SOIL ORGANISMS **91** (3) · December 2019 pp. 97–105

Enchytraeid assemblages at the foot of a talus slope in Skansbukta on the Arctic island of Spitsbergen

Jiří Schlaghamersky[1,]* and Miloslav Devetter[2,3]

[1] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czechia

[2] Institute of Soil Biology, Biology Centre of the Czech Academy of Sciences, Na Sádkách 7, 370 05 České Budějovice, Czechia

[3] Centre for Polar Ecology, Faculty of Science, University of South Bohemia, Na Zlaté stoce 3, 370 05 České Budějovice, Czechia

* Corresponding author, e-mail: jiris@sci.muni.cz

Received 4 June 2019 | **Accepted** 22 November 2019
Published online at www.soil-organisms.de 1 December 2019 | **Printed version** 15 December 2019
DOI 10.25674/so91iss3pp97

Abstract

Enchytraeids are an important component of Arctic ecosystems both as decomposers and part of the foodchain. Compared to other regions of the High Arctic, the enchytraeid fauna of Spitsbergen and some other islands of the Svalbard archipelago have been explored rather well but we still lack information from many areas and specific habitats. In August 2018, potworms (Annelida: Clitellata: Enchytraeidae) were sampled on the lower portion of a talus slope and in the flat area between this slope and the beach of Skansbukta, a bay of the Isfjord(en) on the western coast of Spitsbergen. Objectives were to compare assemblage composition and densities of close-by sites differing in their environmental characteristics, to provide faunistic data for a little explored area within Spitsbergen, and to clarify the true identity of *Marionina argentea* s.l., which had been found here previously. Six taxa on species level were recorded, including a *Mesenchytraeus* species of uncertain identity. Using morphological and molecular characters, *Marionina argentea* s.l. was shown to be *M. mimula*, a species described rather recently from Ireland and Sweden and hitherto not known from the Svalbard archipelago. This species dominated the moist flat area, substantially contributing to the higher enchytraeid density of ca 10 000 individuals/m^2 compared to less than 3 000 ind./m^2 on the lower slope. In the flat area ca 70 % of enchytraeids were present in the uppermost 3 cm layer consisting of mainly live mosses, whereas on the lower slope the distribution of individuals between the 0–3 and 3–6 cm layers was very balanced but no individuals occurred in greater depth, though there was no apparent change in the character of the moss-derived organic soil with depth.

Keywords Soil Animals | Svalbard | Isfjorden | Enchytraeidae | *Marionina mimula*

1. Introduction

Enchytraeids or potworms (Annelida: Clitellata: Enchytraeidae) present a dominant part of soil fauna in tundra habitats and have an important role in decomposition, nutrient cycling and due to their basal position in food chains (Birkemoe et al. 2000). However, many papers on enchytraeids in the Arctic focus on taxonomy and faunistics (e.g. Christensen & Dózsa-Farkas 1999, 2006), whereas those exploring ecological questions often lack information on the species involved (Byzova et al. 1995, Waldrop et al. 2012). Compared to other Arctic regions, the archipelago of Spitsbergen or Svalbard (the prior being historically used for the entire archipelago except Bjørnøya or Bear Island, but nowadays by the Norwegian administration for the main island only) has been explored rather extensively in terms of its enchytraeid fauna (Stephenson 1922, 1924, 1925; Nurminen 1965, 1966; Birkemoe & Dózsa-Farkas 1994; Birkemoe 1995; Dózsa-Farkas 1999; Sømme & Birkemoe

ISSN 1864-6417 (print) · **ISSN** 2509-9523 (online)

1997; Bauer 2002a; Birkemoe et al. 2000; Coulson et al. 2013a, Coulson et al. 2013b, Ávila-Jiménez et al. 2019). Nevertheless, many areas of the archipelago and even of its main island Spitsbergen have never been sampled and for many specific habitats few if any data on enchytraeid fauna are available. The only data on enchytraeids published from the area of Spitsbergen island surrounding the Billefjord(en) are a few species records from the surroundings of 'Bruce City' (Brucebyen) by Stephenson (1922, 1925).

