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Source: Arctic, Antarctic, and Alpine Research, 47(3) : 561-572

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/AAAR0014-046>

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Food choice of invertebrates during early glacier foreland succession

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Abstract

Bryophytes from seven different genera colonized 3- to 6-year-old ground near a receding glacier in central South Norway. Microscopic studies of the gut content in pioneer invertebrates revealed that mosses were grazed upon by four species: an abundant and large Collembola (*Bourletiella hortensis*), a moss-eating Byrrhidae beetle (*Simplocaria metallica*), and two omnivorous Carabidae beetles (*Amara alpina* and *A. quenseli*). The three most abundant moss species were preferred by the moss-eaters: *Pohlia filum*, *Ceratodon purpureus*, and *Bryum arcticum*. Special parts of the moss plant could be selected. Three other Collembola species present were classified as herbivores because they had diatom algae in their gut, indicating that they grazed on terrestrial biofilm. Chironomidae midges hatching from young ponds represented an important element in the gut content of three common predators: the Opiliones *Mitopus morio*, and two Carabidae beetles *Nebria nivalis* and *Bembidion hastii*. The present data show that chlorophyll-based food chains start almost immediately on bare ground, but in a rather invisible way by tiny pioneer mosses and terrestrial biofilm with diatom algae. Pioneer mosses may be regarded as “drivers” in early animal succession, before higher plants establish. Since several of the pioneer invertebrates were herbivores or omnivores, the present community did not fit with the “predator first” hypothesis.

DOI: <http://dx.doi.org/10.1657/AAAR0014-046>

Introduction

Owing to environmental change, glaciers are receding worldwide (Oerlemans, 2005), and large areas of barren ground are becoming exposed. Recent studies have shown that such pristine ground close to the ice edge is rapidly colonized by several invertebrate species, even before higher plants are established (e.g., Kaufmann, 2001; Gobbi et al., 2006; Hågvar et al., 2009; Hågvar, 2010; König et al., 2011; Ingimarsdóttir et al., 2012; Vater, 2012; Bråten et al., 2012; Hågvar, 2012; Raso et al., 2014). Of special interest is the ecological paradox that predators like spiders (Araneae), harvestmen (Opiliones), and certain beetles (Coleoptera, Carabidae) are generally observed before herbivores and plants. This “predator first paradox” has been explained by airborne input of invertebrate prey (Hodkinson et al., 2001, 2002; Coulson et al., 2003). Likewise, the early presence of springtails (Collembola) has been explained by assuming that they are decomposers feeding on inblown organic matter (Hodkinson et al., 2002). Also, springtails have been assumed to feed the predators (König et al., 2011). A key question in this debate is what all these pioneer animals are eating, but documentation of their feeding habits has been lacking.

Recently, molecular studies of gut content using deoxyribonucleic acid (DNA) have revealed the food choice of pioneer predators in an Austrian glacier foreland (Raso et al., 2014). Springtails were identified as a main prey for all predators, and intraguild predation was also documented. However, except for spiders, which ingest fluid food, a direct inspection of gut contents under the microscope may also be rewarding. While prey identification by DNA only documents presence/absence, gut contents spread under the microscope may give more quantitative information. Moreover, identification by DNA is limited to comparison with a set number of assumed food items, which may not cover the whole span of potential food items.

Based on microscopic analyses of gut contents, Hågvar and Ohlson (2013) described an unexpected pioneer food web on a fresh,

barren moraine in south Norway. The invertebrate community was largely fed by three cryptic food sources: ancient carbon from the glacier, and unnoticed algae and mosses. Ancient carbon released by the glacier was assimilated by aquatic chironomid midge larvae in young ponds, and adults with a radiocarbon age of 1040 years were subsequently eaten by the terrestrial predators, primarily carabid beetles, spiders, and harvestmen. These live predators thus achieved radiocarbon ages of 340–1100 years. Springtails were only eaten to a limited degree by these predators. Furthermore, springtails themselves were mainly herbivores. Several species fed on biofilm produced by terrestrial diatom algae, and one large species, *Bourletiella hortensis*, grazed on tiny pioneer mosses.

Here we describe in detail the gut content of these pioneer invertebrates. We illustrate photographically how fragments of plant material and chitinous parts of invertebrates can be identified, sometimes to species level. Because specific fragments can be counted, the analyses may give semiquantitative information. Emphasis has been laid on documenting mosses as a food resource for certain pioneer invertebrates. The data shed new light on how a pioneer food web is established during the first few years of a glacier foreland succession.

Methods and Study Area

STUDY AREA

The study was performed on the foreland of the large (73 km²) Hardangerjøkulen glacier in south-central Norway, just in front of the retreating snout of the Midtdalsbreen glacier, at about 1400 m above sea level (60°34′30″N, 7°27′40″E) (Bråten et al., 2012). All samples were taken from 3- to 6-year-old ground, between 2008 and 2011, on a moraine formed in 2005. Figure 1, parts A and B, show the moraine in 2009 with lids of pitfall traps visible, and the large area released from ice in 2010, respectively. During the period 2006–2011, the glacier snout receded 111 m (Atle Nesje, personal communication).

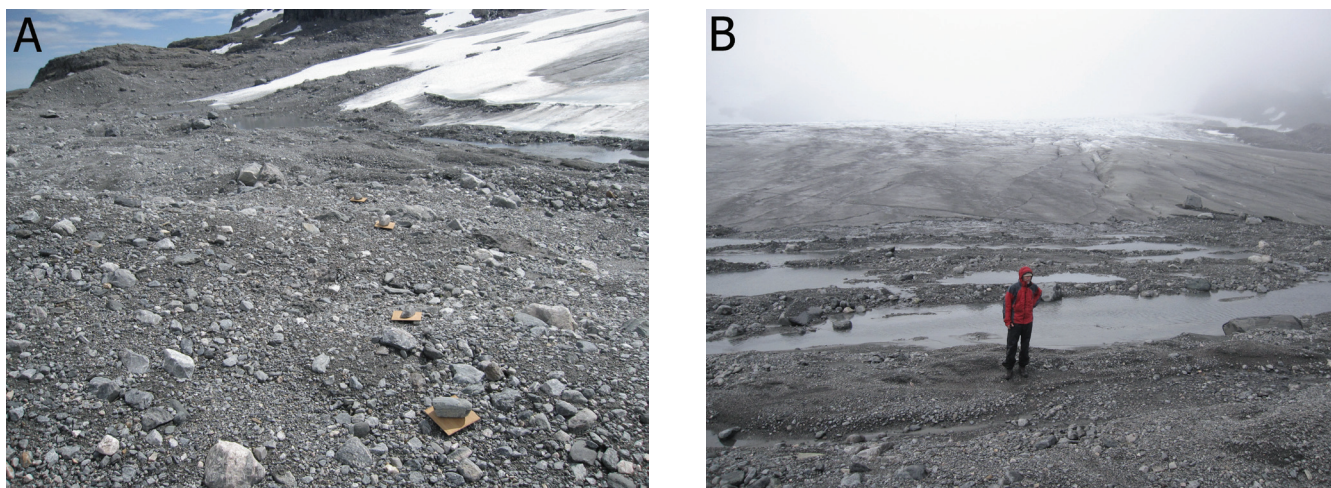


FIGURE 1. (A) Photo from the 2005 moraine taken on 5 August 2009. Lids covering pitfall traps are seen. The distance to the glacier edge was about 75 m. (B) During summer 2010, the glacier edge receded 34 m, exposing most of the ground behind the person. Photo 31 August 2010.

