peat accumulation and decay play a decisive role in shifts between glacial and interglacial periods via affecting CO_2 levels in the atmosphere. Other scientists doubt a strong role of peat bogs in the course of glacial-interglacial cycles (Rohde & Malmer 1997). However, latest models suggest that carbon taken up by peatlands have substantial effects on the global carbon cycle and changes in climate (Kleinen et al. 2012). Whatever their role, however, peatlands have been an important part of Holocene European landscapes and their initiation, development and persistence has varied with climate and human activities (e.g. Cubizolle et al. 2012, Grootjans et al. 2012). In the Czech Republic peaty areas occupied about 50,000 ha (Veselý 1954), but have gradually been reduced by human activities to about one half of this area (Kolibáčová et al. 2001) and are listed as peatlands within Wetland Ramsar Sites in the Czech Republic (AOPK ČR – Nature Conservation Agency of the Czech Republic, www.ochranaprirody.cz/wps/portal/cs/aopkcr). Undisturbed peatland areas are however smaller because Nature Reserves have relatively large buffer zones. On the other hand there are many smaller peatland sites of about several hectares in size and even peat plots covering small areas can provide refuge habitats for peatland biota in landscapes strongly altered by human activities.

Some groups of soil fauna such as testate amoebae can be used to study the past as their shells are preserved in peat for millennia and can be used for palaeoclimatic reconstruction (Amesbury et al. 2008). Soft bodies of nematodes are not preserved in peat layers. However, nematodes are a very promising group for detecting recent changes in environmental conditions (Wilson & Kakouli-Duarte 2009, Neher 2010). Wasilewska (1991) and Háněl (1997) document marked changes in nematode communities associated with a rapid decrease in soil carbon content following drainage of peat meadows. Nematodes such as the plant-parasite *Paratylenchus* increase greatly in abundance after drainage and can contribute to the mineralization of carbon, which is immobilized in peat layers.

Many of the species of nematodes that occur in peaty soils are also common in surrounding ecosystems but there are also specific components. Studies on nematodes in European mires have revealed great variations in the composition of their communities, as first reported by Overgaard Nielsen (1949) in Denmark and Banage (1962) in England. In addition, there are studies on peat soil nematodes extending from northern latitudes to Central Europe by Sohlenius et al. (1997) and Sohlenius & Boström (1999) for those in mires in Sweden. Solov'eva (1986) documents the nematodes in bog meadows in Karelia and Shlepetene (1986) the nematode faunas of mires in Lithuania. The nematodes in peat-soil systems in Poland have been extensively studied (e.g. Dmowska 1993, Ilieva-Makulec 2000, 2004, Háněl 2007, Wasilewska 1991, 2002, 2006). There is a paper by Šály (1981) on peat-moor nematodes in Slovakia (Šály 1981) and data on peat bog nematodes at a number of other localities in his other studies (e.g. Šály & Žuffa 1980). The latest study on peatland nematodes in Slovakia is by Renčo & Murín (2013). Háněl (1997) evaluates soil nematode assemblages in peat meadows and the changes that occurred after drainage in South Bohemia. Hoschitz & Kaufmann (2004) give an account of nematodes in a high mountain peat bog in Austria.

The southern mountain range in Bohemia in the Czech Republic is mainly covered with forests. Nevertheless, there are many smaller or larger areas of peat bogs there, which are very valuable natural sites. These peat bogs covered considerably larger areas in the past but have been, step by step, reduced for silvicultural purposes or drained to establish meadows and pastures. Some sites were damaged by the extraction of peat. According to AOPK ČR the total area of peatland in the Šumava Mts. is 102 km^2 (10,200 ha). The web-site of the Šumava National Park (www.npsumava.cz) gives an estimate of 5,900 ha, which includes sites of a minimum size of 0.5 ha and minimum peat-layer thickness of 30 cm. Free-living nematodes in the Šumava Mts., which are also referred to as the Bohemian Forest or Silva Gabreta, were mainly studied in spruce forests, which were damaged by industrial emissions or bark beetle outbreaks followed by large-scale salvage logging (Háněl 1992, 1996, 1998, 1999, 2004). The root-fungal feeders of the family Tylenchidae mostly dominate the soil nematode faunas in spruce forest. Within this trophic group small species of *Filenchus*, which feed on fungi, prevail in healthy spruce forests and are much rarer in dead spruce forests. After salvage logging understorey grass densities increase and *Aglenchus agricola*, which feeds on epidermal cells and root hairs of grass, outnumbered *Filenchus* species and are the dominant representative of the family Tylenchidae (Háněl 2004). *Aglenchus agricola* is also the most dominant nematode recorded in a *Nardus stricta* L. stand growing between spruce forest and a peat bog (Háněl 1999), where a relatively abundant populations of the predacious *Jensenonchus sphagni* and *Tripyla setifera* were also recorded. The peat bogs in the Šumava Mts. have a specific flora and fauna (Albrecht et al. 2003) but their soil microfauna is practically unknown. The present paper is the first study of the nematode fauna inhabiting these peat bogs. The aim of this study was: (i) to survey free-living nematodes assemblages in two large peat bogs in the Šumava Mts., and (ii) to evaluate the naturalness of these nematode assemblages as a possible bioindicator for detecting the effect upon biota of expected future changes in climate and environment.

MATERIALS AND METHODS

Descriptions of the sites

The peat bogs in the Šumava Mts. started developing ca. 10,000–13,000 years ago (Svobodová & Soukupová 2000) when the climate was cold and wet (Quitt 1971) in areas of the Moldanubicum where the parent rocks are silicates (mainly metamorphosed paragneisses with migmatites, and Variscan granitoids in some areas) (Svoboda 1966, Ložek 2001). Prevailing soil types in mires are acidic raised and transitional histosols, typical and gleyed (Petruš & Neuhäuslová 2001) with pH of 2.7–3.9 (Skuhravý & Mrázková 2000).

