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State of Nordic bryology today and tomorrow.
Abstracts and shorter communications from a meeting
in Trondheim December 1995

Edited by Lars Söderström and Tommy Prestø



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Moen, A. & Selnes, M. 1979. Botaniske undersøkelser på Nord-Fosen, med vegetasjonskart. - *K. norske Vidensk. Selsk. Mus. Rapp. bot. Ser.* 1979-4: 1-96.

Kapittel

Gjærevoll, O. 1980. Fjellplantene. - s. 316-347 i *Voksø, P.* (red.) *Norges fjellverden*. Forlaget Det Beste, Oslo.

Høeg, H.I. 1994. En pollenanalytisk undersøkelse av Tverrlisætri i Grimsdalen, Dovre kommune, Oppdal. - s. 193-200 i *Mikkelsen, E.* (red.) *Fangstprodukter i vikingtidens og middelalderens økonomi*. Universitetets Oldsaksamling Skr. Ny Rekke 18.

Monografi/bok

Bretten, S. 1973. Slekta *Draba* i Knutshø-Finshøområdet på Dovre. Sider ved dens systematikk og autøkologi. - *Hovedfagsoppg.* Univ. Trondheim. 113 s. Upubl.

Rønning, O.I. 1972. Vegetasjonslære. - Universitetsforlaget, Oslo. 101 s.

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Gulmøkkmose
Splachnum luteum
(foto: A. Moen)

Klåved
Myricaria germanica
(foto: E. Fremstad)

Furuskog og myr
Ledalen, Holtålen
(foto: T. Arnesen)

Grasmark med mogop
Pulsatilla vernalis
Dovrefjell
(foto: E. Fremstad)

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Abstract

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This volume contains papers based on lectures presented at a bryological meeting in Trondheim 15-16 December 1995, entitled "State of Nordic bryology today and tomorrow". The aim of the meeting was to present the spectrum of bryological research carried out in the Nordic countries at present. A wide range of current research projects in bryology is covered, dealing with taxonomy, genetics, population biology, population ecology, palaeoecology and conservation biology. Some additional contributions contain reviews of past and present bryological research in individual Nordic and Baltic countries.

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Introduction

The present volume is the result of a meeting arranged by the Nordic Researchers Network of Bryologists at the Norwegian University of Science and Technology (former University of Trondheim) 15–16 December 1995. The aim of the meeting was to present the wide range of current research in bryology carried out in the Nordic countries.

There were approximately 40 participants from nine countries, but as the lectures were open to the public, additional persons from Trondheim attended parts of the meeting.

Financial support for the meeting has primarily come from Nordisk forskerutdanningsakademi (NorFa) with additional support from the Faculty of Science and from the Department of Botany at the Norwegian University of Science and Technology. We are grateful for their support and also to the institutions who provided financial support to individual participants.

The dean of the Faculty of Science, Prof. Kolbjørn Hagen, opened the meeting. Several of the participants served as chairpersons during the meeting.

The arrangement committee consisted of Lars Söderström, Kristian Hassel and Tommy Prestø, all from the Norwegian University of Science and Technology with help from many of the participants from Trondheim.

We wish to thank all the participants and those who otherwise contributed to the meeting and the publication of this volume.

Lars Söderström, Tommy Prestø and Kristian Hassel.

Trondheim, June 1996

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Programme

Friday 15 December 1995

Meeting place: Auditorium II, Main Building, Rosenberg

9.00 – 9.30
9.30 – 10.00

Registration

Opening

Prof. Kolbjørn Hagen, Dean of the Faculty of Science.

Lars Söderström, Chairman of the Researchers Network of Nordic Bryologists.

Session 1. Chairperson Prof. K. I. Flatberg

10.30 – 11.10
11.10 – 11.30
11.30 – 11.50

Dale H. Vitt, Edmonton. Bryophyte diversity. Patterns of rarity

Irene Bisang, Stockholm. Bryophyte - vascular plant interactions in a sea shore meadow

Lillian Hansen, Trondheim. Genetics and morphology of *Sphagnum cuspidatum* and *S. viride*

Session 2. Chairperson Prof. D. H. Vitt

13.00 – 13.20
13.20 – 13.40
13.40 – 14.00
14.00 – 14.20
14.20 – 14.40
14.40 – 15.00

Sinikka Piippo, Helsinki. The past, present and some future aspects of Finnish Bryology

Nele Ingerpuu, Tartu. A short survey of bryological research in Estonia in the past and today

Austra Āboliņa, Riga. Bryological investigations in Latvia

Ilona Jukonienė, Vilnius. Review of bryological investigations in Lithuania

Tommy Prestø, Trondheim. Monitoring of bryophytes in boreal rain forests. Effects of forestry

Lars Söderström, Trondheim. Conservation of bryophytes in Europe. The European Red Data Book

Session 3. Chairperson Prof. T. Koponen

15.30 – 15.50
15.50 – 16.10
16.10 – 16.30

Nils Cronberg, Copenhagen. Genetic diversity of bryophytes. Examples from *Sphagnum* and *Hylocomium*