PITFALL TRAPPING

Invertebrates for gut analyses were collected in pitfall traps (diameter 6.5 cm) (Bråten et al., 2012; Hågvar, 2012). In 2008, 20 pitfall traps, containing ethylene glycol preserving fluid, were operated on the moraine, and in 2011, 50 traps with propylene glycol were used. Trapping periods are shown later in Table 2. Animals were killed by the preserving fluid and could not feed on each other within the traps. Gut contents of the springtails *Lepidocyrtus lignorum* and *Isotoma viridis* were also studied in pitfall material from soils aged 32–63 years old (Bråten et al., 2012; Hågvar, 2012).

GUT CONTENT STUDIES

Gut contents were studied in 11 surface-active species: five beetles, one harvestman, and five springtails (Fig. 2). For springtails, contents were studied on slides at up to 1000× magnification while embedded on a 3:1 mixture of glycerol and lactic acid. Large specimens, like *B. hortensis*, were squeezed to spread the gut content. Guts of beetles and harvestmen were dissected from the dorsal side, and the contents spread and examined under the microscope in the same medium. The crop content of beetles was included. Spider guts were not examined

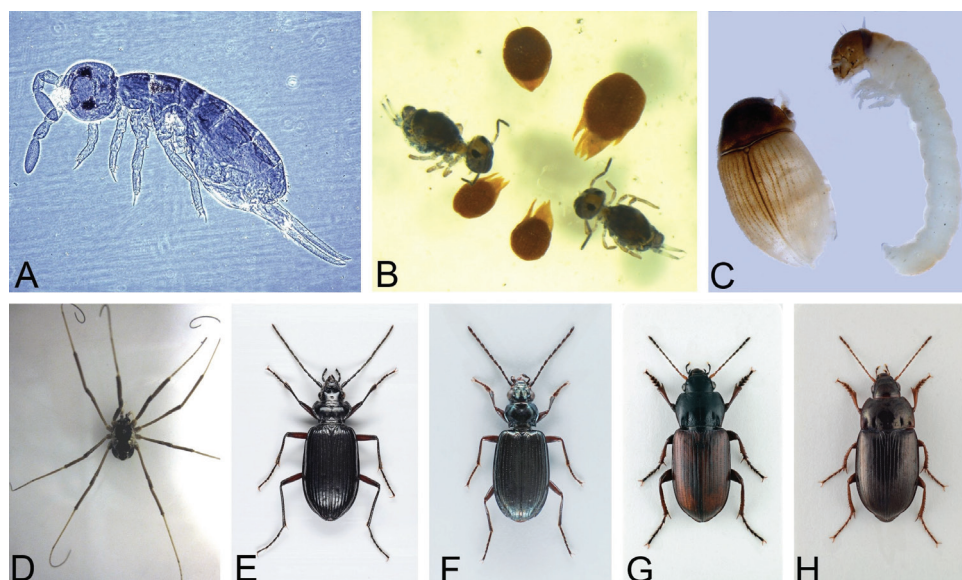


FIGURE 2. Some pioneer invertebrates on a 3- to 6-year-old moraine, representing different taxa and feeding groups. (A) *Agrenia bidenticulata* (Collembola), a super-pioneer feeding on terrestrial diatom algae in biofilm. (B) *Bourletiella hortensis* (Collembola), a moss and fungus feeder. It is shown together with nutrient-rich bulbils of the moss *Pohlia filum*. (C) *Simplocaria metallica* (Byrrhidae), a moss-eating beetle; larva and a newly hatched adult from a pioneer moss patch. (D) The predator *Mitopus morio* (Opiliones). (E) The predator *Nebria nivalis* (Carabidae). (F) The predator *Bembidion hastii* (Carabidae). (G) The omnivore *Amara alpina* (Carabidae). (H) The omnivore *Amara quenseli* (Carabidae). The last two eat moss in addition to invertebrates.

owing to their liquid, unidentifiable content. However, those of beetles and harvestmen often contained numerous chitinous prey fragments that could be identified to group and sometimes species level. This was possible because of the limited number of prey species present. Chitinous fragments of claws, jaws, or furca from springtails, for instance, could be identified to species. Moss fragments could similarly be identified to genus or species, based on cell and leaf structure. Several guts of *B. hortensis* also contained fungal hyphae, which might be confused with moss rhizoids. The rhizoids of *Pohlia filum*, *Ceratodon purpureus*, *Bryum arcticum*, and *Funaria hygrometrica* could, however, be recognized by their oblique cell walls. We also distinguished between Ascomycota and Basidiomycota by the presence of “clamped hyphae,” which are characteristic for the

latter group. Furthermore, Ascomycota spores are aggregated in characteristic asci.

STUDIES ON MOSS COLONIZATION

Early colonization of mosses was documented by different methods (Table 1). Pitfall traps from 2008 contained in-blown moss fragments and diaspores, which were identified to species or genus. Qualitative data from sticky traps at 6–30 cm height in 2008 and at 5–104 cm height in 2011, as well as data from 25–30 fallout traps in 2010 and 2011 (Flø and Hågvær, 2013), confirmed wind transport of moss diaspores. Moss species established on the 2005 moraine were documented in a short field survey in 2009, and by a thorough survey in 2011

TABLE 1

Records of various pioneer bryophytes in the field, and in guts of some invertebrates. All data are from 3- to 6-year-old ground, on a 2005 moraine. Relative occurrence of bryophyte species in the field in 2011 is indicated by number of stars, and occurrence in sticky traps has been qualitatively marked with “Present”. For gut analyses, the number of guts is given in which a specific moss was found.

Year	Field studies						Gut analyses			
	2008	2009	2011	2008–2011	2010	2011	2008	2008–2011	2008–2011	2011
Data from	Pitfall traps, inblown fragments	Pioneer moss colonies (short survey)	Pioneer moss colonies (good survey)	Sticky traps, qualitative data	Pan traps	Pan traps	<i>Bourletiella hortensis</i> (Collembola)	<i>Amara alpina</i> (Coleoptera, Carabidae)	<i>Amara quenseli</i> (Coleoptera, Carabidae)	<i>Simplocaria metallica</i> (Coleoptera, Byrrhidae)
Sample size	In total, 74 fragments	In total, 24 colonies	Stars indicate relative numbers		Min. no. of bulbils	Min. no. of bulbils	In total, 139 guts	In total, 17 guts	In total, 6 guts	In total, 30 guts
<i>Ceratodon purpureus</i>	13	15	*****				26	1		14
<i>Bryum arcticum</i>	3	3	***							
<i>Bryum</i> sp.	18			Present			17	2 (one is capsule)		6
<i>Pohlia filum</i> , colonies		2	*****							
<i>Pohlia filum</i> , bulbils			*****	Present	5	11	15 (indicated by primordial leaves)	1 (with crushed bulbil)	1 (with crushed bulbil)	4 (with crushed bulbil)
<i>Pohlia</i> sp., leaves	31			Present			50	7	4	20
<i>Pohlia drummondii</i> , bulbils	7									
<i>Kiaeria starkei</i>	2									
<i>Racomitrium canescens</i>		3	*							
<i>Funaria hygrometrica</i>		1	**						3	
<i>Jungermannia polaris</i>			*							
<i>Jungermannia</i> sp., capsule								2		

(Table 1). In addition, 20 randomly located 1 m² quadrats were inspected for the extent of moss cover in 2008, 2009, and 2011.

NUTRIENT CONTENT OF MOSS BULBILS

Bulbils are onion-like diaspores typical for the *Pohlia* genus, which develop into new plants (Hågvær, 2012). Wind-transported and locally produced bulbils represent a potential food source for invertebrates. The presence of starch grains within cells of bulbils was identified using Lugol's iodine.