There are basically two types of peat bogs or mires, with natural vegetation of the *Oxycocco-Sphagnetea* and *Scheuchzerio-Caricetea fuscae* classes (Soukupová 1996, Sofron 2001): (i) Raised mountain peat bogs (sloping mires, mountain mires) that develop on gentle slopes on high altitude plains in the surroundings of springs and were formed by paludification. (ii) Alluvial valley peat bogs (valley raised-bogs, valley mires) that develop along rivers and their tributaries and formed by terrestrialization. Those areas of mountain peat bogs covered with woody plants are generally covered by the association *Sphagno magellanici-Pinetum mughi* with dwarf pine *Pinus x pseudopumilio* (Wilk.) Beck and those of valley peat bogs with the association *Pino rotundatae-Sphagnetum* with *Pinus rotundata* Link. Treeless areas are occupied by fen communities of the alliances *Sphagno recurvi-Caricion canescentis*, *Leuco-Scheuchzerion palustris*, *Caricion demissae*, *Sphagnion medii* or *Oxycocco-Empetrion hermaphroditi*. In the contact zones there are dwarf and bog spruce forests *Sphagno-Piceetum* and *Mastigobryo-Piceetum*, along with waterlogged birch, willow and alder woods.

These peat bogs are valuable refuges for relic populations of invertebrates and details of the vegetation and fauna can be found in Albrecht et al. (2003) or papers devoted to particular groups such as the one on oribatid mites by Starý (2006). To carry out a preliminary survey of free-living nematodes in these habitats two peat bogs were studied.

Rokytská Slať peat bog: Ombrotrophic nutrient-poor mountain peat bog west of Roklanský potok stream (a part of the Modrava peat bogs complex) with 69 small lakes, area 142 ha, 1073–1119 m a. s. l., 49° 01’ 10.6” N, 13° 25’ 06.4” E. Samples were taken from patches of vegetation growing on peaty soils (microhabitats) on 16 July 2001 as follows:
R1: Central part of the lagg with *Pinus* × *pseudopumilio* (Wilk.) Beck, *Sphagnum russowii* (Warnst.) Cardot, *Vacinium myrtillus* L., *Vaccinium uliginosum* L.;
R2: Inner margin of the central part of the *Pinus* × *pseudopumilio*, *Vaccinium uliginosum*, *Eriophorum vaginatum* L., *S. russovii*, *Sphagnum magellanicum* Brid., *Aulacomnium palustre* (Hedw.) Schwaegr., *Mylia anomala* (Hook.) Mitt.;
R3: Central open part of the lagg, *Eriophorum vaginatum*;
R4: Central open part of the lagg, *Sphagnum magellanicum*, *Vaccinium uliginosum*;
R5: Central open part of the lagg, *Polytrichum strictum* Menz. et Brid.;
R6: Central open part of the lagg, *Sphagnum majus* (Russow) C.E.O. Jensen;
R7: Central open part of the lagg, *Drosera rotundifolia* L.;
R8: Central open part of the lagg, transitional zone between waterlogged Norway spruce *Picea abies* (L.) Karst. and dwarf pine *Pinus* × *pseudopumilio* wood with *S. russowii*;
R9: Central open part of the lagg, *Pinus* × *pseudopumilio* with *Vacinium myrtillus* and *Sphagnum* spp.;
R10: Ravine below peat bog with *Betula nana* L., *Vacinium uliginosum*, *Melampyrum pratense* L., mosses;
R11: Slough in the phytocoenosis *Carici rostratae-Sphagnetum recurvi* with bog moss *Sphagnum fallax* H. Klinggr.

Chalupská Slať peat bog: Transitional mountain-valley peat bog with a large central lake in a shallow valley of the Vydří potok stream north of Borová Lada, area 137 ha, 898–940 m a. s. l., 49° 00’ 11.2” N, 13° 39’ 43.0” E. Samples were taken from patches of vegetation growing in peaty soils (microhabitats) on 17 July 2001 as follows:
C1: Central part of peat bog ca. 1 m from the lake, *Eriophorum angustifolium* Honck., *E. vaginatum*, *Oxycoccus palustris* Pers., *Sphagnum fallax*;
C2: Central part of peat bog ca. 5 m from the lake, crowberry *Empetrum hermaphroditum* (Lge.) Hager., *Eriophorum vaginatum*, *Vacinium uliginosum*, *Melampyrum pratense*, *Sphagnum magellanicum*, *Calluna vulgaris* (L.) Hull.;
C3: Central part of peat bog ca. 10 m from the lake, *Eriophorum hermaphroditum*, *E. vaginatum*, *Vacinium uliginosum*, *Melampyrum pratense*, *Sphagnum magellanicum*, *Calluna vulgaris*;
C4: Central part of peat bog ca. 10 m from the lake, *Vacinium uliginosum*, *V. myrtillus*, *Aulacomnium palustre*, *Sphagnum flexuosum* Dozy et Molk., *S. magellanicum*, *Pleurozium schreberi* (Brid.) Mitt.;
C5: Norway spruce forest with blueberry *Vaccinium vitis-idaea* L., *V. uliginosum*, *V. myrtillus*, *Sphagnum flexuosum*, *Dicranum scoparium* Hedw., sample taken from a patch of *S. flexuosum*;
C6: Norway spruce forest with *Vaccinium vitis-idaea*, *V. uliginosum*, *V. myrtillus*, *Sphagnum flexuosum*, *Dicranum scoparium*, sample taken from a patch of *D. scoparium*;

C7: *Pinus x pseudopumilio* and *Betula pubescens* Ehrh. with *Vaccinium myrtillus*, *V. vitis-idaea*, *Eriophorum hermaphroditum*, *Oxycoccus palustris*, *Pleurozium schreberi*, *Aulacomnium palustre*, *Sphagnum magellanicum* and *S. flexuosum*;
C8: Moor near the north-eastern margin of the Chalupská Slať peat bog, *Menyanthes trifoliata* L., *Carex rostrata* Stok., *C. panicea* L., *C. pulicaris* L., *Trichophorum alpinum* (L.) Pers., *Eriophorum angustifolium*, *Potentilla erecta* (L.) Hampe and *Andromeda polifolia* L.;
C9: Moor near the north-eastern margin of the Chalupská Slať peat bog, *Carex vulgaris*, *Sphagnum fuscum* (Schimp.) Klinggr., *Polytrichum strictum*, *Oxycoccus palustris* and *Andromeda polifolia*.