The present paper reports on a sampling of enchytraeids conducted in the end of August 2018 as a follow-up to a hitherto unpublished study conducted in 2012–2014 (Schlaghamerský & Devetter, in prep.). During that first study a total of four transects (representing terrestrial environmental gradients), stretching between bird cliffs and the sea shore, were sampled along the coast of Billefjord(en). The main reason for the present study was that the lowest position on the slope that had been sampled in the bay Skansbukta in 2012 was characterized by high densities of the semiaquatic *Marionina argentea* (Michaelsen, 1889), a very characteristic 'species' that was recently shown to represent a species complex of at least five cryptic species (Rota 2013, Martin et al. 2015). Apparently, conditions here differed from the upper part of the transects due to groundwater coming close to the soil surface, even when seepage water was not visible at the exact sampling site (but was observed close-by). To get a better understanding of the role of seepage water and to clarify the true species identity of the encountered *M. argentea* s.l., we re-sampled the foot of the mountain slope in Skansbukta. We used this opportunity to learn more about the structure of the local enchytraeid assemblage and the effect of marked habitat differences on a small spatial scale by not only re-sampling the lower portion of the slope, but also the adjacent flat terrain very gradually levelling off towards the sea shore, thus extending our original transect from the cliff base to the foot of the slope by some 10 m. We also sampled the soil into greater depth than during the preceding study. The obtained results are presented below.

2. Material and methods

The study site was the foot of the mountain slope on the northern shore of the bay Skansbukta in the southwestern part of Billefjord(en) (ca 78°31'39.8"N, 16°2'39.7"E). The mountain slope below the upper part, which consisted of steep cliffs of solid rock, was formed by scree (talus), which was partially loose (in particular in the upper and middle parts of the slope) but to a greater extent filled-in with finer particles and covered by tundra vegetation. The cliffs are ca. 70 m high (from the cliff base at ca. 180 m a.s.l., i.e. above the talus slope, to the top at ca. 250 m a.s.l.) and consist of layers of anhydride, dolomite, limestone, cherts, siltstones, siliceous sandstones and siliceous (spiculitic) shales (Sessford & Hormes 2013). These rocks also form the talus slope and affect soil characteristics. At the foot, below the maximum change of slope, the terrain was flat or only very softly inclined towards the sea shore. It was made up of pre-recent beach deposits and colluvial material vegetated mainly by mosses (Sessford & Hormes 2013). Close to the northwest of the sampling area, seepage water formed small brooks, starting either some metres above or at the very foot of the slope, and the flat area between slope base and beach was boggy. The two actual sampling plots were devoid of surface water bodies at the time of sampling. One (termed Lower Slope below) was on the slope at ca. 5–10 m above the foot of the mountain, the other (termed Flat Area below) some 2–6 m away from the rising ground and ca. 100 m from the sea shore (at ca. 4 m a.s.l., Sessford & Hormes 2013), so that the distance between both was approximately 10 m. The Flat Area had a distinct micro-relief, due to Arctic 'patterned ground' with elevated parts and depressions that might have originated by frost cracking but apparently also served as intermittent fluvial channels, both vegetated primarily by different species of mosses. Presumably, these channels are flooded periodically during wet periods. Soil cores taken here had distinct layers of sandy mineral soil and buried organic horizons, whereas cores taken at elevated ground in-between the channels were basically moss cushions, containing predominantly decomposing moss material below the upper live portion. We did not dig down to permafrost within the sampling plots and no data on the thickness of the active layer above permafrost have been published from Skansbukta. However, our own, unpublished data show that some 400 m to the north and about one third of the talus slope up-hill permafrost starts at 60 cm below ground and further above, at the cliff base, at 90 cm below ground. Soil temperature measurements in 10 cm depth at the cliff base (ca 180 m a.s.l., southwestern aspect), using dataloggers, showed temperatures to range between -12 and 33°C (annual mean ± SD for 1th July 2018 to 30th June 2019: -1.1 ± 7.5°C); on the date of sampling, temperatures of 6.5 to 8°C were measured (own unpublished data).

In each sampling plot (ca 5 m x 5 m in area), five soil samples were randomly taken, using a soil corer (16.6 cm^2 working area), as deep as the partially very rocky ground allowed. Too shallow soil cores were discarded; for actual depths see Table 1. In the Flat Area, stratified random sampling covered channels (two cores, with mineral soil below 4 cm depth but including several thin buried organic horizons) and higher ground (three cores, mineral soil only in one – from 13 cm depth). Soil cores were subdivided into 3-cm thick layers, packed into plastic bags and transported to the field camp and later back to the first author's laboratory (packed to prevent warming-up of the samples). The samples were taken on the 28th of August 2018 and reached the lab on the 2nd of September. In the laboratory, the samples were stored at 4°C and subsequently subjected to wet funnel extraction (min. 48 h without heating, retrieval of extracted specimens and exchange of water after 24 h). The obtained specimens were kept in water-filled Petri dishes at 4°C and identified alive to species using a compound microscope with Nomarski contrast. Voucher specimens were partially fixed in Bouin's solution for subsequent whole-mounting and partially in pure ethanol (diluted to 80 %) for DNA extraction and molecular barcoding. Some of the barcoding was done in-house, some in the laboratory of Prof. Christer Erséus at the University of Gothenburg (Sweden). Obtained sequences (COI, in a few cases 16S) were compared with sequences in publicly accessible databases (BOLD, GenBank) and in the database of Christer Erséus, including not yet published sequences.