Einar Heegaard, Bergen. Ecology of *Andreaea* in western Norway

Hanna Jalkanen, Helsinki. Population biology of *Plagiomnium undulatum* in Finland

Session 4. Chairperson Dr. L. Hedenäs

16.40 – 17.00
17.00 – 17.20
17.20 – 17.40

Kristian Hassel, Trondheim. Diaspore bank and germination ability of an expanding species

Linda Dalen, Trondheim. Survival ability of bryophyte diaspores in water

Hans Martin Hanslin, Trondheim. Interactions in moss carpets. The influence of density and environmental factors on plant growth and competition

Saturday 16 December 1995

Meeting place: Auditorium III, House G (Red Building), Rosenberg

Session 5. Chairperson Dr. N. Ingerpuu

9.00 – 9.20
9.20 – 9.40
9.40 – 10.00

Virpi Aalto, Helsinki. The effects of detergents and ammonium nitrate on the growth and morphology of aquatic mosses

Lars Hedenäs, Stockholm. Harsh bryophyte environments – 100 000 years ago

Marika Kose, Tartu. Some ideas about peat stratigraphy or what possibilities the peat bulk density method gives us

Session 6. Chairperson Dr. L. Söderström

10.30 – 10.50
10.50 – 11.10
11.10 – 11.30

Bengt Gunnar Jonsson, Umeå. Riparian communities in the Cascade Mountains, Northwest USA

Henrik Weibull, Uppsala. Factors affecting bryophyte distribution patterns on siliceous boulders in deciduous forests

Kjell Ivar Flatberg, Trondheim. Norwegian bryology at present

Session 7. Chairperson Dr. K. Damsholt

14.00 – 14.20
14.20 – 14.40
14.40 – 15.00
15.30 – 16.00

Timo Koponen, Helsinki. Characters useful in the taxonomy of *Philonotis*

Viiivi Virtanen, Helsinki. Phylogeny of Bartramiaceae. The research plan

Hans Blom, Trondheim. *Schistidium* in northern Europe. An overview

Closing session

Nordic Researchers Network of Bryologists 1992–95

Lars Söderström

Department of Botany, Faculty of Chemistry and Biology, Norwegian University of Science and Technology, Trondheim, N-7055 Dragvoll, Norway

In 1992, prof. Timo Koponen, Helsinki, took the initiative to establish a network of bryologists in the Nordic Countries. This initiative was positively met by many professional bryologists and an application for establishing a network was submitted to Nordisk forskerutdanningsakademi (NorFa). The application was approved and the **Nordic Researchers Network of Bryologists** was established with the first meeting in Kilpisjärvi 3 August 1992. The original members were Timo Koponen, Helsinki (coordinator and chairman), Kell Damsholt, Copenhagen, Reino Fagerstén, Kuopio, Kjell Ivar Flatberg, Trondheim, Matti Haapasaari, Kuopio, Lars Hedenäs, Stockholm, Pekka Isoviita, Helsinki, Jette Lewinsky-Haapasaari, Kuopio, Sinikka Piippo, Helsinki, Lars Söderström, Trondheim, and Tauno Ulvinen, Oulu. The meetings have also been attended by several other bryologists on an irregular basis.

After serving as coordinator for two years, Timo Koponen resigned in late 1993 and Lars Söderström, Trondheim took over as coordinator. In 1994 the network was expanded with Nils Cronberg, Lund, Arve Elvebakk, Tromsø, Bengt Gunnar Jonsson, Umeå, Krister Karttunen, Helsinki, Sanna Laaka, Helsinki, Viivi Virtanen, Helsinki, Risto Virtanen, Oulu, Esben Warncke, Aarhus, and Rune Økland, Oslo. In 1995 the network was expanded again with participants from the Baltic states. Originally, only Estonian bryologists were considered (i.e. Nele Ingerpuu, Tartu, Leiti Kannukene, Tallinn, Mare Leis, Tartu, Kai Vellak, Tartu) but very soon also Austra Āboliņa, Riga, and Ilona Jukonienė, Vilnius, were included.

During the first year of the project, several possible courses were outlined and one

course, **Nordic peatland bryophytes: their ecology and taxonomy** was held in Lammi 8–13 August 1993 followed by an excursion through central Sweden and Norway 14–17 August 1993. The course was limited to sixteen students but many more applied. During the following years, many courses were planned but we failed to obtain financial support for them. However, the idea of common Nordic courses had been accepted and locally arranged courses were announced in all Nordic countries using the contact net of the network members. It is our hope that this will be a permanent result of the network.

Several research projects have been discussed during the meetings and some of them may be performed in cooperation by network members. The network has administered a project to map the distribution of bryophytes in the Nordic countries. This project was initiated at one of the first meetings and data has been collected ever since. Two workshops have been held to agree on common policy for the different countries, and on the taxa to be mapped and the nomenclature used. The first workshop was held in Stockholm 6 March, 1994, and the second in Tartu, Estonia, 28 October, 1995. The mapping will result in three volumes published at one year intervals. The first volume (hepatics) was published in 1995, the second (Musci A-I) will be published before summer 1996 and the last volume in 1997. Originally we mapped only the Nordic countries, but with the inclusion of the Baltic members in the network, Estonia, Latvia and Lithuania are included in the two last volumes.