Sampling and identification of nematodes

Peat soil samples were collected by my late colleague Dr. Vladimír Balík (specialist in testate amoebae) who also supplied details of the microhabitats. From each microhabitat a sample of 10×10 cm was collected from a depth of 10–15 cm, using a metal frame and a garden trowel, and carefully hand-mixed. A part of each sample was used for a study of testate amoebae the results for which are unpublished. From the rest of each sample 20 grams of the wet substrate were used for a semi-quantitative estimate of nematode populations. Nematodes were isolated from peat soil using modified Baermann funnels, preserved in a 3.5% solution of formaldehyde and mounted in glycerol on slides as described by Háněl (2010). In the tables nematode abundance is expressed as the number of individuals per 10 grams of fresh peaty soil. A total of 4,278 nematodes were identified.

For the determination of species (Table 1) I used mainly the latest books of Andrássy (2005, 2007, 2009), the book by Brzeski (1998), and a lot of other publications dealing with individual taxonomic groups of nematodes and mostly cited in the books mentioned above; plus the latest papers. Nematodes were allocated to trophic groups (Table 2) using information in Yeates et al. (1993) and more recent papers (e.g. Okada et al. 2005).

Nematode community indices and statistical analyses

Numbers of nematode species and genera and the Shannon index H‘gen (using natural logarithms and calculated for genera) were used as indices of nematode diversity. Maturity index (MI), Plant parasite index (PPI) and the PPI/MI ratio according to Bongers (1990) and Sum maturity index ΣMI according to Yeates (1994) were used to evaluate maturity of nematode assemblages and assess their natural condition. *Cp*-values of nematode taxa were used according to Bongers & Bongers (1998). STATISTICA Cz (StatSoft Inc. 2001) and CANOCO for Windows (Ter Braak & Šmilauer 2002) were used for statistical evaluation of the data (*t*-test on *ln*(x+1) transformed abundance, Mann-Whitney *U* test, Detrended Correspondence Analysis, Principal Component Analysis, Cluster Analysis).

RESULTS

Species, genera and orders of nematodes

A total of 90 species were recorded for the two peat bogs, 69 at Rokytská Slať and 66 at Chalupská Slať (Table 1). Some species could not be identified because few specimens were collected or their body measurements differed from those recorded for described species. These species belonged to 46 genera and at each peat bog 34 genera were recorded (Table 2). Significant differences ($p<0.05$) in the abundances of the different genera recorded at the two pest bogs were detected only for *Rhabdolaimus*, *Heterocephalobus*, *Deladenus*, and *Jensenonchus* (*t*-test on *ln*(x+1) transformed abundance, Mann-Whitney *U* test).

The percentage of individuals belonging the different nematode orders at Rokytská Slať and Chalupská Slať were as follows: Monhysterida (1.14 and 1.82, respectively), Araeolaimida (19.03 and 32.25), Chromadorida (0.04 and 0.28), Rhabditida (6.74 and 8.71), Aphelenchida (3.86 and 6.06), Tylenchida (22.85 and 16.37), Enoplida (5.88 and 2.65), Alaimida (0.41 and 0.50), Mononchida (7.02 and 0.55) and Dorylaimida (33.04 and 30.82%). The abundance of Mononchida was significantly greater ($p<0.05$) at Rokytská Slať than Chalupská Slať but the abundance of the other orders did not differ significantly at these two peat bogs.

Multivariate analyses of nematode assemblages

Species presence was analyzed using the ordination methods in the CANOCO package. Detrended Correspondence Analysis with detrending by segments extracted four ordination axes with cumulative percentage variance of species data 14.3%, 22.3%, 26.7%, and 29.3%, which revealed that the length of gradient along the first ordination axis was 2.890 SD. Because the correspon-

Table 1. Check-list of nematode species and the frequency of their occurrence F[%] recorded in the patches of vegetation at Rokytská Slať (R) and Chalupská Slať (C). Classes: Torquentia (TO), Secernentia (SE) and Penetrantia (PE)