As all the taken soil cores were to be used for enchytraeid extraction, one thin slice along the entire length of each soil core was separated by a knife and these slices were pooled to obtain one composite sample per plot for the analysis of some soil characteristics. Due to the small amount of the obtained substrate (incl. moss layer) its chemical characteristics were measured in water leachate (Table 1). The obtained values thus neither reflected potential within plot variability nor did they present total element contents. They served solely for the purpose of a rough comparison of both sampling plots, showing neutral soil pH in both plots, more than twofold higher conductivity and exceedingly higher carbon, nitrogen and calcium contents in the Lower Slope than in the Flat Area. Total organic carbon contents were also measured in the entire individual soil cores from which enchytraeids had been extracted (Table 2). This measurement was preceded by HCl fumigation to remove carbonates (generally present in excess levels in Spitsbergen soils). Due to the high content of solid organic matter present, we considered losses due to leaching or wash out during the enchytraeid extraction stage as negligible when comparing the organic carbon contents of the two plots. The cores from the Flat Area contained significantly less carbon than those from the Lower Slope (Mann-Whitney U test: $p = 0.0158$), which was caused, in particular, by the low C content of the two cores taken in the fluvial channels (the difference was not significant, $p = 2$, when only the other three cores from the Flat Area were included in the test).

3. Results

3.1 Species composition

In total, 104 enchytraeid specimens, representing 6 taxa on species level, were obtained and identified (Table 3). No other annelids were extracted from the samples. The given species number is based on the assumption that *Marionina argentea* sensu lato was represented by a single taxon. Examination of morphological characters in adult specimens and, in particular, molecular barcoding, including a comparison with unpublished molecular sequences obtained elsewhere (Erséus and Klinth, pers. com.), showed with high probability that all the specimens actually belonged to *Marionina mimula* Rota, 2013 (for more taxonomic details see below). The majority of enchytraeid individuals (82) was extracted from the samples taken in the Flat Area at the foot of the

Table 1. Chemical and physical parameters of the two compared plots at the foot of a hillslope in Skansbukta (Spitsbergen) based on water leachate (1:5) from one composite sample per plot (Cond. – conductivity, N – nitrogen, $C_{org.}$ –organic carbon, $C_{inorg.}$ – inorganic carbon).

site	pH (H_2O)	Cond. [µS/cm]	P-PO_4^{3-} [mg/l]	N-NH_4^+ [mg/l]	N [mg/l]	$C_{org.}$ [mg/l]	$C_{inorg.}$ [mg/l]	Ca [mg/l]	Mg [mg/l]	K [mg/l]	Na [mg/l]
Lower Slope	7.0	394	13.8	25.6	188	1632	67	439	41.5	119	15.7
Flat Area	7.1	177	14.3	6.67	58.2	546	36	327	26.4	13.4	38.2

Table 2. Depth and total carbon content of soil cores (1–5 per plot) taken in the two compared plots at the foot of a hillslope in Skansbukta (Spitsbergen). Soil cores 3 and 4 in the Flat Area were taken in fluvial channels incised into higher ground (dry at the time of sampling).

site	Lower Slope					Flat Area				
Soil Core	1	2	3	4	5	1	2	3	4	5
Depth [cm]	9	9	12	7	12	15	18	13	12	12
% Corg	26.3	19.9	28.8	26.9	27.8	15.3	22.1	3.5	2.9	16.2

Table 3. Enchytraeid species and corresponding numbers of specimens obtained from the two compared plots at the foot of a hillslope in Skansbukta (Spitsbergen). Soil cores 3 and 4 in the Flat Area were taken in fluvial channels incised into higher ground (dry at the time of sampling).

