

CHAPTER 1

THE FAUNA: A PLACE TO CALL HOME

TABLE OF CONTENTS

Types of Interactions	1-1-2
Bryological Fauna	1-1-2
Dispersal	1-1-3
Limitations	1-1-3
The Inhabitants	1-1-3
Cover and Nesting Materials – Terrestrial	1-1-5
Bryophyte Individuality	1-1-5
Food Value of Bryophytes	1-1-6
Vitamins	1-1-8
Food Chain Effects	1-1-9
Seasonal Differences in Habitat and Diet	1-1-9
Habitat Differences in Nutrient Availability	1-1-9
Consumption Rates	1-1-11
New and Exciting Directions	1-1-11
Summary	1-1-13
Acknowledgments	1-1-13
Literature Cited	1-1-13

CHAPTER 1

THE FAUNA: A PLACE TO CALL HOME



Figure 1. A bird nest of the New Zealand fantail (*Rhipidura fuliginosa*) in a New Zealand *Nothofagus* forest, exhibiting a potpourri of vegetal material, including bryophytes. Could that be *Dawsonia* on the left? Photo by Rosemary Lovatt, with permission.

Types of Interactions

When I first became interested in bryophytes, I turned to the aquatic habitat, a place I had loved as a child and young adult. This soon led me to the organisms that lived among them. But literature on the subject was extremely difficult to find. This did not seem to be a high priority topic among bryologists, and those who studied animals seemed to think bryophytes were unimportant.

It is with great pleasure that I write this book, because there are now many fascinating stories of bryophyte – animal interactions, from housing to building materials (Figure 1) to food to safe sites. It appears that ecologists are beginning to recognize the importance of bryophytes, including them in studies, and publishing their studies in a very wide array of journals. That literature is easier to find now due to the internet, and when contacted, these wonderful scientists have been willing to share their stories and their photographs with all of us.

Bryological Fauna

Imagine yourself as a tiny mite in the forest. Everything around you must seem gigantic! But there, amidst the rocks and pine needles, a miniature forest beckons. It is a moss. This moss is your home. Here you can feel secure, protected from the drying wind and flecks of sun, hidden from the hungry birds, yet able to find tiny morsels for your own diet.

The bryophyte world is full of life, creating a habitat unlike any other (Ramazzotti 1958). Yet we know almost nothing of it. What loss might there be if the mosses were to disappear? What bird might be unable to construct a nest? What ant would have no place to hide its winter cache of seeds? What lemming might freeze its feet? The animals of the forest and field, stream and rock, have a very different view of the mosses and liverworts from that of the human inhabitants of the planet. These relationships will begin to unfold in this volume.

The habitats provided by mosses and liverworts are widely varied and worldwide, from mosses on roofs (Corbet & Lan 1974) to epiphytes (Fly *et al.* 2002) to turf-forming moss polsters (von der Dunk & von der Dunk 1979). In this volume we will explore the wide-ranging sizes and uses of the bryophyte dwellers and users. We will compare the terrestrial habitat, where nematodes are often most abundant, closely followed by rotifers (Figure 2), to the aquatic habitat, which can be quite different, and where Chironomidae (midges) are often the most abundant.

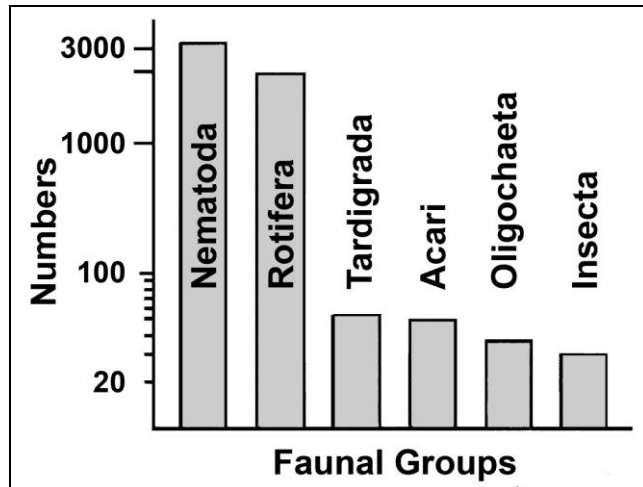


Figure 2. Comparison of relative abundance (log scale) of common bryophyte-inhabiting invertebrate fauna. Redrawn from Sayre & Brunson 1971.

Dispersal

Dispersal is necessary for both bryophytes and their inhabitants. Some, perhaps most of the microinhabitants, ride on a magic flying carpet, transported to their new location as a passenger on the bryophyte. Janiec (1996) trapped microfauna that were transported by the wind to areas with established plants near a glacier on King George Island of the South Shetland Islands. After six weeks of exposure, 859 individuals were trapped. Nematodes comprised 71%, tardigrades 22%, and rotifers 7%. The number of individuals caught depended on the distance from a colonized area and the presence of plant parts, suggesting that the plant parts contributed to their dispersal.

Limitations

Bryophytes provide a habitat with a number of constraints that can prove to be of value to their tiny inhabitants. Most obviously, their small size limits the organisms that can live there. This affords small organisms protection from larger predators. And the bryophytes have a slow growth rate, permitting them to be a nursery to organisms that are initially small, but forcing these youngsters to leave before they are large enough to turn cannibal and consume their own offspring. The perennial nature of most bryophytes, rendering them present when many tracheophytes are absent or unable to provide cover, also provides a suitable overwintering habitat for numerous organisms, from the small ones living among the stems and leaves to the larger ones that live under them or use them as nesting material. Their C_3 habit permits the bryophytes to survive and sometimes even grow when the environment is

cold and other plants are dormant, often absent above the substrate surface. Thus, in a world of predators, the bryophytes offer a safe site to numerous organisms that dominate this miniature world.

In the Antarctic, water limits the flora and fauna (Kennedy 1993). Kennedy suggested that water, rather than dispersal or temperature may limit many organisms from colonizing in the Antarctic. He demonstrated that there was a close relationship between the substrate biota and gradients in meltwater, seepage, and upwelling. Furthermore, microarthropod abundance is "directly proportional" to microvariation in relative humidity. Even the algal food source migrates upward in response to added water.

The Inhabitants

Large bryophyte mats typically host a wide variety of micro and macroinvertebrates (Ino 1992; Glime 1994; Peck & Moldenke 1999). The presence of a wide diversity of feeding strategies in a moss community suggests that the moss serves as a site of multiple pathways for nutrient cycling (Merrifield & Ingham 1998).