STATISTICS

Since chironomid midges was an important prey, differences in the frequency of midge eye fragments in guts were tested between sampling periods, males and females, and between newly hatched and fully pigmented animals. Statistical analysis was performed with the software R, version 2.14.2 (R Development Core Team, 2012). We used non-parametric tests, given that the data were not normal distributed according to Shapiro-Wilk test (R package "stats"). Wilcoxon signed-rank test was used when comparing two data sets, and Kruskal-Wallis rank sum test when testing more than two groups. When the Kruskal-Wallis rank sum test was significant, it meant that one of the three groups was different from at least one of the others. Hence, we needed to perform a multiple comparisons test after Kruskal-Wallis from the package "pgrmss."

TAXONOMY

Nomenclature of vascular plants accords with Lid and Lid (2005), bryophytes follow Frisvoll et al. (1995), springtails concur with Fjellberg (1998, 2007), beetles agree with Silfverberg (2010), and harvestmen follow Fauna Europaea (<http://www.faunaeur.org/index.php>).

Results

PIONEER BRYOPHYTES: FIELD DATA AFTER 3–6 YEARS

In 2008, after 3 years exposure, 18 of the 20 plots contained no visible vegetation, one had a small moss patch of a few square centimeters, the other a single plant of *Poa alpina*. However, by 2009, tiny moss colonies were observed within 17 of 20 plots, covering 0.02% of the moraine slope toward the glacier, and 2.1% of the slope away from the glacier. Two years later (2011), mosses

were visible on all study plots, covering about 0.4% and 6% of the two slopes, respectively. Scattered higher plants were also present, mainly *P. alpina* and *Festuca vivipara*.

Table 1 lists the bryophyte species recorded on the 2005 moraine between 2008 and 2011, and four of the species are illustrated in detail (Fig. 3). The 74 bryophyte fragments and diaspores blown into pitfall traps in 2008 testify to their early wind dispersal. This material contained at least four species: *C. purpureus*, *B. arcticum*, *Pohlia drummondii*, and *Kiaeria starkei*. *Pohlia (drummondii or filum)* leaves were dominant, followed by leaves of *Bryum* sp. and *C. purpureus*. Of special interest were seven bulbils of *P. drummondii*. In 2009, 24 small moss colonies were randomly sampled on the slope away from the glacier. They comprised mainly *C. purpureus*, with some *Racomitrium canescens*, *B. arcticum*, *P. filum*, and *F. hygrometrica*. A detailed survey in 2011 revealed six bryophyte species: *C. purpureus* was dominant followed by *P. filum* (often with bulbils, Fig. 2, part B), and *B. arcticum*. Three additional species were rarer: *F. hygrometrica*, *R. canescens*, and the liverwort *Jungermannia polaris*.

The continuous dispersal of moss diaspores into pioneer ground was demonstrated using sticky traps in 2008–2011, which confirmed wind transport of *Bryum* and *Pohlia* fragments and bulbils of *P. filum*. Pan traps in 2010–2011 also collected bulbils of *P. filum* (Table 1).

Figure 4 illustrates grains of starch within bulbil cells of *P. filum*. Bulbils may represent a valuable food source for pioneer animals.

GUT CONTENT OF BRYOPHYTE FEEDERS

Table 1 lists the moss species found in the gut of the springtail *B. hortensis* and three beetles—*Amara alpina* and *Amara quenseli* (Carabidae), and *Simplocaria metallica* (Byrrhidae). Whereas the two *Amara* species were omnivorous, also eating invertebrate prey (see below), *S. metallica* was an obligate moss feeder.

S. metallica

Among 30 animals collected in 2011, 21 guts contained visible contents, which was always moss. This slow-moving beetle grazed on the most abundant pioneer mosses, mainly *Pohlia* sp. (probably *P. filum*), but also *C. purpureus* and *Bryum* sp. (probably *B. arcticum*) (Table 1, Fig. 5). *Pohlia* and *Ceratodon* were found together in 13 guts, and in three cases, all three mosses were present. Although *Bryum* was observed in only 6 guts, it dominated

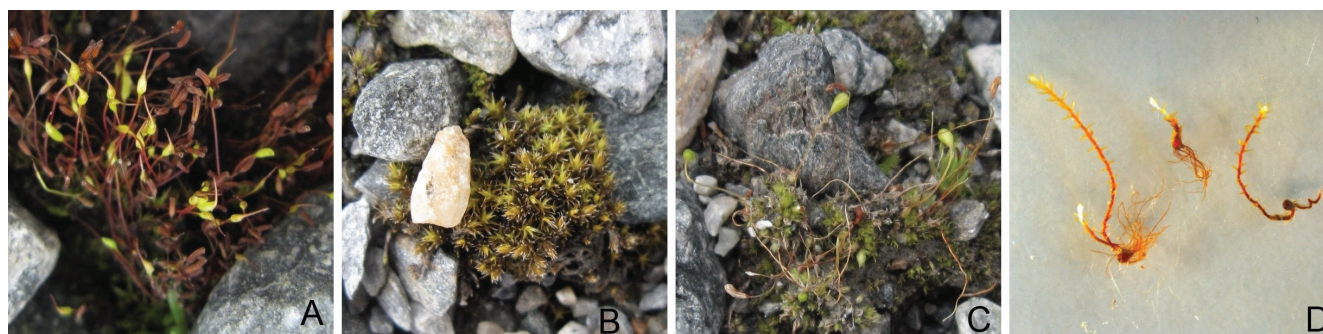


FIGURE 3. Some pioneer mosses. (A) *Ceratodon purpureus*. (B) *Racomitrium canescens*. (C) *Funaria hygrometrica*. (D) Inblown bulbils of *Pohlia filum* which had started to grow shoots and rhizoids in a small pond.

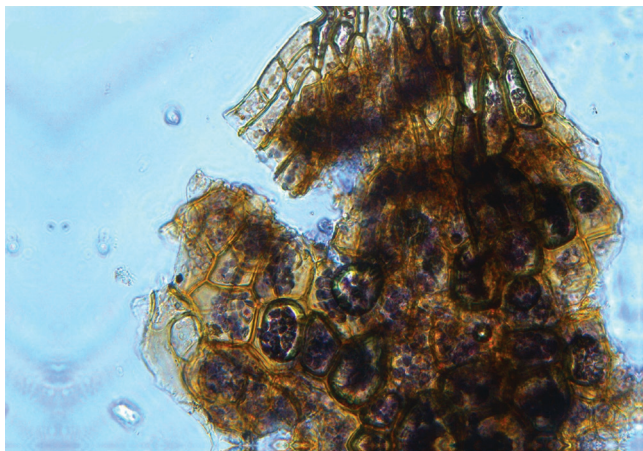


FIGURE 4. Starch grains within cells of a bulbil of the moss *Pohlia filum*. The grains have been colored blue-black in contact with Lugol's iodine. The upper part of the picture shows the basis of a small primordial leaf, without a mid-vein, that is situated on the top of the bulbil (see Figure 2, part B).

in 3. Generally, young shoots with small leaves were preferred. Many small fragments of moss stems indicated that the shoots had been successively chewed from the top. Larger moss fragments, however, were also ingested. Primordial leaves without a mid-vein, characteristic of the tip of *Pohlia* bulbils, were found in four guts. Crushed bulbils were also seen in these four guts, probably from *P. filum*. Rhizoids, probably two from *Bryum* sp., and one from *Pohlia* sp., occurred in 3 guts and probable moss paraphyses, elongate structures that shelter the sex organs, were found in 1. A few fungal hyphae were observed in 2 guts. Males and females shared a similar diet.