site	**Lower Slope**					**Flat Area**				
Species / soil core	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
***Bryodrilus diverticulatus* Černosvitov, 1929**	-	-	-	-	-	-	1	-	-	1
***Henlea glandulifera* Nurminen, 1970**	1	-	-	1	1	-	1	3	2	1
***Henlea perpusilla* s.l. Friend, 1911**	2	2	-	-	1	4	1	8	1	-
***Henlea* spp.**	-	-	-	-	-	-	1	3	-	-
***Marionina mimula* Rota, 2013**	2	-	-	1	3	4	7	25	-	18
***Mesenchytraeus flavus* (Levinsen, 1884)**	-	-	-	-	-	-	-	1	-	-
***Mesenchytraeus* sp. 2 - KDF**	1	-	-	-	1	-	-	-	-	-
***Mesenchytraeus* spp.**	-	3	-	1	2	-	-	-	-	-
Enchytraeidae in total	6	5	0	3	8	8	11	40	3	20
			22					**82**		

hillslope, where five species were found. Four species-level taxa were identified in samples from the Lower Slope, including an unknown *Mesenchytraeus* species (see taxonomic remarks below). The obtained difference in numbers of species between the two sites was minor and might have been accidental. The assemblage in the Flat Area was dominated by *Marionina mimula* (68 % of specimens) whereas on the Lower Slope its representation was 26 %; here *Mesenchytraeus* specimens were dominant (37 %).

3.2 Densities and vertical distribution

Total enchytraeid densities were 9 993 individuals/m^2 ± 8 901 ind./m^2 (SE) in the Flat Area and 2 649 individuals/m^2 ± 2 311 ind./m^2 (SE) on the Lower Slope. The higher density in the Flat Area was mainly due to one of the soil cores (No. 3) taken in an intermittent channel, in which a 3–4 cm thick moss layer topped sandy mineral soil. Most of the enchytraeids were present in the upper 3 cm of organic material here, though there were several thin organic horizons buried in the underlying mineral sediments. This soil core yielded 40 specimens, whereas only three specimens were extracted from the other core taken in an intermittent channel (showing a very similar distribution of organic and mineral matter). The remaining three soil cores (consisting of a live moss layer and moss-derived organic soil) taken in this area yielded 39 specimens. On the Lower Slope, enchytraeids were on average equally distributed in the 0–3 cm and 3–6 cm soil layers while entirely lacking in the deeper layers, though there was no visible change in the character of the moss-derived organic soil. In the flat terrain, a few individuals were found at greater depth, a single one down to the 12–15 cm layer (two soil cores included this layer), but 70 % of individuals were present in the top 3 cm (Fig. 1).

3.3 Taxonomic remarks

All measurements given below are based on live specimens. Barcoding refers to COI if not specified otherwise.

Marionina mimula: In total, 34 adult or subadult (but almost mature) specimens of *Marionina argentea* s.l. were examined. Body lengths 1.9−3.5 mm; body widths at XII 140−192 µm; 18−23 segments; 3 pairs of primary pharyngeal glands (anterior two dorsally broadly collected, third unconnected, elongate ventral lobes only) and 1 pair of secondary pharyngeal glands in V (behind first primary pair); 3 pairs of preclitellar nephridia at VII/VIII−IX/X; dorsal vessel originating in XII (XIII), observations of anterior bifurcation inconsistent, both prostomial (lumbricilline) and pharyngeal (marionine) type recorded (the latter possibly due to the incomplete view of the interior organs in live specimens, obstructed, e.g., by coelomocytes); posterior margin of brain indented; coelomocytes dark in transmitted light, oval, 15−35 µm long; 1−2 yolky eggs present; male copulatory organ (‘penial bulb’) 40−57 µm long and 24−36 µm wide; sperm funnel 36−56 µm long and 18−34 µm wide, collar width 19 µm. Spermatheca with oval ampulla, ca. 25 µm long and 12−22 µm wide, communicating dorso-laterally with oesophagus by short ental duct (ca 18−26 µm when stretched), ectal duct 30−46 µm long and 9−12 µm wide (depending on contraction), with a rosette of ‘ectal’ glands around its orifice and smaller glands along the duct. The observed characters were in fair agreement with the species description of *M. mimula*, taking into account that measurements given by Rota (2013) refer to fixed material. In total 17 specimens from Skansbukta were barcoded (10 in the first author’s department, 7 by Erséus and Klinth, of the latter no COI sequence could be obtained in two specimens, in their case a short 16S barcode allowed identification). All obtained sequences matched sequences obtained earlier by Erséus for *Marionina mimula,* including a specimen from one of the type localities on the Swedish Northsea coast (Erséus, pers. comm.). Several specimens (not barcoded) had gregarines or spores (probably also gregarine) in their coelom.