Fauna of bryophytes may be divided between those that are **bryophilous**, *i.e.*, those that typically live among bryophytes, and the casual visitor, sometimes referred to as **bryoxenous** (Ramazzotti 1958; Gadea 1964). Gerson (1982) divided these bryofauna into four categories:

- bryobionts:** animals that occur exclusively associated with bryophytes, *e.g.* *Cyclidium sphagnetorum* (a ciliate protozoan) on *Sphagnum* (*cf* Figure 3)
- bryophiles:** animals that are usually associated with bryophytes but can be found elsewhere
- bryoxenes:** animals that regularly spend part of their life cycle among bryophytes
- occasionals:** animals that may at times be found associated with bryophytes but do not depend on them for survival



Figure 3. *Cyclidium* sp. This genus includes *C. sphagnetorum*, a species that occurs only on *Sphagnum*. Photo by Yuuji Tsukii, with permission.

Chernov (1985) named the bryophyte-dwelling invertebrates **semi-edophores**, a term that means partly living in soil. This naming is consistent with the treatment of mosses as part of the litter, a practice common in soil biology. In aquatic systems, those tiny organisms that live on the bed of a river or lake and are barely visible to the human eye are termed **meiofauna** – those that pass through a 0.500 mm sieve and are retained on a 0.045 mm sieve (International Association of Meiobenthologists 2008).

Usage of this term has expanded to include organisms living on bryophytes that provide a moist film of water during at least part of the year. Maggie Ray (Bryonet 7 July 2005) stated that there are three groups of meiofauna that commonly live in the film of water on the bryophyte surface and that can achieve an **ametabolic** state. These are tardigrades, free-living nematodes, and rotifers. This **cryptobiotic** or **ametabiotic** state permits them to join the bryophytes in being dormant during those periods when the bryophyte is dehydrated or under a blanket of snow. She states that these cryptobiotic animals are "virtually indestructible." This permits them to survive environmental extremes such as high and low temperatures, high and low pH, very high pressure and very low vacuum, and low moisture. Upon return of the habitat to a "livable" and hydrated state, the animals absorb water, expand, and return to an active life. Hence, one might find eggs, "tuns" (stage in which body metabolism is undetectable), and cysts. Maggie points out that they do not age while they are in their cryptobiotic state and can remain that way for decades, making ideal study organisms for those interested in space travel and cellular research.

Bryophytes are such an important part of the **niches** of some invertebrates that their name indicates they are "of the moss." A Google search for *muscorum* has revealed 33 of these names among the protozoa and invertebrates (Table 1), and there are probably more, as well as those with *bryophila* or *muscicola* and other bryological epithets such as *Cyclidium sphagnetorum* or *Bryometopus sphagni*.

One particularly important **xerophytic** community is the **cryptogamic crust** (Figure 4) found in prairies and deserts. These bryophyte masses are associated with lichens and algae and inhabited by fungi, bacteria, and other micro-organisms. Among 38 taxa (nematodes, tardigrades, mites, arachnids, springtails, other small insects) in New Mexico, 29 occurred on mossy patches (Brantley & Shepherd 2002). Twenty-seven species occurred on mixed lichen and moss patches, and 21 on lichen patches. Fifteen taxa occurred on all three types. Mosses supported the highest abundance, followed by mixed lichen and mosses, then by lichens. Richness and abundance were both higher in winter (March) than in summer (August) for all crust types in these dry habitats, reflecting differences in moisture stress.



Figure 4. Hydrated cryptogamic crust of *Syntrichia ruralis* and other desiccation-tolerant organisms. Photo by Michael Lüth, with permission.

Table 1. Names of protozoa and invertebrates including *muscorum* as the specific epithet. The list was derived from an internet Google search, especially ITIS search, for *muscorum*. Accessed on 7 October 2008 at <<http://www.itis.gov/servlet/SingleRpt/SingleRpt>>.

Protozoa

Assulina muscorum (Rhizopoda)
Chilodontopsis muscorum (Ciliophora)
Gastrostyla muscorum (Ciliophora)
Histriculus muscorum (Ciliophora)
Holosticha (= *Keronopsis*) *muscorum* (Ciliophora)
Oxytricha (= *Opistotricha*) *muscorum* (Ciliophora)
Pusilloburius (= *Pseudoglaucoma*) *muscorum* (Ciliophora)
Rhabdostyla muscorum = *Opercularia coarctata* (Ciliophora)
Sathrophilus (= *Saprophilus*) *muscorum* (Ciliophora)
Steinia muscorum (Ciliophora) name validity not verified
Strongylidium muscorum (Ciliophora) name validity not verified
Stylonychia muscorum (Ciliophora)
Urostyla muscorum (Ciliophora)

Nematoda

Hemiplectus muscorum (nematode)
Prionchulus muscorum (nematode)

Arthropoda: Arachnida

Gnaphosa (= *Pithonissa*) *muscorum* (Araneae – spider)
Liochthonius muscorum (Araneae – spider)
Tegeocranellus muscorum (Acari – mite)

Arthropoda: Isopoda

Philoscia (= *Oniscus*) *muscorum* (moss wood louse)

Arthropoda: Pseudoscorpiones

Neobisium muscorum (Neobisiidae – moss scorpion)

Arthropoda: Insecta

Acerella muscorum (Protura)
Acrotona muscorum (Coleoptera: Staphylinidae)
Bombus (= *Apis*) *muscorum* (Hymenoptera: Bombidae – moss carder bee)
Anthrenus museorum = *Byrrhus* (= *Anthrenus*) *muscorum* (Coleoptera: Dermestidae)
Entomobrya (= *Degeeria*) *muscorum* (Collembola – springtails)
Leptothorax (= *Myrmica*) *muscorum* (Hymenoptera: Formicidae)
Liothrips muscorum (Thysanoptera: Thripidae)
Lissothrips muscorum (Thysanoptera: Thripidae)
Mniophila muscorum (Coleoptera – leaf beetle)
Neanura muscorum (Collembola: Neanuridae)
Peromyia muscorum (Diptera: Cecidomyiidae)
Tetramorium muscorum (Hymenoptera: Formicidae – Guinea ant)

Mollusca

Pupilla muscorum (Gastropoda – snails)

Bryophytes can be especially important in contributing to species diversity of ecosystems. Sudzuki (1971) found that among 17 stations along five lakes on Mt. Fuji in Japan, the populations of rhizopods, gastrotrichs, rotifers, and nematodes were richest in the mosses. The mosses by Lake Kawaguchi had the highest overall species richness, ranging as high as 77 species, whereas gravels had richness as low as 19 species.