	species in orders	F[%] R	F[%] C
TO	Monhysterida		
1	*Cylindrotheristus* sp. (cf. *vesentiniae* (Andrássy, 1962))	9.1	–
2	*Eumonhystera longicaudatula* (Gerlach & Riemann, 1973)	72.7	66.7
3	*Eumonhystera* Andrássy, 1981 sp.	18.2	11.1
TO	Araeolaimida		
4	*Aphanolaimus attentus* de Man, 1880	–	11.1
5	*Rhabdolaimus aquaticus* de Man, 1880	9.1	–
6	*Rhabdolaimus* cf. *minor* Cobb, 1914	36.4	–
7	*Rhabdolaimus terrestris* de Man, 1880	45.5	11.1
8	*Chronogaster boettgeri* Kischke, 1956	18.2	–
9	*Plectus acuminatus* Bastian, 1865	27.3	66.7
10	*Plectus communis* Bütschli, 1873	72.7	77.8
11	*Plectus decens* Andrássy, 1985	90.9	77.8
12	*Plectus geophilus* de Man, 1880	18.2	44.4
13	*Plectus longicaudatus* Bütschli, 1873	63.6	44.4
14	*Plectus parietinus* Bastian, 1865	–	11.1
15	*Plectus* cf. *turricaudatus* Truskova, 1976	9.1	–
16	*Wilsonema otophorum* (de Man, 1880)	9.1	–
17	*Wilsonema schuurmansstekhoveni* (De Coninck, 1931)	27.3	33.3
18	*Euteratocephalus spiraloides* (Micoletzky, 1913)	9.1	11.1
19	*Metateratocephalus crassidens* (de Man, 1880)	27.3	22.2
20	*Metateratocephalus gracilicaudatus* Andrássy, 1985	81.8	22.2
TO	Chromadorida		
21	*Prodesmodora arctica* (Mulvey, 1969)	–	11.1
22	*Achromadora semiarmata* Altherr, 1952	9.1	11.1
SE	Rhabditida		
23	*Teratocephalus costatus* Andrássy, 1958	18.2	11.1
24	*Teratocephalus dadayi* Andrássy, 1968	45.5	11.1
25	*Teratocephalus lirellus* Anderson, 1969	18.2	11.1
26	*Teratocephalus paratenuis* Eroshenko, 1973	9.1	22.2
27	*Teratocephalus terrestris* Bütschli, 1873	36.4	44.4
28	*Heterocephalobus elongatus* (de Man, 1880)	–	55.6
29	*Acrobeloides basilogoodeyi* (Brzeski, 1961)	9.1	11.1
30	*Acrobeloides nanus* (de Man, 1880)	45.5	66.7
31	*Deficephalobus humophilus* Zell, 1987	9.1	–
32	*Rhabditis terricola* Dujardin, 1845	18.2	22.2
33	*Bunonema reticulatum* Richters, 1905	18.2	11.1
34	*Bunonema richtersi* Jägerskiöld, 1905	9.1	–
35	*Steinernema* Travassos, 1927 juv. (dauer larvae)	–	11.1
SE	Aphelenchida		
36	*Aphelenchoides conimucronatus* Bessarabova, 1966	72.7	66.7
37	*Aphelenchoides* cf. *parasubtenius* Shavrov, 1967 s.l.	54.5	66.7
38	*Aphelenchoides saprophilus* Franklin, 1957	9.1	33.3
39	*Aphelenchoides* Fischer, 1894 sp. 1	27.3	–
40	*Aphelenchoides* Fischer, 1894 sp. 2	–	11.1
41	*Aphelenchoides* Fischer, 1894 sp. 3	–	11.1
SE	Tylenchida		
42	*Aglenchus agricola* (de Man, 1884)	45.5	44.4
43	*Filenchus discrepans* (Andrássy, 1954)	27.3	55.6
44	*Filenchus facultativus* (Szczygieł, 1970)	18.2	11.1
45	*Filenchus infirmus* (Andrássy, 1954)	9.1	22.2
46	*Filenchus istvani* Zell, 1988	9.1	–

Table 1. (continued)

	species in orders	F[%] R	F[%] C
47	*Filenchus misellus* Andrássy, 1958 s.l.	63.6	77.8
48	*Filenchus orbus* (Andrássy, 1954)	–	11.1
49	*Filenchus spicatus* (Brzeski, 1986)	27.3	11.1
50	*Filenchus vulgaris* (Brzeski, 1963)	–	11.1
51	*Tylenchus davainei* Bastian, 1865	9.1	11.1
52	*Malenchus acarayensis* Andrássy, 1968	18.2	22.2
53	*Malenchus gratiosus* Andrássy, 1981	45.5	55.6
54	*Malenchus neosulcus* Geraert & Raski, 1986	27.3	–
55	*Pleurotylenchus sachsi* (Hirschmann, 1952)	9.1	–
56	*Lelenchus leptosoma* (de Man, 1880)	9.1	–
57	*Ecphyadophora tenuissima* de Man, 1921	18.2	–
58	*Ditylenchus elegans* Zell, 1988	36.4	33.3
59	*Ditylenchus ferepolitor* (Kazachenko, 1980)	9.1	44.4
60	*Ditylenchus parvus* Zell, 1988	–	11.1
61	*Ditylenchus silvaticus* Brzeski, 1991	–	11.1
62	*Ditylenchus tenuidens* Gritzenko, 1971	9.1	11.1
63	*Helicotylenchus* Steiner, 1945 sp. juv.	9.1	–
64	*Paratylenchus nanus* Cobb, 1923	9.1	–
65	*Gracilaus straeleni* (de Coninck, 1931)	–	11.1
66	*Crossonema menzeli* (Stefański, 1924)	9.1	–
67	*Deladenus* cf. *aridus* Andrássy, 1957	–	55.6
PE	Enoplida		
68	*Ironus ignavus* Bastian, 1865	–	11.1
69	*Prismatolaimus dolichurus* de Man, 1880	63.6	88.9
70	*Prismatolaimus* de Man, 1880 sp.	9.1	–
71	*Tripyla setifera* Bütschli, 1873	27.3	–
PE	Alaimida		
72	*Alaimus jaulasali* Siddiqi et Husain, 1967	27.3	33.3
73	*Paramphidelus dolichurus* (de Man, 1876)	18.2	–
PE	Mononchida		
74	*Mononchus truncatus* Bastian, 1865	–	11.1
75	*Jensenonchus sphagni* (Brzeski, 1960)	63.6	11.1
PE	Dorylaimida		
76	Dorylaimidae (*Drepanodorylaimus* Jairajpuri, 1966) spp. (1♀ + juvs.)	–	11.1
77	*Mesodorylaimus* cf. *bastiani* (Bütschli, 1873)	–	11.1
78	*Paractinolaimus macrolaimus* (de Man, 1880)	9.1	11.1
79	*Epidorylaimus agilis* (de Man, 1880)	9.1	–
80	*Epidorylaimus consobrinus* (de Man, 1918)	9.1	–
81	*Eudorylaimus altherri* Tjepkema, Ferrris & Ferris, 1971	9.1	–
82	*Eudorylaimus brevis* (Altherr, 1952)	45.5	33.3
83	*Eudorylaimus discolaimioideus* (Andrássy, 1958)	45.5	44.4
84	*Eudorylaimus familiaris* Winiszewska-Ślipińska, 1987	63.6	11.1
85	*Eudorylaimus* Andrássy, 1959 sp.1	72.7	77.8
86	*Eudorylaimus* Andrássy, 1959 sp.2	36.4	–
87	*Eudorylaimus* Andrássy, 1959 sp.3	–	11.1
88	*Aporcelaimellus obtusicaudatus* (Bastian, 1865)	–	11.1
89	*Tylencholaimus* cf. *chathami* Yeates, 1979	–	11.1
90	*Tylencholaimus stecki* Steiner, 1914	–	22.2
	total number of species	69	66