***Mesenchytraeus* spp.:** Although the genus *Mesenchytraeus* includes, in general, mid-sized to very large species, the specimens obtained in the present study were mostly small juveniles. A few, though still small, were classified as subadult (the mere presence of a not fully developed spermatheca was not taken as a decisive criterion because this apparently forms early in this genus). A single juvenile specimen (5 mm, 26 segments) stood out by its greenish spindle-shaped coelomocytes (ca 36 µm long) and somewhat enlarged chaetae of the lateral bundles in IV–VII (this often applied only to one of three chaetae in a bundle). Primary pharyngeal glands were present in IV/V and V/VI, secondary ones in V and VI. The brain was short, its hind margin deeply incised. Barcoding allowed to identify this specimen as *Mesenchytraeus flavus*, a species which had been reported from the archipelago before (Nurminen 1966, Birkemoe & Dózsa-Farkas 1994) and was found by us also in further samples from Spitsbergen (own unpublished data). Two small gregarines in syzygy were present in the coelom. All other *Mesenchytraeus* specimens differed in having oval coelomocytes of a length of ca. 18–24 µm that were dark in transmitted light due to rather coarse refractile granules. Two specimens were barcoded and had sequences identical to a taxon called '*Mesenchytraeus* sp. 2 KDF' available in the BOLD Systems database (6 sequences) from material provided by Klara Dózsa-Farkas from Spitsbergen (Christer Ersús and Mårten Klinth, pers. comm.). As some of the other specimens were very small juveniles with few visible characters, we list all non-barcoded specimens as '*Mesenchytraeus* spp.'. Nevertheless, we assume that these probably all belonged to the same species (*Mesenchytraeus* sp. 2 KDF), sharing the following characters (as far as visible): coelomocytes as above; 1–3 chaetae per bundle laterally and 3–5 ventrally; 4 pairs preclitellar nephridia from VI/VII to IX/X; 2 pairs of primary pharyngeal glands at IV/V and V/VI, each followed by a pair of secondary ones. One subadult specimen (3.2 mm, 24 segments; subsequently fixed in Bouin solution) had a rather long seminal duct (the sperm funnel was rudimentary) and a short spermathaeca with a knob-like ampulla without any diverticula and not connected to the oesophagus. In another subadult specimen (4.4 mm, 27 segments) the chaetal formula was noted as 2,3,4–3,2 : (3),(4),5,6,5–(5),4,3,2; the dorsal vessel originated in XII (possibly even further back); the brain was 122 µm long (89 µm when measured medially from the anterior branching to the posterior indentation) and 74 µm wide. This specimen was fixed in pure ethanol but DNA extraction failed to provide a usable sequence for barcoding. The third and last examined subadult (front part fixed in Bouin solution, rear part in pure ethanol and barcoded,