Varga (1992a, b) has found that some rare bryophytes in Sweden [*Plagiobryum zierii* (Figure 5) & *Saelania glaucescens* (Figure 6)] harbor a bryofauna that helps in monitoring air pollution. Not only do the invertebrates have high concentrations of lead, but the fauna in polluted

cushions is diminished compared to that from unpolluted sites.



Figure 5. Lead accumulates in the fauna of this *Plagiobryum zierii*. Photo by Michael Lüth, with permission.



Figure 6. *Saelania glaucescens* is a moss whose bryofauna can be used to monitor air pollution. Photo by Michael Lüth, with permission.

Cover and Nesting Materials – Terrestrial

Moss mats and cushions can make ideal cover and nesting material for a variety of organisms. They serve to buffer both temperature and moisture, while providing sufficient spaces for gas exchange. There are many tiny spaces ideal for laying eggs and protecting young larvae from predators or desiccation. For larger organisms, the leafy stems are easily woven into suitable nests, and the projecting leaves render stability to the completed product. Thus it is not surprising to find that many organisms actually depend on bryophytes for their homes and shelters.

Bryophyte Individuality

But to what extent do individual bryophyte species differ in their provisions for these animals? Learner *et al.* (1990) found no relationship between taxon richness and macroinvertebrate fauna on bank slopes of river corridors where bryophytes were included in the assessment. This suggests that bryophytes might form functional groups that differ in their form from other plants but otherwise differ little within the functional group in the means by which they shelter organisms.

Two communities of bryophytes on Signy Island in the Antarctic support this growth form or functional group suggestion for richness. Davis (1981) found that there was little difference in assimilation or respiration of the plant

and faunal components of the *Polytrichum strictum* (Figure 7) and *Chorisodontium aciphyllum* (Figure 8) turf compared to the *Calliergidium austro-stramineum* (Figure 9), *Calliergon sarmentosum* (Figure 10), and *Sanionia uncinata* (Figure 11) mat with *Cephaloziella varians* (Figure 12), but among the faunal taxa (protozoa, Rotifera, Tardigrada, Nematoda, Acari, and Collembola) of these bryophytes, the standing crops of Collembola and Acari differed between the two associations. Thus, while richness differed little, the types of species did differ. Interestingly, it appeared that no bryophytes were eaten by these organisms. Rather, the bryophytes form unique habitats that provide safe sites for the small invertebrates that seek shelter there.



Figure 7. *Polytrichum strictum*, a turf-former that provides habitat for invertebrates on Signy Island in the Antarctic. Photo by Michael Lüth, with permission.

Bryophytes can play a role in the larger ecosystem picture as well, affecting organisms in other niches. Some mosses in the Antarctic provide habitat for a variety of arthropods indirectly rather than directly by modifying the underlying soil (temperature, moisture, structure) in ways that make it suitable for a variety of arthropods (Gerson 1969).



Figure 8. *Chorisodontium aciphyllum*, a common invertebrate habitat on Signy Island in the Antarctic. Photo by Jan-Peter Frahm, with permission.



Figure 9. *Calliergidium austro-stramineum*, a moss that forms a functional group for fauna similar to that of *Chorisodontium aciphyllum* (Figure 8). Photo by Bill Malcolm, with permission.



Figure 10. *Calliergon sarmentosum*, a common invertebrate habitat on Signy Island in the Antarctic. This moss forms a functional group for fauna similar to that of *Chorisodontium aciphyllum* (Figure 8). Photo by Michael Lüth, with permission.



Figure 11. *Sanionia uncinata*, a moss that forms a functional group for invertebrate fauna similar to that of *Chorisodontium aciphyllum* (Figure 8). Photo by Michael Lüth, with permission.



Figure 12. Leafy liverwort *Cephaloziella varians*, growing here with a member of the **Polytrichaceae**. Photo by Kristian Peters, with permission.

Are Bryophytes an Important Food Source?

The answer to that question seems to depend on who you are. But there is clear evidence that some organisms do eat bryophytes. And they seem to have their preferences for both species and parts.

For example, in *Ulota phyllantha* (Figure 13), the consumer (apparently an isopod) has a preference for the lamina, leaving behind hair-like structures that are the costa remains (Robin Stevenson, pers. comm. 19 February 2014). In others, gemmae are preferred. Stevenson has suggested that in *Orthotrichum lyellii* (Figure 14), where gemmae are prolific, being edible might be an adaptation for dispersal of the gemmae.



Figure 13. *Ulota phyllantha* very badly affected by grazing. Those hair-like structures are remaining costae – the leaf lamina has been eaten. Photo courtesy of Robin Stevenson.



Figure 14. *Orthotrichum lyellii*, a moss with prolific gemmae. Photo by Malcolm Storey, through Discover Life.



Figure 15. *Orthotrichum lyellii* leaf with gemmae. Photo by Hermann Schachner, through Creative Commons.

Food Value of Bryophytes

Because most bryophytes exist uneaten in herbaria around the world, biologists have long held the view that bryophytes are not effectively a part of the food chain. They have low caloric value (3.7–4.8 Kcal/g; Forman 1968, 1969; Rastorfer 1976a, b), large quantities of holocellulose

and crude fiber (Walton 1985) that makes them hard to digest, and are often endowed with a plethora of secondary compounds (Asakawa 1981; see chapter on antiherbivory).

In comparison to evergreen and deciduous shrubs in the alpine tundra, with ~5,560 cal/g ash-free dry mass, bryophytes would seemingly provide considerably less energy (Bliss 1962). Nevertheless, the caloric values for twenty herbaceous tracheophyte species had a mean of $4,601 \pm 29$ cal/g ash-free dry mass, whereas seven species of moss averaged $4,410 \pm 70$ cal/g, ranging from a high of 4,780 in *Polytrichum juniperinum* (var. *alpestre*) (Figure 16) to 4,211 in *Sphagnum girgensohnii* (Figure 17), a difference hardly worth noting.



Figure 16. *Polytrichum juniperinum*, a moss with 4780 measured calories/g ash free dry mass. Photo by Janice Glime.