Table 2. Mean abundance (mean) and minimum–maximum abundance (min–max) of nematodes per 10 g of fresh peaty soil and dominance (D%) and frequency of occurrence (F%) of nematode genera recorded in patches of vegetation at Rokytská Slať and Chalupská Slať. For the key to abbreviated names see Fig. 2

peat bog		Rokytská Slať peat bog				Chalupská Slať peat bog			
genera in trophic groups	name	mean	min–max	D%	F%	mean	min–max	D%	F%
bacterivores									
Plectus Bastian, 1865	*Plectu*	12.2	1.0–38.0	10.88	100.0	30.4	2.5–95.50	30.15	100.0
Acrobeloides Cobb, 1924	*Acrdes*	3.1	0.0–22.0	2.72	54.6	4.6	0.0–14.0	4.58	66.7
Prismatolaimus de Man, 1880	*Prisma*	4.2	0.0–26.5	3.73	72.7	2.2	0.0–5.0	2.15	88.9
Teratocephalus de Man, 1876	*Terato*	4.2	0.0–32.0	3.77	63.6	2.1	0.0–8.5	2.04	44.4
Rhabdolaimus de Man, 1880	*Rhbdol*	4.4	0.0–31.0	3.90	63.6	0.1	0.0–0.5	0.06	11.1
Metateratocephalus Eroshenko, 1973	*Metate*	2.9	0.0–7.5	2.60	90.9	1.4	0.0–6.0	1.38	44.4
Eumonhystera Andrássy, 1981	*Eumonh*	1.2	0.0–6.5	1.10	81.8	1.8	0.0–4.5	1.82	66.7
Heterocephalobus Brzeski, 1960	*Heceph*	–	–	–	–	1.4	0.0–6.0	1.38	55.6
Euteratocephalus Andrássy, 1958	*Eutera*	0.9	0.0–10.0	0.81	9.1	0.1	0.0–0.5	0.06	11.1
Wilsonema Cobb, 1913	*Wilson*	0.4	0.0–3.0	0.37	36.4	0.6	0.0–3.0	0.55	33.3
Alaimus de Man, 1880	*Alaimu*	0.2	0.0–1.0	0.20	27.3	0.5	0.0–2.5	0.50	33.3
Chronogaster Cobb, 1913	*Chrono*	0.6	0.0–4.5	0.49	18.2	–	–	–	–
Bunonema Jägerskiöld, 1905	*Bunone*	0.1	0.0–1.0	0.12	18.2	0.2	0.0–2.0	0.22	11.1
Paramphidelus Andrássy, 1977	*Paramp*	0.2	0.0–2.0	0.20	18.2	–	–	–	–
Prodesmodora Micoletzky, 1923	*Prodes*	–	–	–	–	0.2	0.0–2.0	0.22	11.1
Rhabditis Dujardin, 1845	*Rhabdi*	0.1	0.0–0.5	0.08	18.2	0.1	0.0–0.5	0.11	22.2
Achromadora Cobb, 1913	*Achrom*	0.1	0.0–0.5	0.04	9.1	0.1	0.0–0.5	0.06	11.1
Cylindrotheristus Wieser, 1956	*Cyther*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
Aphanolaimus de Man, 1880	*Aphano*	–	–	–	–	0.1	0.0–0.5	0.06	11.1
Deficephalobus De Ley et Coomans, 1990	*Defice*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
fungivores									
Aphelenchoides Fischer, 1894	*Aphdes*	4.3	0.0–14.0	3.86	90.9	6.1	0.0–15.0	6.06	77.8
Ditylenchus Filipjev, 1936	*Dityle*	2.4	0.0–8.5	2.11	54.6	2.3	0.0–7.5	2.26	66.7
Tylencholaimus de Man, 1876	*Tylmus*	–	–	–	–	0.3	0.0–1.5	0.33	33.3
Deladenus Thorne, 1941	*Delade*	–	–	–	–	0.3	0.0–0.5	0.28	55.6
root-fungal feeders									
Filenchus Andrássy, 1954	*Filenc*	17.0	0.0–123.5	15.18	81.8	7.7	0.0–18.0	7.61	77.8
Malenchus Andrássy, 1968	*Malenc*	5.1	0.0–17.0	4.55	54.6	4.0	0.0–10.0	3.97	55.6
Tylenchus Bastian, 1865	*Tylenc*	0.1	0.0–0.5	0.04	9.1	1.6	0.0–14.5	1.60	11.1
Aglenchus Andrássy, 1954	*Aglenc*	0.7	0.0–3.0	0.65	45.5	0.6	0.0–3.0	0.61	44.4
Ecphyadophora de Man, 1921	*Ecphya*	0.1	0.0–0.5	0.08	18.2	–	–	–	–
Pleurotylenchus Szczygieł, 1969	*Pllenc*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
Lelenchus Andrássy, 1954	*Lelenc*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
plant parasites									
Paratylenchus Micoletzky, 1922	*Paraty*	0.1	0.0–1.0	0.08	9.1	–	–	–	–
Helicotylenchus Steiner, 1945	*Helico*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
Gracilacus Raski, 1962	*Gracil*	–	–	–	–	0.1	0.0–0.5	0.06	11.1
Crossonema Mehta et Raski, 1971	*Crosso*	0.1	0.0–0.5	0.04	9.1	–	–	–	–
omnivores									
Eudorylaimus Andrássy, 1959	*Eudory*	35.7	0.5-114.0	31.90	100.0	27.7	4.0-101.0	27.51	100.0
Epidorylaimus Andrássy, 1986	*Epidor*	0.5	0.0–3.5	0.45	18.2	–	–	–	–
Aporcelaimellus Heyns, 1965	*Aprcll*	–	–	–	–	0.3	0.0–3.0	0.33	11.1
Dorylaimidae	*Dormid*	–	–	–	–	0.2	0.0–2.0	0.22	11.1
Mesodorylaimus Andrássy, 1959	*Mesodo*	–	–	–	–	0.2	0.0–1.5	0.17	11.1
predators									
Jensenonchus Jairajpuri et Khan, 1982	*Jensen*	7.9	0.0–26.5	7.02	63.6	0.5	0.0–4.5	0.50	11.1