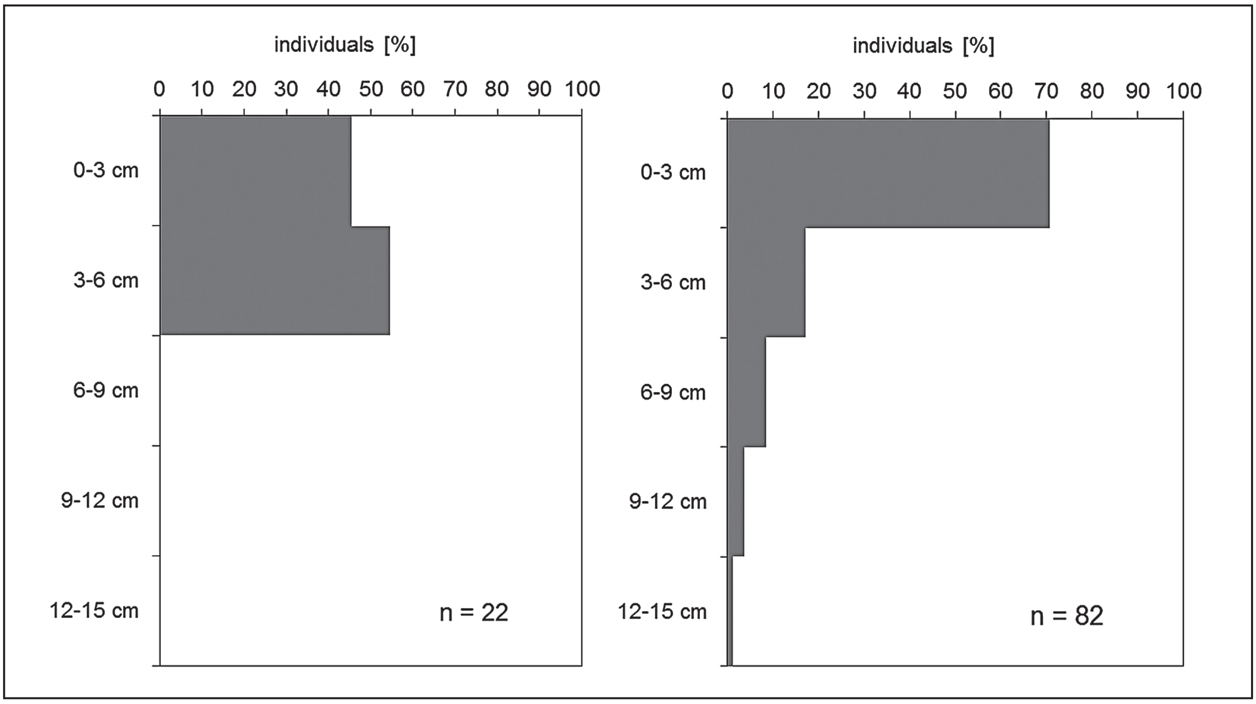

Figure 1. Enchytraeid vertical distribution at the two sites at the foot of a talus slope at Skansbukta (Spitsbergen): Lower Slope (left) and Flat Area (right).

identical with *Mesenchytraeus* sp. 2 KDF) was 3.1 mm and 21 segments long, with the dorsal vessel originating in XII. Numbers of chaetae in dorso-lateral bundles were 1,2–2,1, ventral bundles were not well visible (3 chaetae per bundle seen). Hyaline egg cells were present in XII; no sperm funnels were seen. Spermathecae (immature) were short, restricted to V, finger-like, at a slightly enlarged apical end with a rather thick wall around a moderately sized lumen (ampulla), not connected to the oesophagus; no ectal or other distinct glands associated with the spermatheca were visible, but the surface of the ectal duct was irregular.

***Henlea* spp.:** *Henlea perpusilla* is considered a species complex (Schmelz & Collado, 2010); those 9 of our specimens that were sequenced matched specimens from Spitsbergen identified by Klara Dózsa-Farkas as *H. perpusilla.* According to Erséus (pers. comm.) the same lineage (one of several) has been found in mainland Scandinavia, Greenland and Central Europe. *Henlea glandulifera* may also be a species complex as there are several distinguishable lineages (Erséus, pers. comm.). Our material was identical to a lineage found only on the archipelago of Svalbard but also clustered with an apparently closely-related lineage known both from Svalbard and mainland Norway (Erséus, pers. comm.). Four specimens, either small juveniles or injured, could not be assigned to species with certainty and are listed as *Henlea* spp.