The interest in conservation of bryophytes among Nordic bryologists is pronounced and

the Nordic countries are among the leading in monitoring and protecting rare bryophytes. A workshop was arranged in Uppsala 9 April, 1994 to increase co-operation between the Nordic countries, and to compare the criteria and methods used.

Several students of bryology have visited bryologists at other Nordic universities. This mobility of students has been strongly supported by the network members and all have been willing to accept students from other universities for longer or shorter periods.

This bryological meeting is held as the final arrangement for this period of funding of the **Researchers Network of Nordic Bryologists**. It is very positive that so many bryologists and especially so many students from the Nordic and Baltic countries attend the meeting.

Network Meetings

- 3-6.8.1992 Kilpisjärvi, Finland
- 8-9.12.1992 Trondheim, Norway
- 25-27.3.1993 Helsinki, Finland
- 10-11.8.1993 Lammi, Finland
- 5.3.1994 Stockholm, Sweden
- 11-13.5.1994 Copenhagen, Denmark
- 12-14.11.1994 Kuopio, Finland
- 8.4.1995 Uppsala, Sweden
- 27-29.10.1995 Tartu, Estonia
- 15-16.12.1995 Trondheim, Norway

Workshops and symposia

- 6.3.1994 Workshop on "Distribution of bryophytes in Norden" in Stockholm
- 9.4.1995 Workshop on "Endangered bryophytes in the Nordic countries" in Uppsala
- 28.10.1995 Workshop on "Distribution of bryophytes in north-western Europe" in Tartu
- 15-16.12.1995 Symposium on "State of Nordic bryology today and tomorrow" in Trondheim

The past, present and some future aspects of Finnish bryology

Sinikka Piippo

Botanical Museum, University of Helsinki, P.O. Box 47, FIN-00014 Helsinki University, Finland

The Botanical Museum was established in 1828, the year the University of Helsinki was re-founded after its destruction in the Turku fire. The first bryophyte checklist was actually a list of the herbarium specimens published by William Nylander in 1859 together with Anders Thiodolf Saelan. The number of specimens in the bryophyte collections remained low for decades. The change was created by S.O. Lindberg.

The status of bryological research in Finland as well as the study of Finnish bryoflora have been revised by Collander (1965), Isoviita & Koponen (1967) and Koponen (1976, 1982,

1985a, 1987). Figure 1 shows the main Finnish bryologists from 1830 until today.

Sextus Otto Lindberg (1835–89)

Sextus Otto Lindberg, originally a Swedish medical doctor, came to the University of Helsinki as the professor of botany in 1865 as the only applicant for the chair (see Buch 1935, Elfving 1935, Koponen 1989a). He held the position until his death.

S.O. Lindberg described ca. 50 new bryophyte species from the fairly well-known Fennoscandia. His studies on the taxonomy and nomenclature of European hepatics creat-

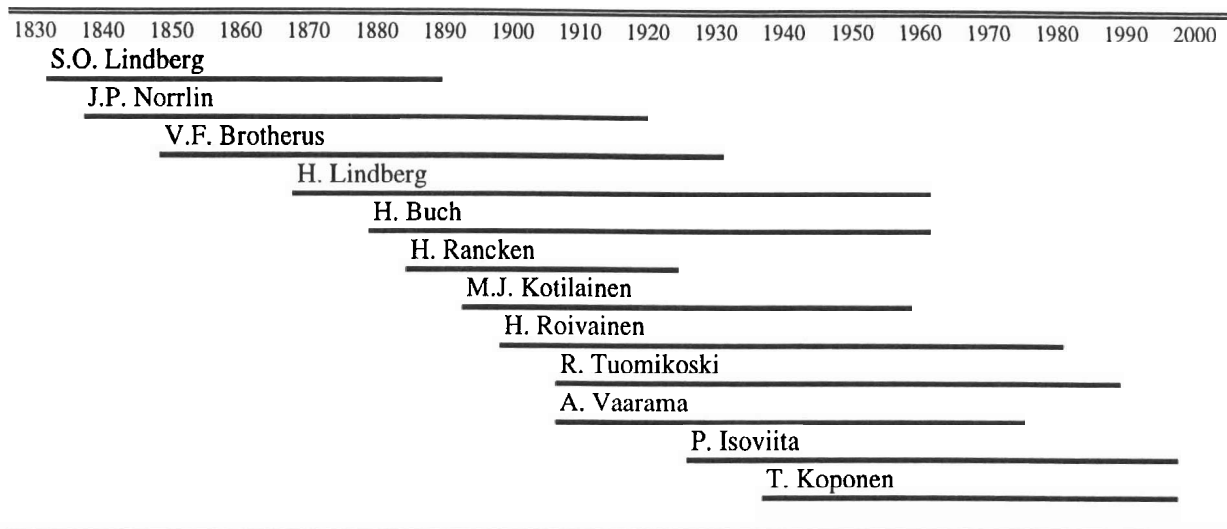


Figure 1. The main Finnish bryologists from 1830 until today.

ed the foundation for the classification of hepatics. He gathered a wide herbarium, in total 47 758 specimens, representing 5 046 moss and hepatic species. About half of these, 23 763 specimens of 921 species, are from Fennoscandia. Since Lindberg was very interested in the nomenclature his collections contain numerous types.