Table 2. (cintinued)

peat bog genera in trophic groups	name	Rokytská Slať peat bog mean	min–max	D%	F%	Chalupská Slať peat bog mean	min–max	D%	F%
Paractinolaimus Meyl, 1957	*Paract*	0.8	0.0–8.5	0.69	9.1	2.3	0.0–20.5	2.26	11.1
Tripyla Bastian, 1865	*Tripyl*	2.4	0.0–16.5	2.15	27.3	–	–	–	–
Ironus Bastian, 1865	*Ironus*	–	–	–	–	0.5	0.0–4.5	0.50	11.1
Mononchus Bastian, 1865	*Mononc*	–	–	–	–	0.1	0.0–0.5	0.06	11.1
insect parasites									
Steinernema Travassos, 1927 juv.	*Steinl*	–	–	–	–	0.4	0.0–3.5	0.39	11.1

dence analysis explained only a small part of variance in species composition and the gradient length along the first ordination axis was <3 SD, a Principal Component Analysis (PCA) was used (Fig. 1). Samples from both peat bogs were scattered along the first ordination axis. Along the second ordination axis the greater part of samples from Rokytská Slať were in the upper part and those from the Chalupská Slať in the lower part of the ordination diagram. PCA of the nematode genera abundance (*ln*(y+1) transformed) resulted in a similar picture (Fig. 2).

Dendrogram based on a Cluster Analysis of the *ln*(y+1) transformed abundances of genera placed the samples on the right hand side of the PCA first ordination axis in the upper cluster (except for C9) and those on the left hand side of the PCA first ordination axis in the lower cluster (Fig. 3). It is very likely that the composition of the nematode assemblages was more influenced by the conditions in individual peaty patches of soil than their being located at a particular peat

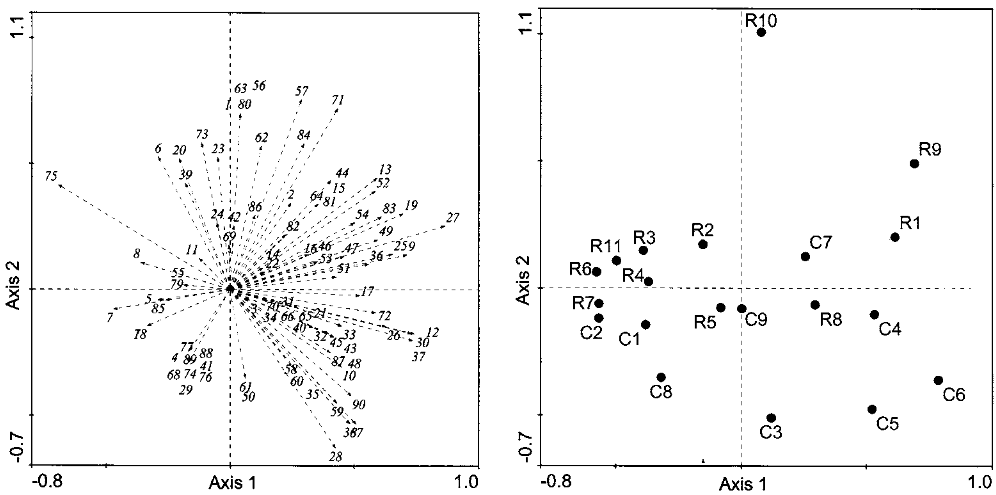

Fig. 1. Principal component analysis of species occurrence (for species numbers see Table 1) in patches of vegetation at Rokytská Slať (R) and Chalupská Slať (C). Eigenvalues for ordination axes 1, 2, 3 and 4 were 0.200, 0.109, 0.089 and 0.083, respectively. Cumulative percentage variance of species data for ordination axes 1, 2, 3 and 4 were 20.0, 30.9, 39.8 and 48.2, respectively.

Table 3. Mean abundance (mean) and minimum–maximum abundance (min–max) of nematodes per 10 g of fresh peaty soil and dominance (D%) and frequency of occurrence (F%) of the different nematode trophic groups and mean and minimum–maximum values (min–max) of nematode community indices recorded for patches of vegetation at Rokytská Slať and Chalupská Slať

peat bog	Rokytská Slať peat bog				Chalupská Slať peat bog			
trophic groups and indices	mean	min–max	D%	F%	mean	min–max	D%	F%
bacterivores	34.8	8.0–84.0	31.09	100.0	45.7	4.0–109.0	45.31	100.0
fungivores	6.7	0.0–20.5	5.97	90.9	9.0	0.0–24.0	8.93	88.9
root-fungal feeders	23.1	0.5–138.5	20.58	100.0	13.9	0.0–40.0	13.78	77.8
plant parasites	0.2	0.0–1.0	0.16	27.3	0.1	0.0–0.5	0.06	11.1
omnivores	36.2	0.5–117.5	32.35	100.0	28.4	4.0–101.0	28.22	100.0
predators	11.1	0.0–26.5	9.86	81.8	3.3	0.0–25.5	3.31	22.2
insect parasites	0	0–0	0	0	0.4	0.0–3.5	0.39	11.1
sum of all individuals	112.0	12.5–263.0	100.0	100.0	100.8	20.5–232.5	100.0	100.0
species	20	10–33			19	4–30		
genera	13	9–21			12	4–20		
H'gen	1.79	1.42–2.10			1.75	1.09–2.29		
ΣMI	3.04	2.52–3.39			2.89	2.16–4.03		
MI	3.21	2.71–3.58			2.98	2.18–4.21		
PPI	2.00	2.00–2.02			2.00	2.00–2.00		
PPI/MI	0.63	0.56–0.74			0.72	0.48–0.92		

bog. Nevertheless, the nematode faunas at the two bogs differed. For example, as can be seen in Table 1 and 2, there was a greater frequency of occurrence and abundance of *Jensenonchus sphagni* at Rokytská Slať than Chalupská Slať.