4. Discussion

4.1 Species composition of enchytraeid assemblages

According to Dózsa-Farkas (1999) and Coulson & Refseth (2004), 33 enchytraeid species have been reported from the Svalbard archipelago. However, two of the listed *Fridericia* species should be considered nomina dubia according to Schmelz (2003): *F. leydigi* Vejdovský, 1878 (the actually identity of the Svalbard specimens being *F. connata*) and *F. bulbosa* (Rosa, 1887). A variety of species with a bulbous spermathecal ampulla without diverticula has been recorded under the name of *F. bulbosa* (Schmelz 2003, Rota 2015). Though, according to Rota (2015), *F. bulbosa* is a valid species known from Italy, this has very specific habitat requirements (oak woods and meadows on limestone). This makes its occurrence on Svalbard highly improbable, the more so, as the similar species *F. bulboides* has been repeatedly recorded here. Excluding further a number of marine-littoral species of *Lumbricillus* leaves a pool of some 20 species that can be potentially found in terrestrial habitats of Svalbard. However, assemblages actually reported from individual habitats are substantially poorer in species. Birkemoe et al. (2000) found only two species, *Henlea glandulifera* and *H. perpusilla,* in a *Cassiope* heath at Ny-Ålesund, and six species in a *Salix* heath in Adventdalen. The other four species were *H. ventriculosa* (d'Udekem, 1854), *Bryodrilus librus* (Nielsen & Christensen, 1959), then reported as *B. parvus* Nurminen, 1970), *B. diverticulatus*, and *Mesenchytraeus argentatus* Nurminen, 1973. The overlap with the assemblage found in the present study is thus very high, a substantial difference is only the presence and partially dominant position of *Marionina mimula* at the Skansbukta study site. This is the first report of this species from the Svalbard archipelago, but it would have been previously identified as *Marionina argentea* or, possibly, *M. aporus* (Stephenson, 1925). Like all species of the *M. argentea* complex, *M. mimula* is of very small body size and semiaquatic. Bauer (2002a) reported the species composition (but not representation) of enchytraeid assemblages collected at several sites and in several microhabitats from the Kongsfjord(en) area around Ny-Ålesund (thus from the same part of Spitsbergen as Birkemoe et al. 2000). In samples most similar to those taken in the present study (combining samples taken in the tundra with a soil corer and bulk samples of vegetation, such as moss cushions) she found from one to four species. *H. perpusilla* was present in all of them and the four-species assemblage included also *H. glandulifera*, *B. diverticulatus* and a non-identified *Marionina* species. Her species-richest site, where she took five soil cores of organic material with willow leaves and six qualitative samples of wet moss at a small lake, hosted six species: *H. glandulifera*, *H. perpusilla*, *Marionina argentea* (Michaelsen, 1889), *M. aporus*, *Mesenchytraeus argentatus* and a non-identified *Mesenchytraeus* species. Again, there is a substantial overlap with the species composition found in the present study. As *M. argentea* is a complex of cryptic species (see above), it might have been *M. mimula*, though the presence of another representative of this complex cannot be excluded (in fact, *M. aporus* could also be incorporated in *M. argentea* s.l.). Dózsa-Farkas (1999) identified enchytraeids from samples taken on the island of Nordaustlandet and on the small island of Phillipsøya north of it, but also from Bockfjord(en) on the northern coast of Spitsbergen island. Although she had only one or two soil samples of 20 cm^2 area and 5 cm depth from each sampling site, she found up to 9 species per site (at two sites on the Oxfordhalvøya, with moist, densely vegetated habitat, represented by one and two samples). These assemblages included also one or two *Lumbricillus* species and it is thus possible that these were close to the coast and brackish. She found four species in soil with dense vegetation taken below a bird cliff, but the same number was also present in a sample from the ‘polar desert’ (both on the north coast of Nordaustlandet). The papers of Stephenson (1922, 1924, 1925) and Nurminen (1965, 1966) list species records with very brief comments on localities and habitats where the individual species had been collected, which hardly allows reconstruction of community composition for specific sites.

4.2 Enchytraeid densities and vertical distribution

We found most enchytraeids in the uppermost 3 cm of the soil cores (of which some 0.5–1 cm were taken by live moss and the rest by rotting material of moss and some vascular plants); our sampling took place during the short ‘Arctic autumn’, but temperatures were still rather high (as reported above) and if there is a downward migration due to falling temperatures, it had not yet occurred. We therefore also assume that if there is increased mortality due to falling temperatures, our sampling preceded such a development.

As most studies on enchytraeids in the Arctic focused primarily on taxonomic and faunistic aspects, few data on enchytraeid densities in terrestrial habitats are available, and even less on vertical distribution, for which reason the latter is not further discussed below. No information on species composition, but rather rich data on densities, were reported by Byzova et al. (1995) from the Hornsund area of Spitsbergen. They sampled several tundra habitats at three to five dates from mid May or early June to the end of August. Mean densities per habitat (site) and date ranged from 120 ± 40 individuals/m^2 on open ground in polygonal tundra to 23 240 ± 4 640 ind./m^2 in mossy/lichenous tundra (data reported here with standard deviations were re-calculated to densities per m^2). On a mossy site near an auk colony, which also included patches of meadow vegetation, a peak density of 18 320 ± 17 840 ind./m^2 was recorded (one of several samplings). These maximal values exceeded those found in the present study approximately twofold. In reality, they were most probably even higher because enchytraeids were extracted from the substrate for one hour only (with heating, but no details on the temperature were reported). O’Connor’s wet funnel method employs gradual heating up of the soil sample surface from 17°C to 45°C over 3 h, thus creating a heat gradient both over time and within the extraction funnel (O’Connor 1962). Graefe’s modification without heating requires at least 0.5 to 2 days exposure in the case of organic soil and 5–10 days for mineral soils (Graefe 1984), see also ISO 23611-3:2007(E) (ISO 2007). Too fast heating up might kill the enchytraeids and these may remain in the soil, whereas less or no heating might prolong the extraction process. We tested enchytraeid extraction (without heating) from Spitsbergen soils previously and obtained only few worms during extraction periods extended beyond the initial 48 hours (own unpublished results). In a detailed study from two sites on the island of Spitsbergen, Adventdalen and Ny-Ålesund, Birkemoe et al. (2000) reported densities for the dominant enchytraeid species and several sampling dates. They found ca. 4 000 to 10 000 ind./m^2 in a *Salix* heath in Adventdalen and ca. 500 to 2 000 ind./m^2 in a *Cassiope* heath at Ny-Ålesund, values that correspond well with the densities found in the present study. Finally, Bauer (2002b) reported substantially lower densities from soil with vegetation samples taken during July at several sites in the Kongsfjord(en) area of Spitsbergen, i.e. also near to Ny-Ålesund: Density ranges from 0 to 2.105 ind./m^2 were found for individual soil cores and sampling dates; where several cores (6 and 13, respectively) were taken in a single habitat at a given site (‘Stuphallet’), mean densities for the two sampling dates were 926 and 130 ind./m^2. These densities were much lower than in the present study. It is not clear from the article if the reported wet funnel extraction for 3–5 h involved heating; if not, extraction time was probably too low to obtain all worms present in the soil samples (see above). In a boreal rich fen in interior Alaska an enchytraeid density of ca. 40 000 individuals/m^2 was found, whereas other vegetation types close-by had lower densities, down to less than 5 000 individuals/m^2 in a black spruce stand on permafrost soil – judging from the provided figure (Waldrop et al. 2012). However, these boreal, i.e. subarctic, conditions, are already very different from the middle to high Arctic ones, present on the west coast of Spitsbergen.