B. hortensis

This was the dominant springtail species (60% of pitfall captures) on 3-year-old ground in 2008. Among 156 mounted individuals from July and August, moss fragments were seen in 64% of guts. A closer study of 139 guts, where the content had been sufficiently exposed (Table 1), showed that 19% were apparently empty, but 54% contained fragments of identifiable moss leaves. *Pohlia* leaves were the most common, followed by *C. purpureus* and *Bryum* sp. (Table 1, Fig. 6). In 15 guts, primordial leaves from *Pohlia* bulbils were recognized, probably *P. filum*, but crushed bulbils were not identified owing to the fine fragmentation of the contents. Fungal hyphae, mainly brown, occurred in 46% of the guts,

in variable amounts (Fig. 6, part D). Most probably these belonged to the Ascomycota, as they lacked a hyphal clamp, and because some asci with spores were seen.

In 47 random guts from the whole season, an estimate was made with respect to the relative volume of different gut content categories. This was based on a subjective evaluation of the relative area covered by leaves, hyphae, et cetera on slides with well-squeezed material. Fragments of moss leaves dominated with 35%, followed by fungal hyphae (25%), mineral particles (18%), unidentifiable matter (15%), pollen (5%), moss rhizoids (1%), and fungal spores (1%). Some pollen grains belonged to pine (*Pinus silvestris*) and must have been lifted at least 400 altitude meters by air currents.

GUT CONTENT OF REMAINING SPRINGTAILS

The remaining species in the 2008 pitfall sample included *Agre-
nia bidenticulata* (24.7%), *Desoria olivacea* (8.0%), *Isotoma viridis* (5.2%), *Desoria infuscata* (1.5%), *Lepidocyrtus lignorum* (0.4%), *Desoria tolya* (0.2%), and *Ceratophysella scotica* (0.1%) (Hågvar, 2012).

The gut contents of *A. bidenticulata* were compact and dominated by mineral particles, making the separate elements difficult to identify. Diatoms occurred in several guts (Fig. 7), indicating feeding on terrestrial biofilm (Hågvar and Ohlson, 2013). Within each of four two-week periods, diatoms were identified in 5%–17% of guts, with a mean of 14%. Guts of *D. olivacea*, *I. viridis*, and *D. infuscata* were also dominated by mineral particles, but diatoms were also recognized in *D. olivacea* (5% of guts) and *I. viridis* (1%). Hyphae were not seen in guts of *A. bidenticulata* and *D. infuscata*, and only a few within one gut among 127 *D. olivacea*. Among 19 *I. viridis*, hyphae were recorded in three, and fungal spores in one. Among the rarer species, hyphae were found in one *D. tolya*, and one *L. lignorum*. The overall conclusion for springtails on 3-year-old ground, excepting *B. hortensis*, was that mineral particles dominated the gut contents. Terrestrial diatoms were present, but fungal hyphae or spores were rarely seen.

By contrast, at experimental sites of 30–40 years of age, *L. lignorum* and *I. viridis* became the dominant species in pitfall traps (Hågvar, 2012). Here the diet of both species changed more toward fungi. In *L. lignorum*, mineral particles still dominated gut contents, but among 13 animals, 7 also had fungal spores and 5 had hyphae. At 63-year-old sites, however, mineral particles were usually absent. Among 24 *L. lignorum* guts, all had spores, sometimes in great amounts, and 18 had hyphae. Similarly, in *I. viridis*, minerals dominated guts on 40-year-old ground, but with a tendency to increased fungal material: among 14 animals, 5 had hyphae and 6 had spores. Eight animals from 63-year-old ground had few mineral particles in their gut, but 7 of them had varying amounts of fungal hyphae.

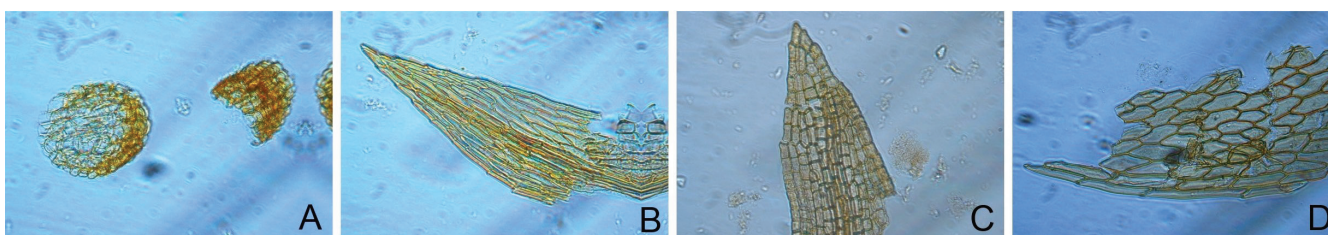


FIGURE 5. Moss fragments from the gut of the beetle *Simplicaria metallica* (Byrrhidae). (A) Sharply cut cross sections of a moss stem. (B) *Pohlia* leaf. (C) Young leaf of *Ceratodon purpureus*. (D) Characteristic cells from a *Bryum* leaf.

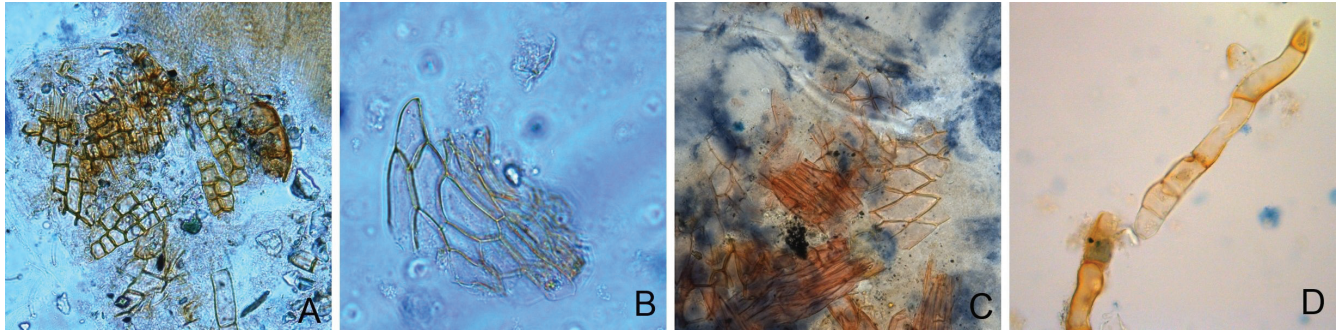


FIGURE 6. Various gut contents of *Bourletiella hortensis* (Collembola). (A) Quadratic cells in leaves of *Ceratodon purpureus*. (B) Primordial leaf from a bulbil of *Pohlia filum*. (C) Rhombic cells of *Bryum* sp. (D) Fungal hypha.

GUT CONTENT OF OMNIVOROUS CARABID BEETLES

A. quenseli

Among six guts examined, four contained identifiable content. Mosses (*Pohlia* sp. and *F. hygrometrica*, Table 1) were found in all four. Chironomid antennae and facet eyes occurred in two (3 and 21 eye fragments, respectively). One gut contained primordial leaves and crushed bulbils, probably of *P. filum* (Fig. 8).

A. alpina

Of 17 guts studied, invertebrate fragments were present in 14, moss in 9, higher plants in 4, and 1 was empty. Except for 2 guts with only animal prey, the rest contained a mix of animal and plant remains, with an approximately equal ratio by volume (Fig. 9). In any animal, different sections of the gut often contained different material. Bryophytes were mainly represented by *Pohlia*, but also *C. purpureus*, *Bryum* sp., and the liverwort *Jungermannia* sp. Primordial leaves from *P. filum* were noted in 3 guts, and crushed bulbil tissue in 1 (Table 1). In 2 guts from 6-year-old ground, embryo

sacs from the perianth of higher plants were identified (Fig. 9, part G). Among animal prey, fragments of facet eyes were present in 12 guts, with a mean of 10 fragments. Additional characteristic fragments of antennae indicated Chironomidae. Chitinous remains of one springtail were identified as *B. hortensis*. Males and females shared similar food habits.