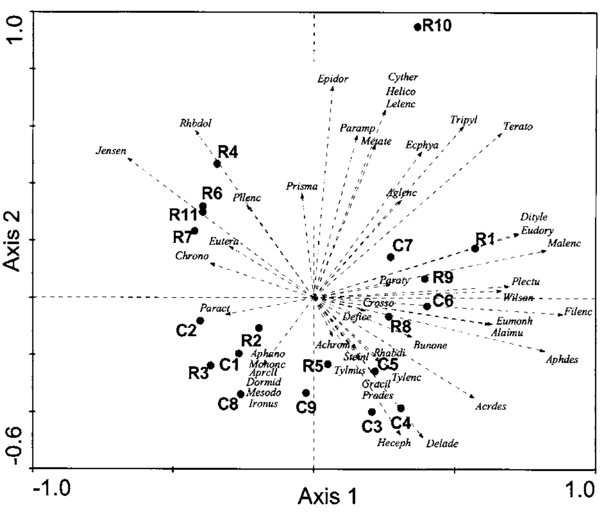

Fig. 2. Principal Component Analysis biplot of nematode genera and vegetation patches recorded at Rokytská Slať (R) and Chalupská Slať (C) using *ln*(x+1) transformed abundance of nematode genera. Eigenvalues for ordination axes 1, 2, 3 and 4 were 0.397, 0.121, 0.085 and 0.081, respectively. Cumulative percentage variance of genus data for ordination axes 1, 2, 3 and 4 were 39.7, 51.8, 60.3 and 68.3, respectively. Abbreviated names of genera are explained in Table 2.

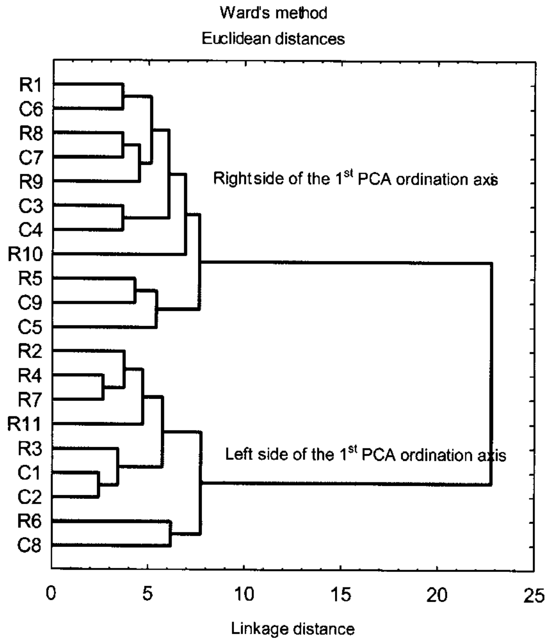

Fig. 3. Dendrogram based on Cluster Analysis of the *ln*(x+1) transformed abundance of nematode genera recorded in patches of vegetation at Rokytská Slať (R) and Chalupská Slať (C); Euclidean distance, Ward's clustering method.

Trophic groups and community indices of the nematodes

The abundances of the different nematode trophic groups and community indices recorded at both peat bogs are in Table 3. In terms of abundance the only significant difference (*t*-test on *ln*(x+1) transformed data, Mann-Whitney *U* test) was recorded for predatory nematodes, with a significantly greater abundance of predators ($p<0.05$) recorded at Rokytská Slať than Chalupská Slať. The only significant difference in community indices was the greater PPI/MI ratio recorded for Chalupská Slať than for Rokytská Slať; Mann-Whitney *U* test, $p=0.035$.

The respective values of the community indices H'gen, ΣMI, MI, PPI and PPI/MI calculated using the mean abundances of the nematode genera recorded at Rokytská Slať and Chalupská Slať were as follows: H'gen=2.38 and 2.24, ΣMI=2.99 and 2.74, MI=3.25 and 2.86, PPI=2.00 and 2.00, and PPI/MI=0.62 and 0.70.

DISCUSSION

Nematodes in peat bogs in the Šumava Mts. and other peatlands in Central Europe

As pointed out in the introduction nematode assemblages in peaty soils vary greatly and their comparison would need a special study. However, due to the predominance of omnivores and bacterivores followed by the root-fungal feeding Tylenchidae and very low population densities of plant parasites the peat bogs studied are similar to the Alpine peat bog (2284 m a. s. l) studied by Hoschitz & Kaufmann (2004). However, in the alpine peat bog the dominant omnivore is *Dorylaimus* and predatory mononchid nematodes are absent. In the peat meadows at low altitudes

(650–666 m a. s. l.) studied by Háněl (1997) there are higher population densities of the plant parasite *Helicotylenchus* and the *r* selected bacterivore *Rhabditis* appears to be more abundant than in Šumava peat bogs. These two genera are dominant in the Horná Orava peatlands in Slovakia (617–780 m a. s. l) studied by Renčo & Murín (2013). On the other hand, Šály (1981) reports a low abundance of *Helicotylenchus* and *Rhabditis* in peat-moors at Orava with the most abundant species the bacterivorous *Prismatolaimus dolichurus*. The abundance of *P. dolichurus* was relatively low, but it occurred at high frequency in Šumava peat bogs (Tables 1, 2). The proportions of the nematodes that are bacterivorous and fungivorous are commonly used in ecological studies but in the present case the high population densities of omnivores (Table 3) complicates the evaluation of the functioning of the detritus food web. The data collected indicate that bacteria and fungi have an equal role in the breakdown of organic matter in the peat bogs studied because the population densities of bacterivores were comparatively small and omnivores have an important role in this trophic food web (McSorley 2012).

Renčo & Murín (2013) characterized the peatlands at Horná Orava as relatively mature and stable. Nevertheless, the high abundance of *Rhabditis* and relatively high values of PPI/MI (1.00–1.61) indicate a nutrient disturbance, see also text below. In the peat meadows studied by Háněl (1997) PPI/MI was 0.79–0.98, whereas in drained meadows it is 0.80–1.34. The data on nematodes in peat bog systems in the middle parts of Central Europe are scarce but might reflect the increasing incidence of eutrophication (nutrient pollution) in this region. It is difficult, however, to verify the hypothesis that changes in peat-bog nematode fauna can indicate eutrophication. Landscapes at low altitudes were subject to anthropogenic influences for centuries before nematology as a branch of natural science was established. In addition, it is important to stress again that there is a great variety of peatland systems. For example, Wasilewska (1991) reports that *Rhabditis* followed by *Tylenchus* are the dominant nematodes in natural sedge-moss-fen peats. In natural sedge-fen peats the most dominant genera are *Tylenchus*, *Prismatolaimus* and *Plectus*, and in natural alder-fen peats *Mesodorylaimus*, *Eudorylaimus* and *Malenchus*. Not even the Biebrza wetlands are unaffected by human activities as ammunition and other "artefacts" from World War II can be still found there. On the other hand large peat bogs in the Šumava Mountains have been very little affected by human activities and can be used as reference sites when monitoring the effect on biota of the expected changes in climate and environment. For this purpose the evaluation of the natural status of peat bog nematode assemblages is an effective tool in bioindication studies.