5. Conclusions

With six species found within a rather small area the enchytraeid assemblage at the base of the talus slope in Skansbukta seems rather rich for Spitsbergen. Also enchytraeid densities were rather high for Spitsbergen standards, showing that the habitat and time of sampling were favourable for this group. In particular, this was true for the flat terrain plot, probably due to higher soil moisture compared to the lower slope. Organic carbon was present in higher supply at the Lower Slope than in the adjacent flat terrain, so its availability was obviously not driving the species richness and overall enchytraeid density. Soil moisture was not directly measured in the present study, but our conclusion is corroborated by the high dominance of *Marionina mimula* in this habitat, a species that can be considered semiaquatic like the other known members of the *M. argentea* species complex (although, it might not be that closely related to other species described from this group, see Rota 2015). It was described from coastal sites in Ireland and Sweden, with grass turf exposed to some sea spray or brackish ground water (Rota 2015). These are conditions in rather good agreement with those at Skansbukta. In terms of ecological function, one has to bear in mind that this is an enchytraeid species of minute body size, substantially smaller than the others found at this site. Also the other species recorded are – as far as we know – not restricted to Svalbard or the Arctic, although *B. diverticulatus* and *H. glandulifera* can be considered species of colder climate, i.e. northern Europe, the Alps, Greenland, Arctic Siberia (Nurminen 1970, 1977; Rota et al. 1998; Christensen & Dózsa-Farkas 1999, 2006; Schmelz & Collado 2010). As *H. perpusilla* is a species complex it might be well possible (as suggested by the comparison of molecular barcodes) that the population of Spitsbergen or of the wider archipelago represents a species in its own right (Ch. Erséus, pers. comm.). Barcoding of the undescribed *Mesenchytraeus* species found in the present study has shown that this species was found in the Svalbard archipelago before. However, its range might be much wider as the enchytraeid fauna of the Arctic and beyond remains poorly explored. In this context we believe that the present study presents a small but useful contribution to our knowledge of enchytraeid biogeography and ecology and on the importance of enchytraeids in terrestrial ecosystems of the Arctic.

6. Acknowledgements

This study was supported by the Czech National Science Foundation (GACR, 17-20838S) and the Czech Polar Research Infrastructure of the University of South Bohemia in České Budějovice with its Josef Svoboda Station on Svalbard (Project CzechPolar2 LM2015078 funded by the Ministry of Education, Youth and Sports of the Czech Republic). We thank Veronika Jílková (Institute of Soil Biology, Biology Centre CAS) for measuring the carbon content of soil cores, Michal Pavonič (Dept of Botany and Zoology, Masaryk University) for measuring further chemical and physical parameters of composite soil samples. We further thank Andrea Tóthová (Dept of Botany and Zoology, Masaryk University), Mårten Klinth and Christer Erséus (both Dept. of Biological and Environmental Sciences, University of Gothenburg, Sweden) for barcoding several voucher specimens and the latter, in particular, for comparing the obtained sequences with own unpublished data, being instrumental in the confirmation of several species identities.

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