GUT CONTENT OF OBLIGATE PREDATORS

N. nivalis

Thirty-two specimens of this large carabid beetle, from one sampling period in 2008 and two sampling periods in 2011, were studied (Table 2, Fig. 10). One gut was empty. Fragments of faceted eyes, often with antennal fragments of Chironomidae, dominated the guts for all sampling periods (Fig. 10, part D). In total, 88% of the guts contained eye fragments, with individual fragments numbering up to 237 (mean = 27). Kruskal-Wallis rank sum test indicated differences between sampling periods ($P = 0.0011$, Chi-squared = 14, $df = 2$). Multiple comparison

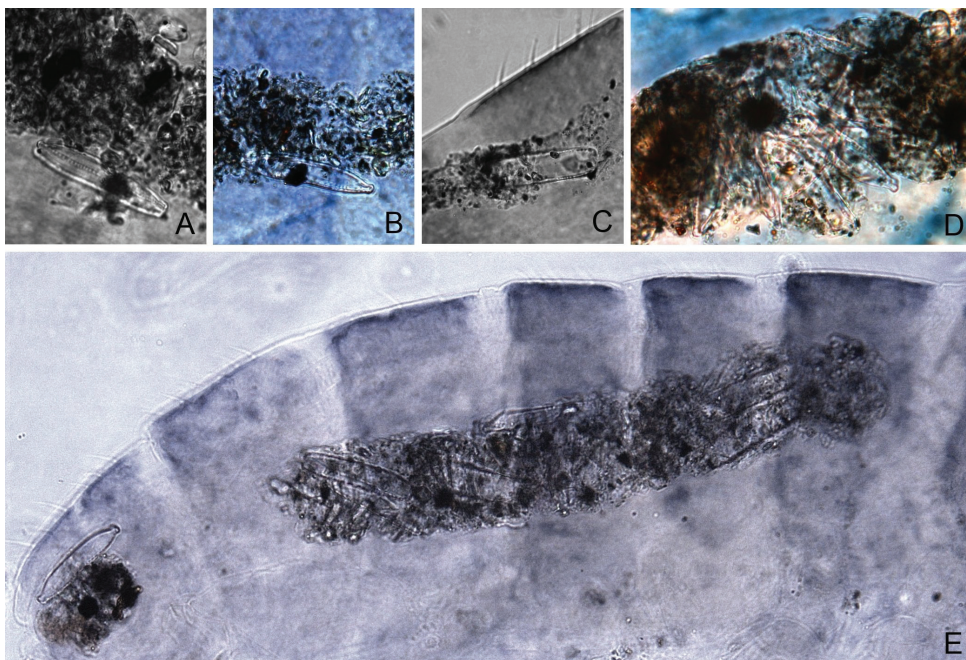


FIGURE 7. Terrestrial diatom algae in the gut of *Agrenia bidenticulata* (Collembola). (A–D) Selected gut sections from various individuals. (E) A complete gut, which was densely filled with diatoms. Based on comparison with diatoms in terrestrial biofilm at this place, A, B, D, and the left diatom in E were identified as *Hantzschia* cf. *amphioxys*, and C and the densely packed diatoms in E were identified as *Pinnularia* cf. *subcapitata*.

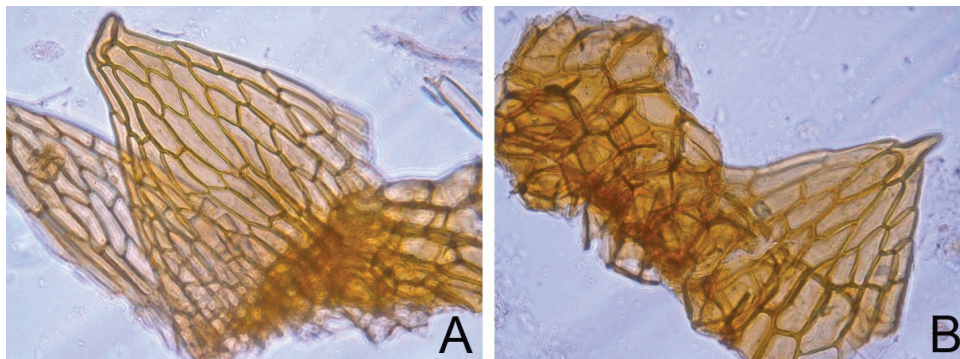


FIGURE 8. Two examples from the gut of *Amara quenseli* (Carabidae) of a crushed moss bulbil, with primordial leaves still attached. Compare with Figure 4, which shows the starch grains within bulbil cells.

test showed that the mean number of eye fragments per gut were significantly greater in June/July 2011 than in July/August 2008 ($P < 0.05$), but not significantly different in individuals collected during two separate periods of 2011. No difference was found between 10 males and 17 females in the total material ($P = 0.58$, $W = 74$), or between 6 teneral and 8 fully colored, black individuals in July 2011 ($P = 0.14$, $W = 12$).

Three springtail species, *A. bidenticulata*, (Fig. 10, parts A–B), *I. viridis*, and *B. hortensis*, identified by their chitinous fragments, were present but always in low numbers, as were two individual spiders (Table 2, Fig. 10, part C). The few tiny moss fragments present were probably ingested inadvertently or may be derived from the gut content of *B. hortensis* prey.

B. hastii

Samples were taken of 47 guts of this small carabid beetle over the same three sampling periods as for *N. nivalis*. Conclusions were similar for the two species (Table 2, Fig. 11). Two guts were empty, and 53% contained eye fragments, often with chironomid antennae. Mean number of eye fragments per gut was 7, with a maximum of 39. Among other contents, five spiders and nine

springtails of two species were identified. Some tiny moss fragments were present as in *N. nivalis*. Number of eye fragments did not differ significantly between the three sampling periods ($P = 0.65$, Chi-squared = 0.88, $df = 2$), nor between 13 males and 21 females ($P = 0.88$, $W = 132$), or between 13 teneral versus 9 fully colored adults in August 2011 ($P = 0.64$, $W = 66$). This species was observed hunting during daytime, especially on moist silty substrates.

M. morio

Harvestman samples ($n = 29$) covered two periods on 3-year-old moraine (Table 2). All specimens were pre-adult or adult. One gut was empty. Typical gut contents (Fig. 12) included eye fragments, often together with chironomid antennae, which were found in nearly half of the guts, although in small numbers. Eye fragment numbers did not differ significantly between the two sampling periods ($P = 0.92$, $W = 102$). Other invertebrate remains found included 22 springtail individuals of four species, one spider, one aphid, and, in two guts, scales from butterfly wings (Table 2). The few tiny moss fragments were insignificant. Four guts contained white, spherical bodies resembling eggs.