Since his schooldays S.O. Lindberg had been in correspondence with numerous foreign bryologists exchanging specimens and reprints. He received valuable specimens, e.g. numerous duplicates of type specimens from South America, Java, Australia, New Zealand, and Japan. Especially remarkable are his studies on the bryophytes of Siberia, Russian Far East and Japan. Perhaps the most valuable set of specimens received by him was the duplicate collection of Professor Johann Jakob Dillenius of Oxford University. Lindberg himself carried out only two expeditions outside Fennoscandia, to Great Britain and Ireland.

Since S.O. Lindberg was extremely interested in bryophyte nomenclature he used a lot of time in finding out a legal name for each species and genus. Therefore he was interested in obtaining all the old bryophyte

literature and herbaria. He either bought old literature himself or asked the Department of Botany to buy it for its library. Because of him many rare books on bryophytes dating back to the 1600's can now be traced to Helsinki.

Due to his collections and bibliophily and by transferring his knowledge to at least one student, Viktor Ferdinand Brotherus, he created a sound basis for Finnish bryology. He wrote ca. 250 scientific papers. Lindberg stressed the significance of identifying plants in the field. The tradition of field recognition still prevails in Finland.

The scientific output of Harald Lindberg (1871–1963), Sextus Otto Lindberg's son, was very wide and he has a large number of publications (310), of which 28 are exclusively on bryophytes (Marklund 1963). In the beginning of his career his father's influence was significant and Harald Lindberg also studied bryophytes, but after S.O. Lindberg's death he changed mainly to other plant groups such as *Taraxacum* and *Hieracium*. He published on bog bryophytes and *Sphagna*.

In 1910 the first chair of head curator was

established in the Botanical Museum and the first curator was Harald Lindberg. He conducted many excursions; besides Fennoscandia to Tunis, Sicily, Spain, Morocco, Cyprus, Balkan and Great Britain, also collecting bryophytes.

Viktor Ferdinand Brotherus (1849–1929)

After his graduation as Master of Science in 1870, Viktor Ferdinand Brotherus started studies in medicine, but had to cancel them shortly after suffering blood-poisoning (see Häyrén 1929, 1931, Kotilainen 1929a, 1949, 1950, Koponen 1989a). In 1871–78 he acted as a teacher in different schools until 1878 when he moved to the Swedish girls school of Helsinki in the position of younger colleague, in which position he acted until his retirement in 1917, teaching natural history and mathematics. Brotherus obtained a PhD degree in 1884. He was honoured with an honorary professorship as late as 1921. He never held an academic position. In old age, he was the most respected scientist of his field, *Altmeister der Bryologie*.

Brotherus continued S.O. Lindberg's way of studying bryophytes in the field. At first he collected in South and Central Finland (e.g. Brotherus 1872). His first longer expedition was to the Kola Peninsula in 1872. He also made two other expeditions to Kola, namely in 1885 and 1887. As a result of these three Kola expeditions he published a revision on the bryophyte flora of Kola Peninsula, *Musci Lapponiae Kolaensis*.

Brotherus also conducted two expeditions to Caucasus, in 1877 and 1881. During these trips he collected a large material from an area, whose bryophyte flora was almost unknown. His doctoral thesis is also based on this material (Brotherus 1884). The thesis was of international standing; it was in French and dealt with the bryogeography of the Caucasus area. Later he published an enumeration of Caucasus bryophytes (Brotherus 1892). In 1896 he conducted a five month excursion to Central Asia (Järvinen &

Koponen 1975).

The papers of Brotherus on Caucasus bryophytes confirmed his worldwide reputation and he started to receive increasing numbers of determination requests. More and more specimens came to Helsinki, but Brotherus also bought specimens from private explorers and collectors. His numbers of publications from different areas increased accordingly.

In 1899 Adolf Engler, the director of the botanical garden and botanical museum of Berlin, completed the vascular plant part of the compilation work "Die natürlichen Pflanzenfamilien". Brotherus' task was to compile the moss part, which meant the arrangement of 14 000 moss species in the most natural system as possible. Completing the task took ten years (1901–09) and it comprises 970 pages and 696 figures. Brotherus was the only person in the world, who could complete this work requiring as much knowledge.

Brotherus was not especially interested in studying Europe, because the area was already then relatively well known. He compiled, however, "Die Laubmoose Fennoskandias" (1923), a handbook with 635 pages. It is still the most important determination guide for Finland.