Nematodes in original peatlands and man-established systems on peatland soils

The number of species and genera of nematodes recorded at Rokytská Slať and Chalupská Slať (69 and 66 species; 34 and 34 genera, respectively) are similar to those recorded in spruce forest ecosystems in the Šumava Mts. surveyed by Háněl (2004). There the number of species varied from 54 to 71 (mean 61) and the number of genera from 29 to 39 (mean 33) per site. Nevertheless, the nematode diversity data for peat bogs came from a single survey whereas those for spruce soils were collected over longer periods of time. The H'gen values for Chalupská Slať and Rokytská Slať calculated using mean generic abundance were in the range of values recorded for spruce forests soils by Háněl (2004). ΣMI and MI values were greater and PPI/MI ratios lower for peat bog soils than spruce forests soils. It is also interesting that the numbers of species and genera at both of the peat bogs studied were practically the same although the sites differed in altitude. In forests the numbers of species and genera of nematodes decrease with altitude (Kozlovsky 2002, Háněl & Čerevková 2010). Multivariate analyses revealed that the composition of the nematode assemblages at both peat bogs overlapped. More studies are necessary, however, as recent data indicate that peat bog systems can play an important role in the preservation of nematode species richness in landscapes at different altitudes in the Šumava Mts. Spruce forest plantations in the region were often established on former peaty soils (Skuhravý & Mrázková 2000). As discussed above, general features of nematode assemblages indicate a less disturbed environment in peat bogs than man-managed spruce soils in the region. Research carried out by Wasilewska (1991) in north-eastern Poland in the ice-marginal valleys of Biebrza and Narew indicate that the number of nematode genera in natural peaty soils can be smaller or greater than in drained peat soil meadows. Similar results are reported for peat and drained meadows in the Czech Republic (Háněl 1997). In natural fens in Poland H'gen varied within the range of values reported for drained meadows, while the values of ΣMI and MI tended to be greater and the PPI/MI ratio tended to be lower at natural sites than in the drained sites (Wasilewska 2002, Table 10). Nematode community indices thus showed a similar response to human activities in natural systems in different areas where peatland communities were replaced by either forests or meadows.

Natural state of the nematode assemblages in peat bogs in the Šumava Mts.
Nematode faunas in floodplain fens in Poland studied by Wasilewska (1991) and Háněl (2007) differ greatly from those recorded for the mountain bogs Rokytská Slať and Chalupská Slať. Nematode assemblages also differed greatly in terms of their trophic group composition. In Biebrza-Narev peatlands omnivores (a great part of Dorylaimida) made up only about 10% of all nematodes (Wasilewska 2006: Fig. 3) whereas in the peat bogs studied they made up about 30%. Omnivores in the peat meadows studied by Háněl (1997) made up 19% and in drained meadows 23% of nematode individuals. In the peatlands studied by Renčo & Murín (2013) omnivores made up about 5% of the nematodes. Barbuto & Zullini (2006) report that predator dominance and a high percentage of Dorylaimida in mossy habitats indicates their high quality. Their results thus support the view that Rokytská Slať and Chalupská Slať are natural undisturbed habitats.

In addition, the undisturbed naturalness of the peat bog studied is supported by the low values of the PPI/MI ratio. Bonger et al. (1997) postulate that the PPI/MI ratio in natural habitats, where higher plants make optimal use of nutrient resources, does not exceed 0.9. This is similar to the situation recorded for Rokytská Slať. At Chalupská Slať the PPI/MI ratio was slightly but significantly greater than at Rokytská Slať. Chalupská Slať is a valley peat bog into which the Roklanský potok stream and its small tributaries flow bringing enriching nutrients that could result in eutrophication, whereas the water at Rokytská Slať comes entirely from precipitation. Precipitation may be nutrient-polluted. But nematodes as an indicator of environmental disturbance indicate that the effect of such pollution on the Rokytská Slať peat bog was small (at least when the samples were collected, in 2001).

Interestingly, the predatory nematode, *Jensenonchus sphagni*, was abundant at Rokytská Slať, which indicated that the nematode assemblages recorded in this peat bog were effectively top-down controlled. *J. sphagni* was described and re-described from *Sphagnum* and evidently prefers natural and semi-natural habitats (Brzeski 1960, Loof & Winiszewska-Ślipińska 1993, Peneva et al. 1998, Háněl 1997, 1999, 2004, Keith et al. 2009). Abundant predators in nematode assemblages generally indicate an undisturbed environment (Wasilewska 1997). At Chalupská Slať *Jensenonchus sphagni* was rare and there was a greater abundance of bacterivores, which although statistically insignificantly, might also along with greater PPI/MI ratio indicate a greater level of habitat disturbance here than at Rokytská Slať.

Generally, the nematode assemblages recorded in the peat bogs studied can be classified as rich in species and genera, mature and undisturbed, with an indication there is a slight nutrient disturbance at least in some parts of the Chalupská Slať peat bog. The peat bogs were characterised by high population densities of omnivorous *Eudorylaimus* and high frequency of occurrence of species typical of *Sphagnum* sites, such as *Plectus decens*, *Metateratocephalus gracilicaudatus*, *Malenchus gratiosus*, *Prismatolaimus dolichurus* and *Jensenonchus sphagni*. Significant changes in this composition of the nematode assemblages can be used an indicator of degradation of the peat bogs in Šumava Mts.

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