Ecologists have long considered that bryophytes had little to offer in nutritional quality (Pakarinen & Vitt 1974). Furthermore, some bryophytes even prevent their consumers from obtaining the nutrition from the non-bryophyte food they have just eaten by complexing the protein in ways that make it indigestible. Liao (unpublished) has found lignin-like protein-complexing tannin compounds in all the boreal forest mosses, except for *Sphagnum* (Figure 17), in his study.

In further support of this concept of low food value, we find that in the Antarctic, where bryophytes form the bulk of the vegetation, the invertebrates (protozoa, Rotifera, Tardigrada, Nematoda, Acari, & Collembola) form a diverse fauna among the bryophyte cushions. Yet despite the paucity of non-bryophyte plant food organisms, most invertebrates apparently do not eat the bryophytes (Davis 1981).

Nevertheless, some animals seem to include liverworts (Barthlott *et al.* 2000), mosses (Smith 1977), and hornworts (Bisang 1996) in their diets. Even among the **apparent** (conspicuous) Antarctic bryophytes, which should be expected to have the highest quantity of antifeedant secondary compounds, some invertebrates are adapted to consume them. Weevils (*Ectemnorhinus similis*) eat 37% of their body weight daily of the moss *Brachythecium rutabulum* (Figure 18), consuming 1.67 mg per day per individual weevil on Marion Island (Smith 1977). Tardigrades worldwide are adapted to living among and consuming mosses. Perhaps antifeedants are not as

important to these organisms as we might suppose. How little we know of the physiological mechanisms that make these feeding relationships successful!



Figure 17. *Sphagnum girgensohnii*. Photo by Janice Glime.



Figure 18. *Brachythecium rutabulum* with capsules, a moss that provides 37% of the body weight daily to the weevil *Ectemnorhinus similis*. Photo by Andrew Spink, with permission.

We know even less about the nutritive value of sporophytes. Yet several instances are known where capsules are a preferred food, especially for snails and slugs (Davidson *et al.* 1990). Stark (1983) found that 14% of the expanded capsules of *Entodon cladorrhizans* (Figure 19) exhibited signs of grazing. Spores can have a lipid content of 30% while vegetative portions may have only 5% (Gellerman *et al.* 1972; Pakarinen & Vitt 1974). Even flowering plants have a lipid content of only 5% in the Arctic (Pakarinen & Vitt 1974).



Figure 19. *Entodon cladorrhizans*, a moss where capsules are grazed. Photo by Bob Klips, with permission.

Not all functions of food are directly for nutrition. Particularly in northern climates, mammals, and perhaps other animals, seem to benefit from the large quantities of arachidonic acid in bryophytes (Al-Hasan *et al.* 1989). With a melting point of -49.5°C , this fatty acid provides greater pliability for cell membranes at low temperatures. Prins (1981) suggested that this property may help to keep foot pads of Arctic rodents from freezing.

In any case, bryophytes appear to form an important component of the diet for a number of invertebrates and some Arctic mammals and birds. Gerson (1969) included among these the **Collembola**, **Diptera**, **Hemiptera**, **Hymenoptera**, **Orthoptera**, **Cryptostigmata**, and **Acarina**. These and many others will be discussed further in the succeeding chapters on individual groups.

Vitamins

Bryophytes may fill specific needs of animals when fresh food is scarce. For example, vitamin B₂ is not available in most plants, but *Barbella pendula* has a high content and causes no noticeable side effects when fed to puppies and chickens (Sugawa 1960). In fact, Sugawa claims that the animals thrive. Asakawa (1990) lists the species used by Sugawa, citing *Barbella pendula*, *B. enervis*, *Floribundaria nipponica* (Figure 20), *Hypnum plumaeforme* (Figure 21), *Neckeropsis nitidula* (Figure 22), and *Ptychanthus striatus* (Figure 23) as all resulting in weight gain in chickens and puppies, implying that the presence of B₂ in these bryophytes may have been instrumental in that gain.



Figure 20. *Floribundaria nipponica*, a moss source of Vitamin B₂ and potential food for puppies and chickens. Photo courtesy of Zen Iwatsuki.

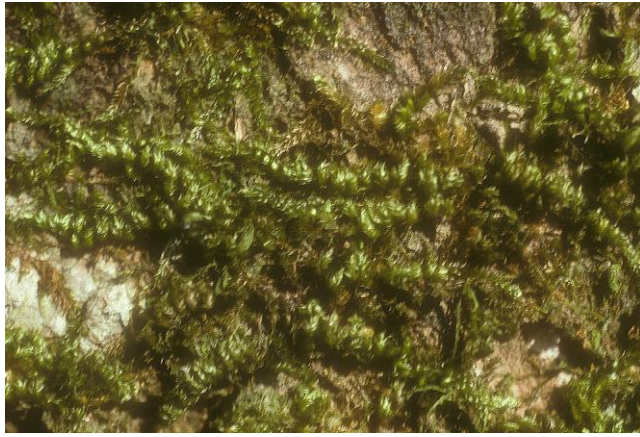


Figure 21. *Hypnum plumaeforme*, a source of Vitamine B₂ and potential food for puppies and chickens. Photo by Janice Glime.



Figure 22. *Neckeropsis nitidula*, a moss source of Vitamine B₂ and potential food for puppies and chickens. Photo by Hyun Ji Huon, through Creative Commons.



Figure 23. *Ptychanthus striatus*, a leafy liverwort source of Vitamin B₂ and potential food for puppies and chickens. Photo by Li Zhang, with permission.

Food Chain Effects

Of concern when bryophytes enter the food web is the ability of bryophytes to retain high levels of radiation. When the Chernobyl accident occurred, bryophytes for hundreds of miles had elevated radiation (Daroczy *et al.*

1988), measurable in mosses two years after the accident (Elstner *et al.* 1987, 1989). These concentrated levels are further concentrated when they enter the food web, and lemmings, which consume them rather extensively in areas affected by the high radiation (Ericson 1977), are but one step into the food web of higher carnivores.

Seasonal Differences in Habitat and Diet

We know virtually nothing about the seasonal changes in diet of invertebrates that might involve bryophytes. And it is likely that bryophytes also change their nutritive value seasonally, but again we are ignorant. We do know that both invertebrates and vertebrates change habitats to survive or take advantage of the seasons (Ovezova 1989). Crafford and Chown (1991) hypothesized that curculionid beetles (**Curculionidae**: Ectemnorhinini) would gain a nutritional advantage by eating bryophytes at low temperatures. Indeed, the cryptogams provided the main source of energy for five out of six of these species on sub-Antarctic Marion Island.