Brotherus also wrote the bryophyte flora of Russian Far East, *Flora Aziatskoy Rossii*, which, however, remained uncompleted. Brotherus published a lot on South East Asia and he became a remarkable determinator for the Japanese bryologists. In total he published 198 species new to science in his publications dealing with Japan (Koponen 1979, 1988). He also wrote *Symbolae Sinicae* (1929), which is still a basic work for Chinese bryology. In total he published at least 176 papers.

In 1924 the herbarium of Brotherus was bought by the University of Helsinki. The

herbarium consists of two separate herbaria: European and extra-European. The European one had 27 800 specimens of 1 200 species, the extra-European had 83 300 specimens of ca. 14 600 species – and every known moss genus. At that time it was the largest private herbarium. The collection includes ca. 1 800 types of species described by Brotherus and a large amount of duplicates of types described by other scientists. After selling his herbarium Brotherus continued his research for five years and added 10 000 specimens into the herbarium. When he died the collections had 120 000 specimens representing 15 500 species.

Brotherus' European collections formed the basis of the General Herbarium of the Bryophyte Museum, and the rest, ca. 90 000 specimens, are kept as a separate "Brotherus herbarium". Its specimens cover almost the whole world. Siberia, Japan, China, the Philippines, Himalayas, Africa, Brazil, New Zealand, and the Hawaiian Islands are especially well represented areas. The collections in Helsinki can be considered as the most important bryophyte collections in the world for international bryological research because of their representativeness.

Brotherus himself had no students, but he liked to help young botanists by determining their specimens. Those were e.g. Mauno Kotilainen, Heikki Roivainen and Hans Buch.

Hans Robert Buch (1883–1964)

Hans Buch was appointed as the first head curator of the cryptogamic division of the Botanical Museum in 1949 and retired in 1953 (Tuomikoski 1953, Roivainen 1965).

Buch was ahead of his time. The basis of his ability to connect many scientific fields was created by his many teachers. He was a student of the plant physiologist Fredrik Elfving and was also influenced by Brotherus and Harald Lindberg. In addition, Buch had frequent contacts with foreign scientists.

The scientific output of Hans Buch focused almost entirely on bryophytes and especially hepatics. Early he widened his research into morphology and physiology. He brought empirical techniques into bryophyte taxonomy. Buch collected rich material for research himself and observed the relationships between habitat and species. His doctoral dissertation in 1911 dealt with asexual dispersal means of hepatics. He also published on organology connected with light and water economy and mineral uptake of bryophytes (1919, 1920, 1921, 1945, 1947). At an early stage he studied the effects of pollution on bryophytes (Buch 1945, 1947). Buch published 85 papers. Most of his publications have been unusual and innovative.

In 1936 he published the book *Suomen maksasammalet* (Finnish hepatic flora), which until now is the only hepatic guide published in the Finnish language. It has also been used abroad because of its good illustrations. Buch also published comprehensive work on the genus *Scapania* (1922, 1928).

Heikki Roivainen (1900–83)

Before he became a Master of Science in 1935 and especially afterwards, Roivainen took part in many practical jobs dealing with plant diseases, pasture and grasses. He got his PhD as late as 1954 (Kotilainen 1960, Koponen 1985b). From 1953 he was first an amanuensis at the Botanical Museum of the University of Helsinki and in 1956 he was appointed as the head curator after Hans Buch.

Roivainen took part as a botanist in the Finnish scientific expedition to Tierra del Fuego, Patagonia and Central Chile in 1928–29. He collected e.g. wetland material from Tierra del Fuego, published as a doctoral thesis in 1954. Even after retirement he travelled and studied these same areas (1969–70).

Roivainen was an exceptionally good vegetation botanist, who knew both vascular

plants, bryophytes and fungi. His interest in bryophytes was possibly created, when he proof read the manuscript of "Die Laubmoose Fennoscandias" by Brotherus. Roivainen published both on Finnish and Tierra del Fuego bryophytes. Other bryologists such as E.B. Bartram and J.J. Engel also published on his collections from South America. He published ca. 150 papers, of which 14 dealt with bryophytes.

Shortly before his death Roivainen was elected an honorary member of Sociedad Latinoamericana de Briologia.

Mauno Johannes Kotilainen (1895–1961)

Mauno Kotilainen acted as a botanist for the Finnish peatland agriculture society during 1925–56 (Kalela 1962, Kivinen 1965, Vasari 1965). Additionally he acted as associate professor of botany in the Faculty of agriculture and forestry and as an extraordinary professor of plant geography in the Faculty of mathematics and natural history. He also taught peatland science and later botany in the Technical Highschool.

In his youth Kotilainen became interested in bryophytes as an unofficial student of Brotherus. His doctoral dissertation in 1924 dealt with northeast Enontekiö bryophytes and vegetation and Brotherus is known to have helped him with identification of the bryophytes. Another remarkable publication was on the boreal element of the bryoflora in Ladoga Karelia (1929b). He wrote 144 papers, of which 13 are purely bryological.