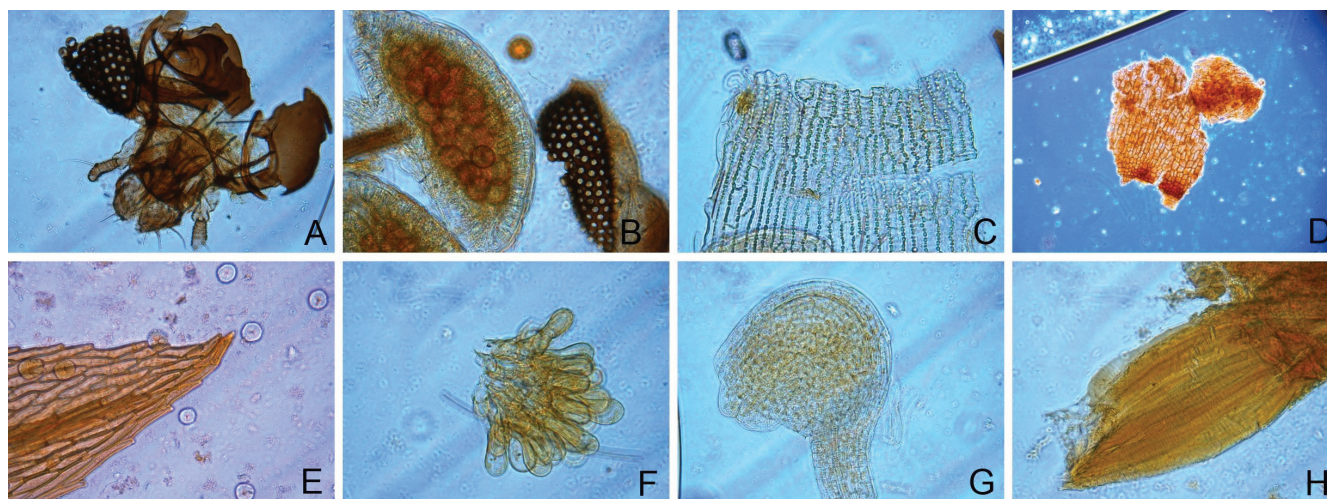


FIGURE 9. Elements from the gut of the omnivore beetle *Amara alpina* (Carabidae). (A) Head of a chironomid midge, with one facet eye. (B) Part of bryophyte capsule with spores from the liverwort *Jungermannia* sp. (probably *J. pumila*), and a facet eye. (C) Capsule wall of *Jungermannia* sp. (D) Capsule wall from *Bryum* sp. (E) *Pohlia* leaf. (F) Probably paraphyses from a moss (*Pohlia* sp.). (G) Embryo sac (nucellus) from a perianth of a vascular plant. (H) Young bud from a vascular plant.

TABLE 2

Invertebrate fragments identified in guts of three pioneer predators, from different sampling periods and years. All data are from 3- to 6-year-old ground, on a 2005 moraine. For each category, the mean number per gut is given, and the percentage of guts containing this category (in parentheses). While facet eyes are given as number of fragments, other categories show the minimum number of individuals, often based on the number of claws, jaws, or furca elements. Accompanying fragments indicate that facet eyes were mainly from Chironomidae (Diptera). All species names of prey refer to Collembola.

Predator species:	<i>Nebria nivalis</i> , Coleoptera, Carabidae			<i>Bembidion hastii</i> , Coleoptera, Carabidae			<i>Mitopus morio</i> , Opiliones	
Period:	26 July– 23 August	29 June– 27 July	27 July– 25 August	26 July– 23 August	29 June– 27 July	27 July– 25 August	26 July– 9 August	9–23 August
Year:	2008	2011	2011	2008	2011	2011	2008	2008
Number of guts	10	14	8	15	10	22	18	11
Facet eye fragments	8.2 (80)	47.4 (100)	16.6 (75)	5.9 (53)	11.1 (60)	5.7 (50)	1.4 (44)	0.9 (45)
<i>Agrenia bidenticulata</i>	0.3 (10)	0.2 (21)	0.1 (13)	0.3 (27)		0.2 (18)	0.1 (6)	0.7 (36)
<i>Desoria</i> sp.							0.1 (6)	0.3 (18)
<i>Isotoma viridis</i>		0.1 (7)						0.1 (9)
<i>Bourletiella hortensis</i>		0.1 (14)		0.1 (7)			0.2 (17)	0.5 (9)
Aphidoidea, aphids							0.1 (6)	
Lepidoptera, butterflies							0.1 (11)	
Araneae, spiders	0.1 (10)		0.1 (13)	0.1 (7)	0.1 (10)	0.1 (14)	0.1 (6)	

Discussion

BRYOPHYTES AS PIONEER ORGANISMS

The bryophytes recorded were typical pioneer species that colonize bare soil. Elven (1975) studied mosses on 10- to 30-year-old ground near two other arms (Blåisen and Kongsnutbreen) of the same glacier and found a similar community, with *C. purpureus*, *P. drummondii*/*P. annotina*, *P. nutans*, and *R. canescens* the most frequent species on young moraines.

Whereas *B. arcticum* and *P. filum* are mainly alpine, *C. purpureus* and *R. canescens* also occur in the lowlands. *F. hygrometrica* is a typical pioneer on bare or burned ground. These pioneer species are highly dispersive but tend to be outcompeted in closed vegetation. The nearest known locality for *C. purpureus*, for instance, is near Finse railway station, 3.5 km away. Moss species established within 3 years, five species were present after 4 years, and after 6 years mosses were present in all 20 square meter plots.

Significant wind transport of moss fragments and bulbils was documented by data from pitfall, sticky, and pan traps. These bulbils and fragments develop rhizoids and start to grow on moist surfaces (Hågvar, 2012). Tiny mosses are thus important pioneers serving as a barely visible food resource for several invertebrates.

BRYOPHYTES AS A FOOD SOURCE

Four pioneer invertebrates, one springtail and three beetles, fed upon altogether five bryophyte/liverwort genera: *Ceratodon*, *Bryum*, *Pohlia*, *Funaria*, and *Jungermannia* (Table 1). *Pohlia* was generally preferred. Few invertebrates are known to eat moss, but the beetle family Byrrhidae (*S. metallica*) is an exception (Koch, 1989). More surprising are the three other moss-eaters: *B. hortensis* (Collembola) and the two omnivorous *Amara* species (Carabidae). Our data show that different parts of the moss plant are selected, suggesting that different species graze mosses in differ-

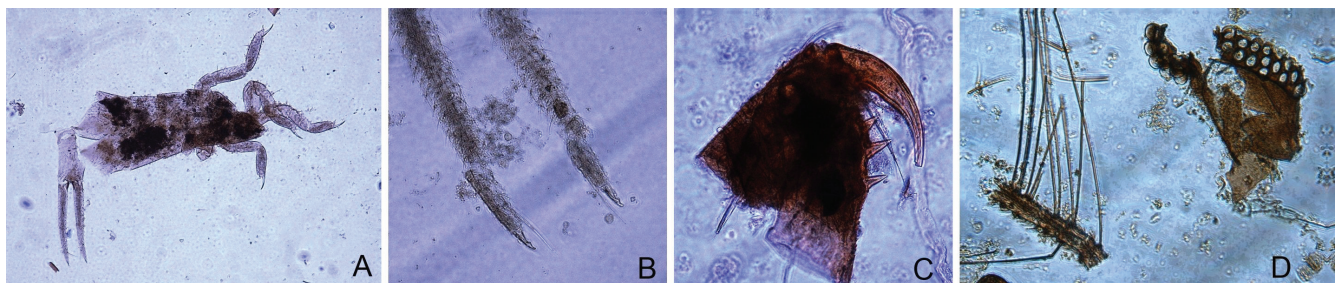


FIGURE 10. Examples of gut content in the predator *Nebria nivalis* (Carabidae). (A) Nearly complete specimen of the springtail *Agrenia bidenticulata*. (B) Furca of the same species. (C) Spider chelicer. (D) Facet eye and antenna fragment of a chironomid midge.