While we seem to know nothing about seasonal diet changes of moss-dwelling invertebrates, we have, however, observed changes in the eating habits of the more conspicuous rodents. Lemmings are known to switch to bryophytes as winter approaches (Prins 1982a), perhaps taking advantage of the high content of arachidonic acid in bryophytes to maintain pliability of cell membranes in their footpads as they run around on frozen ground and snow.

Habitat Differences in Nutrient Availability

Even desert mosses form habitats for a variety of invertebrates (Kaplin & Ovezova 1986). Habitat can play a major role in food value (Figure 24). The avoidance of bryophytes as food seems to be supported where bryophytes form a dominant feature of the physiognomy, *i.e.* the Antarctic, so perhaps apparency theory, the theory that more visible plants contain more antiherbivory compounds, does apply.

Davis (1981) reported that moss was eaten at a rate of less than 0.2 g m⁻² yr⁻¹ by two Antarctic moss invertebrate communities, despite tardigrades, nematodes, rotifers, protozoa, mites, and insects living among them. If such is the case, it supports the model of **apparency**, discussed regarding antiherbivory later in this volume, where the Antarctic bryophytes indeed are the most conspicuous photosynthetic food items available. One would suppose that to avoid herbivory where the slow-growing bryophyte is so conspicuous to would-be consumers, it must either have a high component of secondary compounds to inhibit feeding or lack sufficient food value to make consumption profitable.

This nutritional profitability, as in tracheophytes, differs with habitat. In the high Arctic, not only do the percentages of N and C differ (Figure 24), but the hydric mosses tend to have a higher caloric value (4.57-4.97 kcal/g) and lipid content than do the mesic and terrestrial ones (4.50-4.69 kcal/g) (Pakarinen & Vitt 1974).

Caloric contents likewise differ among terrestrial habitats, with those of alpine regions seemingly lower than those of either coniferous forests (4169 cal/gdw) or northern hardwoods (4179 cal/gdw) (Figure 25; Forman

1968). Oakwoods have the least (3773 cal/gdw) among these studies.

Despite their seemingly lower caloric content, Arctic bryophytes seem to experience greater consumption by mammals than elsewhere (Prins 1982b). Prins (1982a) reported that mosses were found in 20% of Arctic stomach analyses but were only about 1% of the total amount of food consumed. It is clear that a lower proportion of net bryophyte production is grazed than for tracheophytes, and Longton (1984) concluded that bryophytes are utilized primarily via the detritus pathway. Ugh! If they have little caloric content when alive, it would seem that only the microbes could benefit when they are dead. Of course, once eaten they can go up the food chain. It appears that certain temperate animals eat mosses in very limited amounts. Unfortunately, our knowledge of feeding relationships with bryophytes in the tropics is meager.

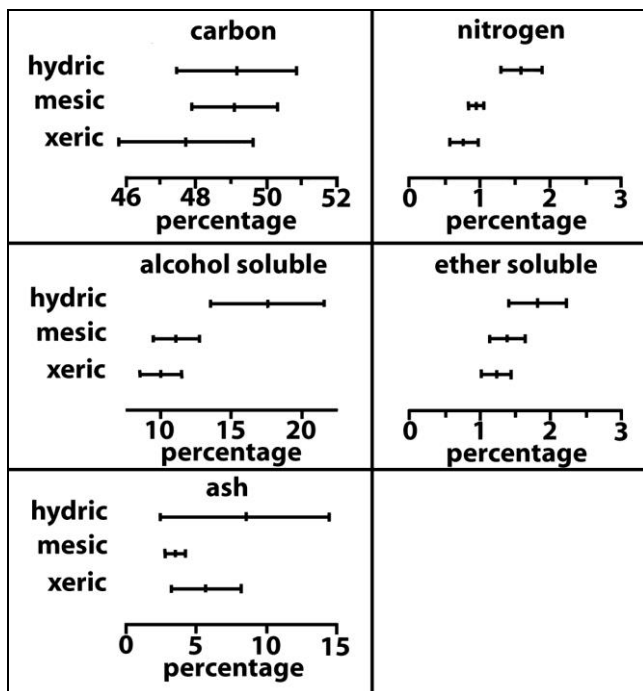


Figure 24. Mean food values (\pm 95% C.I.) of green (living) tissues based on ash-free dry mass of 35 species of Arctic bryophytes. Redrawn from Pakarinen & Vitt 1974.

Markham and Porter (1978) were among the first to take a global approach to examining the constituents of bryophytes. The differences are strongly influenced by the climate, especially temperature. In the Antarctic, bryophytes have higher C:N ratios than do tracheophytes, with larger amounts of holocellulose and crude fiber and lower energy levels, contributing to their undesirability as a food source (Walton 1985). Pakarinen and Vitt (1974) found that even within the Arctic, ratios could differ considerably, with mesic habitats having a higher carbon ratio (Figure 24). Furthermore, as the moss ages, its cellulose content increases, whereas in grasses it decreases (Walton 1985).

Long after Bliss (1962) initiated the study of Arctic and alpine plants and their nutritional value by examining the caloric and lipid content of alpine tundra plants. Sveinbjornsson and Oechel (1991) found little seasonal difference in lipid or carbohydrate content of *Polytrichum*

commune (Figure 26) or *Polytrichastrum alpinum* (Figure 27). Nevertheless, the variability they did find suggests that seasonality of nutrients bears further investigation. Sugar and starch content were negatively associated with each other, with high starch contents occurring in rhizomes and high sugar contents in shoots, suggesting that starch serves as a storage compound.

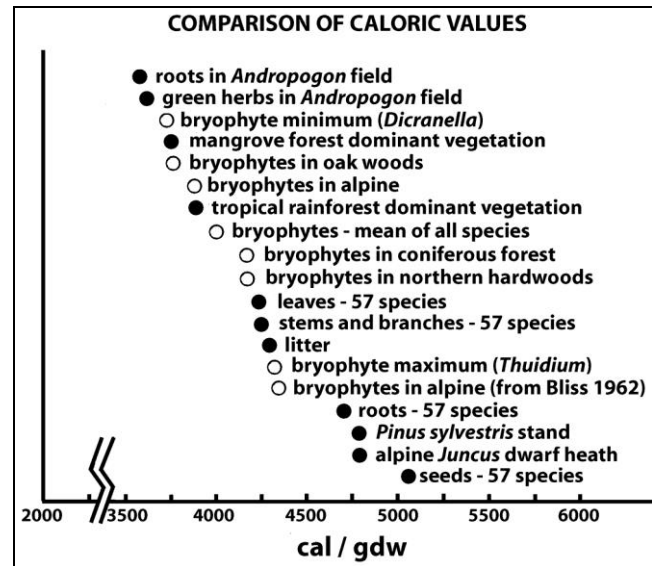


Figure 25. Caloric values (per gram dry weight) of bryophytes (open circles) compared to other plants and plant parts (solid circles). Non-bryophyte data are from Golley 1961; redrawn from Forman 1968.