Kotilainen was a good lecturer both in the lecture theatre and in the field. In 1934–35 he held a comprehensive two-year bryophyte course in the Botanical Department of the University of Helsinki, which provided an enthusiastic start for both Risto Tuomikoski and Antero Vaarama.

Antero Vaarama (1912–75)

Antero Vaarama taught natural sciences and plant protection in Lepaa Garden School

from 1939 to 1945, where his interest in cytology, genetics and plant breeding was started (Anderson 1976, Inoue 1976, Rousi 1976a, b, Koponen 1977). In Lepaa, Vaarama conducted cytological studies on the difficult genera *Rubus* and *Ribes*, trying to develop better edible strains. Vaarama became a biotaxonomist instead of a herbarium taxonomist, because Lepaa and Piikkiö did not have a herbarium or the literature needed. At this time Vaarama started his cytological studies on bryophytes.

In 1955 Vaarama was appointed as professor of botany in Turku, a chair he held until his retirement in 1975. During his years in Turku he concentrated on developing the university and did not have much time for research. Vaarama died one month after his retirement. As late as July 1975 he took part in the Leningrad International Botanical Congress with biosystematics as his topic. He spent some years in the United States and Canada as a visiting researcher.

Vaarama was a pioneer in chromosome studies of bryophytes. He was the first Finnish bryologist, who can be called as a biosystematist. He published 114 papers, of which 28 dealt with bryophytes. Most of his studies were about cytogenetics and hybridizations.

Vaarama studied both chromosome numbers (1950) and special chromosome shapes, e.g. m-chromosomes (1969). Vaarama's study on the bicentric (bikinetochoric) chromosome of *Pleurozium schreberi* is classical (1954). Vaarama was also especially interested in centromere evolution. The progress of chromosome studies of bryophytes in 1960-70's owes a great deal to the studies of Vaarama.

Risto Tuomikoski (1911–89)

Tuomikoski was an exceptionally versatile scientist (Koponen 1989b). His first scientific research (1930) was on insects, dipteras of tree trunks. Even in botany, Tuomikoski was many-sided. His first papers dealt with

vascular plants (1933a, b), but soon he evolved into a talented bryologist (1934, 1935a).

Tuomikoski took part in the two-year bryophyte course of Mauno Kotilainen. Finally the course progressed as far as the family Mniaceae, and Kotilainen was presenting *Mnium affine*, a species considered as difficult. He explained that the problem with the species would probably be resolved if two species were accepted instead of one. At this point, however, Tuomikoski commented that there would be no problem, if three species were accepted. Kotilainen recommended Tuomikoski to prove his statement, which he did in his Master of Science thesis (1935b, 1936).

The study method of Tuomikoski was that of S.O. Lindberg: bryophytes had to be studied and known in the field to solve the variation caused by habitat. An example of this kind of study was his research on the recognition of sphagna without a microscope (1946).

Tuomikoski also used mixed stands and mixed specimens as a study method. The idea is based on the assumption that if related species can be distinguished in a mixed stand, their seen characters are due to genetics and it is justified to approve them at specific level. This method was later both criticized and appreciated (Isoviita 1985, Wyatt et al. 1985).

Tuomikoski attended two expeditions to Canada. The first one was conducted in 1947 to Hudson Bay and James Bay. The other one was to Newfoundland. Buch & Tuomikoski (1955) published the hepatics, and the unfinished moss manuscript was published later (Tuomikoski et al. 1973). The Hudson Bay and James Bay manuscripts (Tuomikoski 1947, 1955) are still unfinished.

Tuomikoski shifted early on to other fields than bryology. He had so many interests that no time was left for bryophytes. Tuomikoski

has published a lot on fungi, insects and later in his life on the grammar of the Finnish language. Bryologists consider him as a bryologist, mycologists as a mycologist, entomologists as an entomologist, and linguistics as a linguist.

In 1961 Tuomikoski was appointed as extraordinary professor of biotaxonomy at the University of Helsinki. In this way he was granted freedom to select his own research interest and field of teaching. At this point he also became interested in phylogenetic systematics, a field nowadays known as cladistics. In the 1960's Tuomikoski left his "testament as a bryologist" by holding the bryophyte club in the Botanical Museum. Reino Fagerstén, Matti Haapasaari, Harri Harmaja, Timo Koponen, Esa Kotanen, Ilkka Kytövuori, Juha Suominen, and Orvo Vitikainen participated. Every year since 1946, Tuomikoski arranged the traditional bryophyte course in the Department of Botany. He retired in 1974.

The present and future

One starting point for our research is the knowledge of our own flora (cf. Isoviita & Koponen 1967, Koponen 1982). To improve this we have started to compile the Finnish bryophyte flora. Until now in Finland we have only the hepatic flora by Hans Buch from 1936. Finland is included in the works of Brotherus (1923), Jensen (1939), and Nyholm (1954-69), although they are not in Finnish. The first part of the Finnish bryophyte flora, Guide to Finnish aquatic bryophytes (in Finnish), was published in 1995.