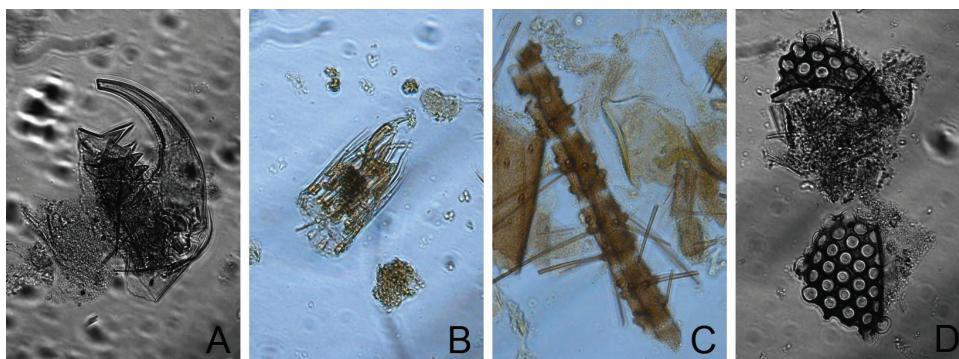


FIGURE 11. Elements from the gut of the smaller predator beetle *Bembidion hastii* (Carabidae). (A) Spider chelicer. (B) Spider claw. (C) Chironomid antenna. (D) Chironomid facet eyes.

ent ways. *S. metallica* seems to chew the whole plant from the top, including the stem, sometimes ingesting larger fragments, while the smaller *B. hortensis* chews single leaves of the same three moss genera. All four moss-eaters consumed some primordial leaves from the tip of *Pohlia* bulbils, and crushed bulbil tissue, rich in starch, was identified in the three beetles (Fig. 4). *A. alpina* showed another feature by having eaten spore capsules of *Jungermannia* and *Bryum*.

Elsewhere, *B. hortensis* feeds on several agricultural plants, damaging the seedlings of cucumber, radish, rape, and common chickweed. Also spores, pollen, fragments of hyphae, and moss, were frequently found in the gut (Honma, 1988). This wide food choice allows *B. hortensis* to establish on pioneer ground as soon as windblown diaspores and fragments of pioneer moss are present. The Arctic springtail *Megaphorura arctica* also feeds partly on mosses on Svalbard, ingesting several species (Hodkinson et al., 1994). Moss leaves, with their soft thin tissues, usually comprising a single layer of cells, were thought to be more easily processed by small mouthparts than those of vascular plants.

VASCULAR PLANTS AS A FOOD SOURCE

Scattered specimens of *F. vivipara* and *P. alpina* colonized the moraine within six years and the embryo sacs in two guts of *A. alpina* (Fig. 9, part G) could derive from one of these graminoid species. *A. alpina* is known to climb plants at night and feed on seeds, for instance those of *Poa arctica* (Chernov, 1988).

BIOFILM AS A FOOD SOURCE

Certain pioneer springtails, *A. bidenticulata*, *D. olivacea*, and *I. viridis*, graze on biofilm created by photosynthesizing diatoms (Hågvar and Ohlson, 2013). Diatoms were present in the guts of the first two species during several sampling periods, indicating that biofilm was a reliable food resource on 3-year-old ground. On Svalbard, certain surface-active Collembola feed on a crust of cyanobacteria (e.g., Birkemoe and Liengen, 2000), which is readily visible after 16 years (Hodkinson et al., 2001). The unidentified gut contents in the Midtdalsbre springtail species may be digested cyanobacteria, although no obvious cyanobacterial crust was observed.

FUNGI AS A FOOD SOURCE

B. hortensis was mainly a moss feeder but fungal hyphae were recorded in 46% of the guts, and dominated in some. Whether these slowly digestible chitinous hyphae accumulate in the gut is an open question. Fungi may represent a valuable food source for individuals when mosses are not nearby. Various bryophytes may host specialized fungi (e.g., Kausarud et al., 2008), and in some cases the hyphae could be ingested inadvertently. No pioneer springtail species had fungi as their main food, probably owing to a lack of decomposing organic material. On older ground, however, fungal feeders like *L. lignorum* and *I. viridis* were more common (Hågvar, 2012), and the relative amounts of hyphae and spores in their gut increased with soil age. These fungal feeders typically belong to later successional stages where decomposing material is more abundant.

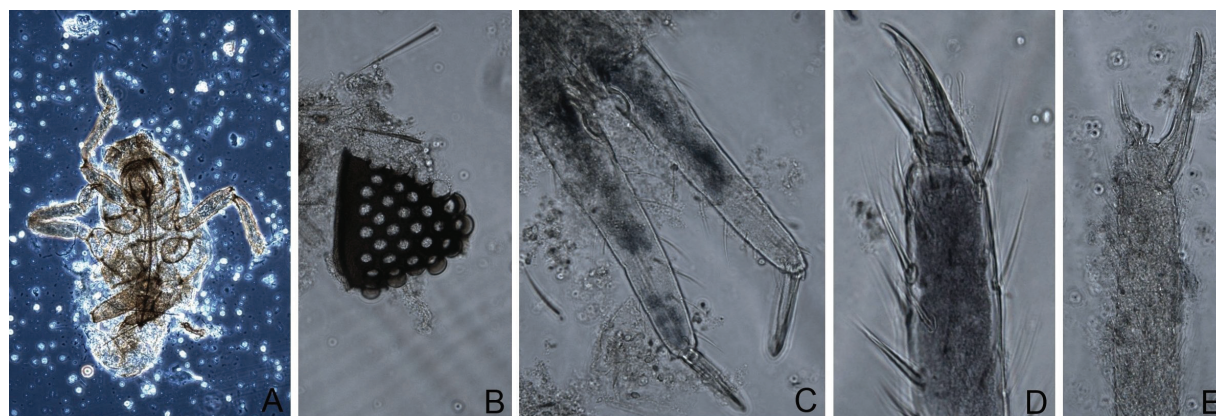


FIGURE 12. Elements from the gut of the large predator *Mitopus morio* (Opiliones). (A) Intact aphid specimen. (B) Facet eye. (C and D) Furca and claw of the springtail *Bourletiella hortensis*. (E) Claw of the springtail *Agrenia bidenticulata*.

PREDATOR FOOD

We assume that many adult chironomid midges end up on the ground, for instance during rain or at night. These midges were numerous in pitfall traps and also periodically numerous in fall-out traps (Flø and Hågvar, 2013). Probably, both dead and alive midges can be found on the ground by the actual predators. Faceted eyes and antennae of chironomids were commonly present in predator guts, independent of sampling period in a given year, sex, and adult beetle age (Table 2). The two omnivorous *Amara* species also ate chironomid midges. We conclude that chironomid midges, developing in adjacent ponds, provide a stable food resource for the predators during the early stages of succession. Springtails, by contrast, were eaten only in small numbers (Hågvar and Ohlson, 2013). The harvestman *M. morio* consumed more springtails than the two carabid species and even ate aphids and butterflies (Table 2). This large, often diurnal, generalist predator feeds efficiently by scanning a broad strip during its walk. It also eats dead invertebrates (Phillipson, 1960a, 1960b). Records of white, spherical bodies in some guts made us suspect that *Mitopus* eats eggs deposited by conspecifics. Intraguild predation among predators appeared limited, comprising a few spiders eaten by each of the three main predators. The food of pioneer spiders, which include a few Linyphiidae species and one Lycosidae species (Bråten et al., 2012) remains unknown. However, a radiocarbon age of 340 years for the lycosid *Pardosa trailli* indicated feeding on locally produced chironomid midges (Hågvar and Ohlson, 2013).