Figure 26. *Polytrichum commune* with capsules. Photo by Michael Lüth, with permission.



Figure 27. *Polytrichastrum alpinum* with dew. Photo by Tom Thekathyl, with permission.

Consumption Rates

There are few quantitative studies of bryophyte consumption. Duke and Crossley (1975) calculated that a rock grasshopper, *Trimerotropis saxatilis* (Figure 28), consumed the moss *Grimmia laevigata* (Figure 29) at a rate of 391 mg m⁻² yr⁻¹ in SE USA. On Marion Island in the Antarctic, an individual beetle, *Ectemnorhinus similis*, ate a mean of 1.67 mg of *Brachythecium rutabulum* (Figure 18) per day in feeding trials, equivalent to 37% of its body weight (Smith 1977). Davidson and Longton (1987) quantitatively investigated the consumption of several moss species by slugs [*Arion rufus* (Figure 30-Figure 31) and *A. subfuscus* (Figure 32)], as discussed in the chapter on invertebrates.



Figure 28. *Trimerotropis saxatilis*, a grasshopper well camouflaged among lichens, also eats the moss *Grimmia laevigata* in southeastern USA. Photo by Carmen Champagne, through Creative Commons.



Figure 29. *Grimmia laevigata* with capsules, food for the grasshopper *Trimerotropis saxatilis*. Photo by Michael Lüth, with permission.



Figure 30. *Arion rufus*, black phase of a slug that eats mosses. Photo © Dr. Roy Anderson, with permission.



Figure 31. *Arion rufus*, a rusty-colored phase of a slug that eats mosses. Photo by James K. Lindsey, with permission.



Figure 32. *Arion subfuscus*, a slug that consumes mosses. Photo © Dr. Roy Anderson, with permission.

Moss litter is not easily broken down and depends on the moss fauna for consumption, returning to the ecosystem as feces (Frak & Ponge 2002). In alpine areas, other litter generally does not depend on fauna for its breakdown. The same secondary compounds that discourage herbivory also interfere with bacterial and fungal decomposition.

New and Exciting Directions

I am excited – a young researcher decided to examine *Funaria hygrometrica* (Figure 33) to see who lived there. This was a great challenge because there are few resources to help in the identification of terrestrial protozoa and algae, especially those that might find mosses to be particularly suitable as homes. But Alen Alex Philip ventured into the realm of the microscopic to explore this cryptic fauna.

What Philip (Philip & Thomas 2016) found was more than he could identify among the 120 kinds of organisms, including Cyanobacteria, algae, Protozoa, Rotifera, Nematoda, and Tardigrada, but he did manage to identify

16 of them to genus. In each of the 15 Indian locations of *Funaria hygrometrica* (Figure 33) collections he found six constant genera: **Cyanobacteria** – **Oscillatoria** (Figure 34); **Protozoa** – **Aspidisca** (Figure 35), **Chilodonella** (Figure 36), **Holosticha** (Figure 37), and **Rotifera** – **Habrotrocha** (Figure 38), **Philodina** (Figure 39). For a short-lived fugitive moss species of exposed, disturbed habitats, this is to me a surprising number of constant genera!



Figure 33. *Funaria hygrometrica*, home to 120 different kinds of meiofauna! Photo by Michael Lüth, with permission.



Figure 34. *Oscillatoria* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo through Creative Commons.

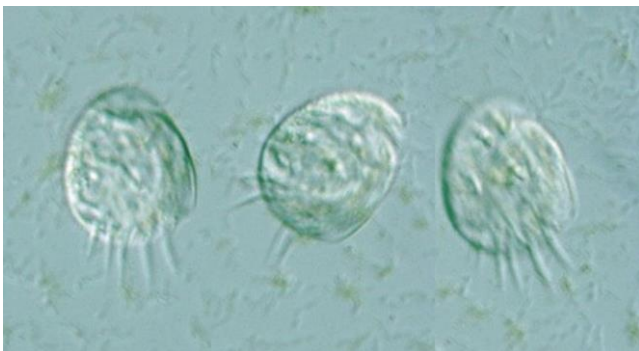


Figure 35. *Aspidisca* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo by Yuuji Tsukii, with permission.



Figure 36. *Chilodonella* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo by Wolfgang Bettinghofer, through Creative Commons.



Figure 37. *Holosticha* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo by Yuuji Tsukii, with permission.

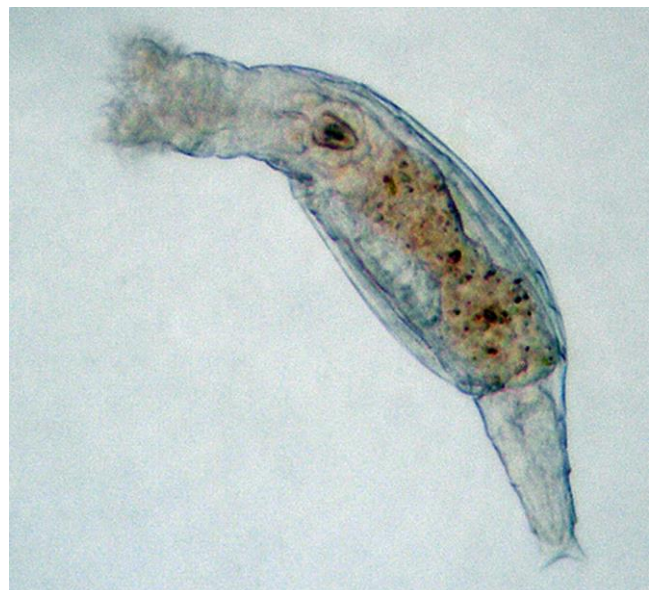


Figure 38. *Habrotrocha* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo by Rkitko, through Creative Commons.



Figure 39. *Philodina* sp., a genus that is a constant member of the meiofauna community of *Funaria hygrometrica* in India. Photo by Wim van Egmond, with permission.