The research conducted in Helsinki is mainly focused outside Finland, because the Bryophyte Museum has especially good collections from many developing countries (Koponen 1985a, 1987). Those countries usually have no bryologists of their own, usually no herbaria, and many areas are still poorly known. Our bryophyte herbarium makes it possible to study any area of the world.

The Bryophyte Museum has a continuous and steady connection with the Department of Ecology and Systematics (former Department of Botany) and many research projects are shared.

Timo Koponen, Professor of Department of Ecology and Systematics, and the former head curator of the Bryophyte Museum (before Prof. Pekka Isoviita), has maintained the old traditions and handed these down to many of his students. He has stressed the global and international nature of our research and conducted several expeditions, e.g. to Japan, China, Tanzania, and New Guinea. He has stressed the importance of field recognition and held moss courses, by which means knowledge and experience are transferred to the next generation. Additionally he took cladistics into practice early in bryology.

Pekka Isoviita has continued the S.O. Lindberg tradition by concentrating on nomenclature. Dr. Ahti Mäkinen has carried out the Hans Buch tradition of monitoring pollution by using moss balls.

In 1994 the European Union recognized the high level of Finnish bryology and lichenology and gave the Bryophyte Museum and Department of Ecology and Systematics "Large Scale Facility" Status "Advanced instruction in Bryology and Lichenology" for 1994–98. The status guarantees the possibility for scientists from other European countries to conduct research in Helsinki. The Academy of Finland is currently funding the project "Biodiversity of SE Asiatic bryophytes".

The projects carried out in Helsinki include the bryophyte flora of Western Melanesia, Finnish bryophyte flora, nomenclature of bryophytes, and bryogeography of Australasia. The following projects are also actively participated in: Bryoflora of China, Flora Neotropica, Australian bryophyte flora, bryophyte flora of tropical Africa, and Californian hepatic flora.

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A short survey of bryological research in Estonia in the past and today

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The first data about the bryophytes on the territory of Estonia can be found in the book of J.B. Fischer from the year 1791. After that several bryofloristic works about the territory named at that time Ehst-, Liv- and Kurland appeared. They contained much information about the present-day Estonia. The work of K.G. Girgensohn (1860) contained a list of 228 species collected from the territory of Estonia. One of the most famous bryologists from the previous century was E. Russow who worked as a professor of botany at Tartu University. His works in the field of sphagnology are world-famous. The bryofloristic work of the Latvian scientist N. Malta about the East Baltic region was also of great importance.

The ecological and bryosociological studies were started by T. Lippmaa (1933, 1935). He worked out a method of describing vegetation by one-layer communities (synusiae). Bryophyte communities played an important part in his works. The research of moss synusiae has been continued by J. Paal (1994) with modern methods. The first key-books were written by L. Laasimer and co-workers in the 1950's. Since the 1960's several papers about topics such as pH-values of moss substrata (Kannukene 1929), growth-forms and their relations to ecological factors (Vilde 1990), peat-moss growth increment (Ilomets 1982) and fertilization effects on the moss cover (Kalda & Kannukene 1966) have appeared. The floristic work was mainly led by L. Kannukene who has carefully studied several areas in Estonia and the Arctic.

The monitoring of bryophytes was started in 1981 by L. Kannukene. In 1994, the list of Estonian bryophytes as a collective work of

six authors appeared (Ingerpuu et al. 1994). The list contains 510 species, but since then 10 more species have been found in Estonia. Since the year 1993, courses of bryology have been held at Tartu University and students have become more involved in bryological research.

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Bryological investigations in Latvia

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The history of bryophyte investigations in Latvia begins in the 19th century. In the beginning floristic investigations dominated (Girgensohn 1860, Bruttan 1891, 1892, Mikutowicz 1908-13, Malta & Strautmanis 1926, Malta 1930, Bušs & Āboliņa 1968, Āboliņa 1968, 1985a, 1985b, 1994, Laivins et al. 1984). The floristic works also continued in the postwar period. At present 488 bryophyte species (113 species of Hepaticopsida and 375 species of Bryopsida) have been registered.

Ecological studies as well as floristic works are performed at the Latvian Forestry Research Institute "Silava". Moss ecology has been studied mostly in forests and mires. The dynamics of moss cover are investigated under the influence of different activities of forestry (amelioration, clear-cutting, thinning, fertilisation, usage of herbicides, etc.). After the study of the succession of amelioration in long-term sample plots (from 1963) it has been concluded that *Polytrichum strictum* is not a species but an ecological modification of *P. juniperinum* from habitats with high groundwater level. This was also shown with transplantation into environments of different ground water tables.

At present the compilation of a key-book of Latvian bryophytes is being prepared.