A PIONEER COMMUNITY WITH SEVERAL FOOD NICHES

Eleven pioneer invertebrates are listed according to their visible gut content (Table 3). Many food sources were available during the 3–6 first years of succession, but they were used differently by different species. Only the three last species were obligate predators. The biofilm- and diatom-eating springtail *A. bidenticulata* was the initial pioneer that tracked the retreating ice edge closely, but disappeared after 30–40 years (Hågvar, 2010, 2012; Bråten et al., 2012; Flø and Hågvar, 2013). Slightly later came another biofilm-grazer, *D. olivacea*, and the moss-eating *B. hortensis*, which also

ingested fungi. Pioneer springtails were thus primarily herbivores. It took 30–60 years for the typical fungus feeders *L. lignorum* and *I. viridis* to achieve high abundance.

Food chains based on living green plants may thus establish almost immediately following ice retreat, allowing both herbivores and omnivores as pioneers. Mosses are thus one of the “drivers” in early succession. Predators predominantly fed chironomid midges, which transported ancient carbon from adjacent aquatic habitats. Hågvar and Ohlson (2013) called this “the invisible carbon source community,” being driven to a large degree by ancient carbon from the glacier and unnoticed diatom algae and pioneer mosses.

COMPARISON WITH OTHER GLACIER FORELAND STUDIES

At the present site, springtails were the first surface active animals on newly exposed ground. Mites of the Actinedida group also arrived early, occurring in pitfall traps after three years (Hågvar, 2012). Early colonization by springtails and mites is a common phenomenon in European glacier forelands. Both groups were documented after 2–4 years in Svalbard (Hodkinson et al., 2004) and in the Alps (Kaufmann et al., 2002), and after less than 10 years on nunataks in Iceland (Ingimarsdóttir et al., 2012). Another common trait in European glacier forelands is the appearance of macroinvertebrate predators before any visible vegetation. In Norway and the Alps, Lycosid and Linyphiid spiders, Carabid beetles, and harvestmen of genus *Mitopus* are early predators (Kaufmann, 2001; Gobbi et al., 2006; Vater, 2012; Bråten et al., 2012; Hågvar, 2012). On Svalbard, harvestmen are lacking, and beetles are absent on forelands, but Linyphiidae spiders colonize rapidly by “aerial ballooning” (Hodkinson et al., 2001; Coulson et al., 2003; Hodkinson et al., 2004).

Despite similar invertebrate colonization patterns on European forelands, little is known about the pioneer food webs. Aside from our work, food choice and trophic levels have been studied in the Rotmoos glacier foreland, Austria. Here stable isotope studies suggested that pioneer predators relied on decomposer prey, with springtails the most important (König et al., 2011). They assumed that the springtails fed mainly on fungi colonizing allochthonous

TABLE 3
Food sources of terrestrial invertebrates on 3- to 6-year-old ground, based on gut content analyses.

Species	Group	Biofilm	Fungal hyphae	Bryophytes	Vascular plants	Invertebrates	Ancient carbon via Chironomidae
<i>Agrenia bidenticulata</i>	Collembola	x					
<i>Desoria olivacea</i>	Collembola	x					
<i>Isotoma viridis</i>	Collembola	x	x				
<i>Lepidocyrtus lignorum</i>	Collembola		x				
<i>Bourletiella hortensis</i>	Collembola		x	x			
<i>Simplocaria metallica</i>	Coleoptera			x			
<i>Amara alpina</i>	Coleoptera			x	x	x	
<i>Amara quenseli</i>	Coleoptera			x		x	
<i>Nebria nivalis</i>	Coleoptera					x	x
<i>Bembidion hastii</i>	Coleoptera					x	x
<i>Mitopus morio</i>	Opiliones					x	x

humic material. DNA from predator guts confirmed springtails as a general prey and also demonstrated intraguild predation (Raso et al., 2014). However, molecular methods only demonstrate prey presence/absence of tested taxa. Neither König et al. (2011) nor Raso et al. (2014) checked gut content of predators or springtails under the microscope. The proportion of springtails to other prey items in predator guts was therefore unknown and fungal-feeding by Collembola remained unconfirmed. Our data from Midtdalsbreen foreland, by comparison, describe a different food web, in which springtails were mainly herbivores, and the predators relied heavily on locally produced chironomid midges. No food choice diagram or food web has been described for pioneer invertebrates in Svalbard forelands based on detailed gut studies, but web-building Linyphiidae spiders probably feed on allochthonous Diptera, especially chironomid midges (Hodkinson et al., 2001; Coulson et al., 2003). A general terrestrial invertebrate food web for Svalbard (Hodkinson and Coulson, 2004) illustrated that both springtails and mites use many different food sources, and also serve as prey. On Svalbard, these groups may be important in the food webs of glacier forelands.

VARIATION IN PIONEER FOOD WEBS

European glacier forelands exist under varying conditions, from the severe climate of the high Arctic to more benign sites farther south. The distances to source communities also vary, and different food items may be available on newly exposed ground in different regions. Many pioneer invertebrates are flexible with respect to food choice and it is reasonable to assume that different environmental conditions shape different food webs. For instance, chironomid-producing ponds are lacking in the Rotmoos site, reducing the potential importance of ancient carbon transfer between aquatic and terrestrial food chains.

Freshly exposed sand, gravel, and stones may be considered a hostile habitat for the human eye. However, Bråten et al. (2012) concluded that pioneer macroinvertebrates often have in common an ability to, or a preference for, living in open or poorly vegetated habitats. Open habitats may have certain advantages. The ground is rapidly heated by sun, and the heat is slowly released during night. In the absence of vegetation, it is easy to move around for surface active predators, but also to find shelter in crevices among stones and gravel. Furthermore, competition could be low for pioneers. Given an adequate food supply, open ground may be a good habitat for several species, and the initial community structure could to a large degree depend on a random colonization sequence.

FUTURE STUDIES

Future food web research in pioneer communities should combine high taxonomic resolution DNA techniques with visual analyses of gut contents under the microscope. Gut content analyses of predatory beetles, based on identifiable exoskeleton or chitinous remains, have historically given valuable results (e.g., Holopainen and Helenius, 1992) as have studies on collembolan guts, with respect to the presence of fungal hyphae and spores (e.g., Bødvarsson, 1970). More such studies would allow us to look for general ecological principles governing the establishment of pioneer communities and resolve whether spiders or other macroinvertebrate predators typically colonize before the microarthropods. Hågvar (2012) noted that pioneer invertebrates include both specialists and generalists, parthenogenetic and bisexual species, and species with short or long life cycles. Several questions remain

open. Is the pioneer ground a sink for several “pioneer” species that depend on continuous colonization? How important are saprophagous species, such as fungal-feeding springtails? How important is allochthonous material as an invertebrate food source? How early do green plant-based food chains operate, and are biofilm and pioneer mosses overlooked as drivers of early succession? The answers may vary between particular situations.

The “predator first paradox” has been much debated, but the “microarthropod first question” may be equally relevant. Linyphiidae spiders are effective pioneer predators, especially suitable for trapping eolian prey, particularly Diptera (Hodkinson et al., 2001, 2004; Coulson et al., 2003). However, if epigeal animal life generally starts with the microarthropods, which may also serve as food for early predators, a key question is what do the pioneer microarthropods eat? Our study is the first attempt to suggest possibilities.

Acknowledgments

Klaus Høiland and Trond Schumacher helped to identify fungal hyphae, and Oddvar Hanssen photographed pioneer carabid beetles. Ronny Steen helped with statistical testing, and Atle Nesje gave information on yearly glacier retreat. Olav M. Skulberg identified diatom algae in Collembola guts. Ole Wiggo Røstad produced compound figures. Two referees gave valuable comments. Thanks to Finse research station for hospitality.

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MS accepted April 2015