This volume will be a new adventure. In the words of Donald Rumsfeldt, then US Secretary of Defense, in a statement to the press in February 2002, "There are known knowns: there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns – the ones we don't know we don't know." This volume will certainly venture toward the ones we don't know we don't know, and hopefully it will take us to places where we begin to discover those unknowns.

Summary

The small size of bryophytes affords protection from predators to small organisms. This also makes them a good nursery for many kinds of invertebrates. Their perennial nature also provides winter cover, not only for tiny invertebrates, but for larger amphibians and reptiles. Therefore, their potential for contributing to the biodiversity of the planet is enormous.

Bryophyte inhabitants may be classified as **bryobionts** (animals occurring exclusively on bryophytes), **bryophiles** (animals usually but not exclusively among bryophytes), **bryoxenes** (animals that spend part of their lives among bryophytes), and **occasionals** (animals that occur among bryophytes but do not depend on them for survival). **Meiofauna** are the tiny organisms on the bed of a river or lake, or in the moist film of a bryophyte.

One reason for the success of many invertebrate inhabitants is their ability to achieve an **ametabolic** or **cryptobiotic** state, thus becoming dormant when the bryophyte becomes dehydrated or frozen.

Bryophytes buffer both temperature and moisture, not only within the bryophyte community, but in the soil beneath them. Bryophytes differ considerably in their form, yet we know little about differences in communities among different species of bryophytes.

Scientists have assumed that bryophytes have little or no food value, but, nevertheless, isopods, lemmings, and a variety of other organisms do eat them. We know virtually nothing about seasonal changes in nutritive

value of bryophytes, nor of seasonal diets of animals that feed on them. Only a few small rodents are known to switch to bryophytes in preparation for winter. Dangers lurk in areas with radiation accumulation in the bryophytes.

Habitat may select for nutritional quality, with alpine taxa having lower caloric values, hydric mosses having higher values and also higher lipid content. Coniferous and northern hardwood forest bryophytes have higher caloric values, bryophytes of oakwoods the least. As bryophytes age, cellulose content increases, further reducing palatability and energy availability.

Acknowledgments

Thank you to Rod Morris for providing the name of the bird that made the nest in the frontispiece. Throughout this volume, Google and Wikipedia have been invaluable. Without the search capabilities of Google, I would never have discovered many of the stories in this volume. With Wikipedia, I could find general information and leads to important primary literature. Members of Bryonet have kindly sent me stories and publications. This volume is the product of worldwide cooperation of scientists of many kinds. Without their help in providing literature, comments, and images, the richness of the forthcoming stories would be lost.

Literature Cited

- Al-Hasan, R. H., El-Saadawi, W. E., Ali, A. M., and Radwan, S. S. 1989. Arachidonic and eicosapentaenoic acids in lipids of *Bryum bicolor* Dicks. Effects of controlled temperature and illumination. *Bryologist* 92: 178-182.
- Asakawa, Y. 1981. Biologically active substances obtained from bryophytes. *J. Hattori Bot. Lab.* 50: 123-142.
- Asakawa, Y. 1990. Terpenoids and aromatic compounds with pharmacological activity from bryophytes. In: Zinsmeister, H. D. and Mues, R. (eds.). *Bryophytes, Their Chemistry and Chemical Taxonomy*, Proceedings of the Phytochemical Society of Europe 29, Oxford University Press, Oxford, pp. 369-410.
- Barthlott, W., Fischer, E., Frahm, J.-P., and Seine, R. 2000. First experimental evidence for zoophagy in the hepatic *Colura*. *Plant Biol.* 2: 1-5.
- Bisang, I. 1996. Tracing a hornwort consuming beast. *Bryol. Times* 86: 1-2.
- Bliss, L. C. 1962. Caloric and lipid content in alpine tundra plants. *Ecology* 43: 753-757.
- Brantley, S. and Shepherd, U. 2002. Microarthropods on different types of cryptobiotic crusts in pinyon-juniper habitat. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, 4-9 August, 2002, Tucson, AZ.
- Chernov, Yu. I. 1985. *The living tundra*. Cambridge University Press, Cambridge, 212 pp.
- Corbet, S. A. and Lan, O. B. 1974. Moss on a roof and what lives in it. *J. Biol. Ed.* 5: 153-160.
- Crafford, J. E. and Chown, S. L. 1991. Comparative nutritional ecology of bryophyte and angiosperm feeders in a sub-

- Antarctic weevil species complex (Coleoptera: Curculionidae). *Ecol. Entomol.* 16: 323-329.
- Daroczy, S., Bolyos, A., Dezsoe, Z., Pazsit, A., Nagy, J., and Nagy, M. 1988. Could mosses be used for the subsequent mapping of the Chernobyl fallout? *Naturwissenschaften* 75(11): 569-570.
- Davidson, A. J. and Longton, R. E. 1987. Acceptability of mosses as food for a herbivore, the slug, *Arion hortensis*. *Symp. Biol. Hung.* 35: 707-719.
- Davidson, A. J., Harborne, J. B., and Longton, R. E. 1990. The acceptability of mosses as food for generalist herbivores, slugs in the Arionidae. *Bot. J. Linn. Soc.* 104: 99-113.
- Davis, R. C. 1981. Structure and function of two Antarctic terrestrial moss communities. *Ecol. Monogr.* 51: 125-143.
- Duke, K. M. and Crossley, D. A. Jr. 1975. Population energetics and ecology of the rock grasshopper, *Trimerotropis saxatilis*. *Ecology* 56: 1106-1117.
- Dunk, K. von der and Dunk, K. von der. 1979. Lebensraum Moospolster. *Mikrokosmos* 68: 125-131.
- Elstner, E. F., Fink, R., Höll, W., Lengfelder, E., and Ziegler, H. 1987. Natural and Chernobyl, USSR, caused radioactivity in mushrooms, mosses and soil samples of defined biotypes in SW Bavaria, West Germany. *Oecologia* 73: 553-558.
- Elstner, E. F., Fink, R., Höll, W., Lengfelder, E., and Ziegler, H. 1989. Radioactivity in mushrooms, mosses and soil samples of defined biotopes in southwest Bavaria, West Germany two years after Chernobyl. *Oecologia* 80: 173-177.
- Ericson, L. 1977. The influence of moles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. *Wahlenbergia* 4: 1-115.
- Fly, J., Hardin, J., and Moran, M. 2002. The effects of tree species and tree age on epiphyte community structure in a temperate deciduous forest. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, 4-9 August, 2002, Tucson, AZ.
- Forman, R. T. T. 1968. Caloric values of bryophytes. *Bryologist* 71: 344-347.
- Forman, R. T. T. 1969. Comparison of coverage, biomass, and energy as measures of standing crop of bryophytes in various ecosystems. *Bull. Torrey Bot. Club* 96: 582-591.
- Frak, E. and Ponge, J. 2002. The influence of altitude on the distribution of subterranean organs and humus components in *Vaccinium myrtillus* carpets. *J. Veg. Sci.* 13: 7-26.
- Gadea, E. 1964. La zoocenosis muscicola en los biotopos altimontanos. *Publ. Inst. Biol. Aplicada* 36: 113-120.
- Gellerman, J. L., Anderson, W. H., and Schlenk, H. 1972. Highly unsaturated lipids of *Mnium*, *Polytrichum*, *Marchantia* and *Matteuccia*. *Bryologist* 75: 550-557.
- Gerson, U. 1969. Moss-arthropod associations. *Bryologist* 72: 495-500.
- Gerson, U. 1982. Bryophytes and invertebrates. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, New York, pp. 291-332.
- Glime, J. M. 1994. Bryophytes as homes for stream insects. *Hikobia* 11: 483-497.
- Golley, F. B. 1961. Energy values of ecological materials. *Ecology* 42: 581-584.
- Ino, Y. 1992. Estimation of the net production of moss community at Langhovde, East Antarctica. *Antarct. Rec. (Tokyo)* 36: 49-59.
- International Association of Meiobenthologists. 2008. What Is Meiobenthology? Accessed on 14 April 2009 at <<http://www.meiofauna.org/phyla34.html>>.
- Janiec, K. 1996. Short distance wind transport of microfauna in maritime Antarctic (King George Island, South Shetland Islands). *Polish Pol.Res.* 17: 203-211.
- Kaplin, V. G. and Ovezova, A. Kh. 1986. Characteristics of the invertebrate complexes of the desert moss, *Tortula desertorum* Broth. *Bjull. Moskovsk. Obshch. Ispyt. Pri.*, Otd. Biol. 91(6): 49-58.
- Kennedy, A. D. 1993. Water as a limiting factor in the Antarctic terrestrial environment: A biogeographical synthesis. *Arct. Alp. Res.* 25: 308-315.
- Learner, M. A., Bowker, D. W., and Halewood, J. 1990. An assessment of bank slope as a predictor of conservation status in river corridors. *Biol. Conserv.* 54: 1-13.
- Longton, R. E. 1984. The role of bryophytes in terrestrial ecosystems. *J. Hattori Bot. Lab.* 55: 147-163.
- Markham, K. R. and Porter, L. J. 1978. Chemical constituents of the bryophytes. *Prog. Phytochem.* 5: 181-272.
- Merrifield, K. and Ingham, R. E. 1998. Nematodes and other aquatic invertebrates in *Eurhynchium oregonum* (Sull.) Jaeg., from Mary's Peak, Oregon Coast Range. *Bryologist* 101: 505-511.
- Ovezova, A. K. 1989. Peculiarities of summer population of *Tortula desertorum* invertebrates in eastern Karakum. *Akad. Nauk Turkmenskoi, Ser. Biol. Nauk* 1989(5): 19-23.
- Pakarinen, P. and Vitt, D. H. 1974. The major organic components and caloric contents of high Arctic bryophytes. *Can. J. Bot.* 52: 1151-1161.
- Peck, J. E. and Moldenke, A. 1999. Describing and estimating the abundance of microinvertebrates in commercially harvestable moss. Eugene District of the Bureau of Land Management, Eugene, Oregon.
- Philip, A. A. and Thomas, S. 2016. Meiobiota associated with *Funaria hygrometrica* Hedw. collected from Pathanamthitta district of Kerala. *SB Acad. Rev.* XIX.OA1: 78-81.
- Prins, H. H. T. 1981. Why are mosses eaten in cold environments only? *Oikos* 38: 374-380.
- Prins, H. H. T. 1982a. Why are mosses eaten in cold environments only? *Oikos* 38: 374-380.
- Prins, H. H. T. 1982b. Why the Arctic dwellers gather moss. *New Scientist* 95: 152.
- Ramazzotti, G. 1958. Note sulle biocenosi dei muschi. *Mem. Ist. Ital. Idrobiol. Dott Marco Marchi* 10: 153-206.
- Rastorfer, J. R. 1976a. Caloric values of three Alaska-Arctic mosses. *Bryologist* 79: 76-78.
- Rastorfer, J. R. 1976b. Composition and bryomass of the moss layers of two wet-tundra-meadow communities near Barrow, Alaska. *Ecol. Stud.* 29: 169-183.
- Sayre, R. M. and Brunson, L. K. 1971. Microfauna of moss habitats. *Amer. Biol. Teacher* 33: 100-102, 105.
- Smith, V. R. 1977. Notes on the feeding of *Ectemnorhynchus similis* Waterhouse (Curculionidae) adults on Marion Island. *Oecologia* 29: 269-273.
- Stark, L. R. 1983. Reproductive biology of *Entodon cladorrhizans* (Bryopsida, Entodontaceae). I. Reproductive cycle and frequency of fertilization. *Syst. Bot.* 8: 381-388.
- Sugawa, S. 1960. Nutritive value of mosses as a food for domestic animals and fowls. *Hikobia* 2: 119-124.
- Suzuki, M. 1971. An analysis of colonization in the freshwater microorganisms. I. Colonization at 17 stations along the 5 lakes of the Mt. Fuji. *Zool. Mag. Tokyo Zool. Soc.* 80(6): 191-201.
- Sveinbjörnsson, B. and Oechel, W. C. 1991. Carbohydrate and lipid levels in two *Polytrichum* moss species growing on the Alaskan tundra. *Holarct. Ecol.* 14: 272-277.

- Varga, J. 1992a. Analysis of the fauna of protected moss species. *Biol. Conserv.* 59: 171-173.
- Varga, J. 1992b. Analysis of the fauna of protected moss species. Symposium on Endangered Bryophytes in Europe – Causes and Conservation, Uppsala, Sweden.
- Walton, D. W. H. 1985. Cellulose decomposition and its relationship to nutrient cycling at South Georgia. In: Siegfried, W. R., Condry, P. R., and Laws, R. M. (eds.). *Antarctic Nutrient Cycles and Food Webs*, Springer-Verlag, Berlin, Heidelberg, pp. 192-199.