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Review of bryological investigations in Lithuania

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The first data on the Lithuanian bryophytes are to be found in the works of botanists of the 18th and 19th centuries (Gilibert 1781, B.S. Jundził 1791, 1811, J. Jundził 1822a, b, c, 1830, Pabrėža 1900). The first special bryological issue was "Zapiski bryologiczne" by Szafnagl (1908) in which 209 moss species occurring in the eastern part of Lithuania and the north-western part of present Belarus were described. More extensive bryological investigations were initiated by Minkevičius (1931, 1935, 1955). Pipinys (1964) studied bryophytes of fens and meadows in the eastern part of Lithuania, with respect to specific composition and distribution according to some ecological factors (pH, humidity, etc.). The liverwort flora have been investigated by Kuzas (1977). Data on bryophyte distribution and ecology have also been accumulated during other botanical and phytosociological investigations (e.g. Reimers & Hueck 1929, Brundza & Povilaitis 1937, Mowszowicz 1957, Bakšytė 1968, and others).

About 400 species of bryophytes are now known in Lithuania. More detailed investigations of specific habitats (stones, tree trunks, open habitats, etc.) are required. Revision of some bryophyte families such as Bryaceae, Grimmiaceae, Pottiaceae is necessary.

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Genetic diversity of bryophytes. Examples from *Sphagnum* and *Hylocomium*

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Bryophytes have maximum species diversity in oceanic areas of the temperate zone, in contrast to most other plants and animals which have maximum diversity in the tropics or subtropics. Is this paralleled by the distribution of infraspecific variation? The investigated species *Sphagnum rubellum*, *S. capillifolium* and *Hylocomium splendens* all belong to a life-form category of bryophytes known as perennial stayers, which is characterised by long persistence, predominant asexual reproduction by clonal growth and more or less rare sexual reproduction. The screening of electrophoretic variation at 12-15 enzyme loci from samples consisting of c. 40 individuals from each of 20, 16 and 21 populations of these species respectively enables some generalisations about genetic diversity. Populations of *Sphagnum* are an order of magnitude less variable than popu-

lations of *H. splendens*, which are as variable as the most variable vascular plant populations. In all species as much as 90-95% of the variation is partitioned within populations, an indication of strong gene flow past or present. The remaining 5-10% partitioned among populations is informative enough to reveal a clear geographic pattern in both *S. rubellum* and *H. splendens*. This pattern is suggested to be a consequence of processes related to the survival in different refugia during the latest glaciation and subsequent post-glacial re-colonisation. Results from the screening of *H. splendens* from Siberia show that populations from an arctic climate may not necessarily be less variable, although sexual reproduction is shown to be rare and correlated with mean July temperature.

Genetic and morphological differentiation between and within populations of *Sphagnum cuspidatum* and *Sphagnum viride*

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The peat mosses *Sphagnum cuspidatum* and *S. viride* are two closely related taxa within sect. Cuspidata. *S. viride* was described as a new species by Flatberg (1988). The two taxa have a slightly different distribution in Norway. *S. viride* is found in the south of Norway at the coast, while *S. cuspidatum* is more widely distributed along the fjords and further up in the north of Norway. *S. cuspidatum* grows in carpets in both bogs and poor fens, while *S. viride* prefers poor fens. They may grow in mixed populations and they then grow in poor fens. Apart from Norway, *S. viride* is also found in Great Britain and on the eastern coast of North America.

In the field the two taxa are differentiated according to colour and sometimes the shape of the branches. *S. cuspidatum* is red at the bases of the fascicles, both at the stem and in the capitulum. There is no red colour in the capitulum in *S. viride*, but there may be some red colouration further down the plant as with *S. cuspidatum*. *S. viride* is also more bright green than *S. cuspidatum*. The branches of *S. viride* are less falcate-cuspidate in the distal part than *S. cuspidatum*. There are also quantitative differences of the cells of the two species.

The aim of this project is to use isozymes as supplemental markers to see whether the present species concept of *S. cuspidatum* and *S. viride* should be maintained to differentiate between the two taxa or not. Another aim is to bring about some documentation of how the genetic variation is structured within and between populations of the two species. A morphological analysis

(morphometry) will also be done in addition to the genetic analysis.

The populations were collected at four locations (Fig. 1), one at Frøya, two at Smøla and one in Klæbu, late in September 1995. At each location about 40 samples of each taxon were collected except in Klæbu where only *S. cuspidatum* was found. At the other locations the two taxa were in mixed stands. The water level and pH were measured at each sample point. The samples were collected along a 40 meter transect and at least one meter apart. After the sampling in the field one plant from each sample was cultivated in a glass tube with nutrient solution. Only the upper 2 cm of the plant was placed in the glass tube. The rest of the plant was stored in a paperbag for morphological analysis.

About 10 different enzyme systems will be used in the genetic analysis. The isozymes will be extracted from the capitulum and the extract loaded on paper wicks for electrophoresis. The main problem is to extract enough of the enzymes for electrophoresis. One reason for this is that peat mosses have hyalin cells whose main function is to store water. The isozymes will be separated by PAGIEF (isoelectric focusing in polyacrylamid gel). This method will hopefully give well defined banding patterns which will make the interpretation easier.

In the morphological analysis the length and the width of leaves of the stem and the divergent branches will be measured in addition to the size of the cells in these leaves.

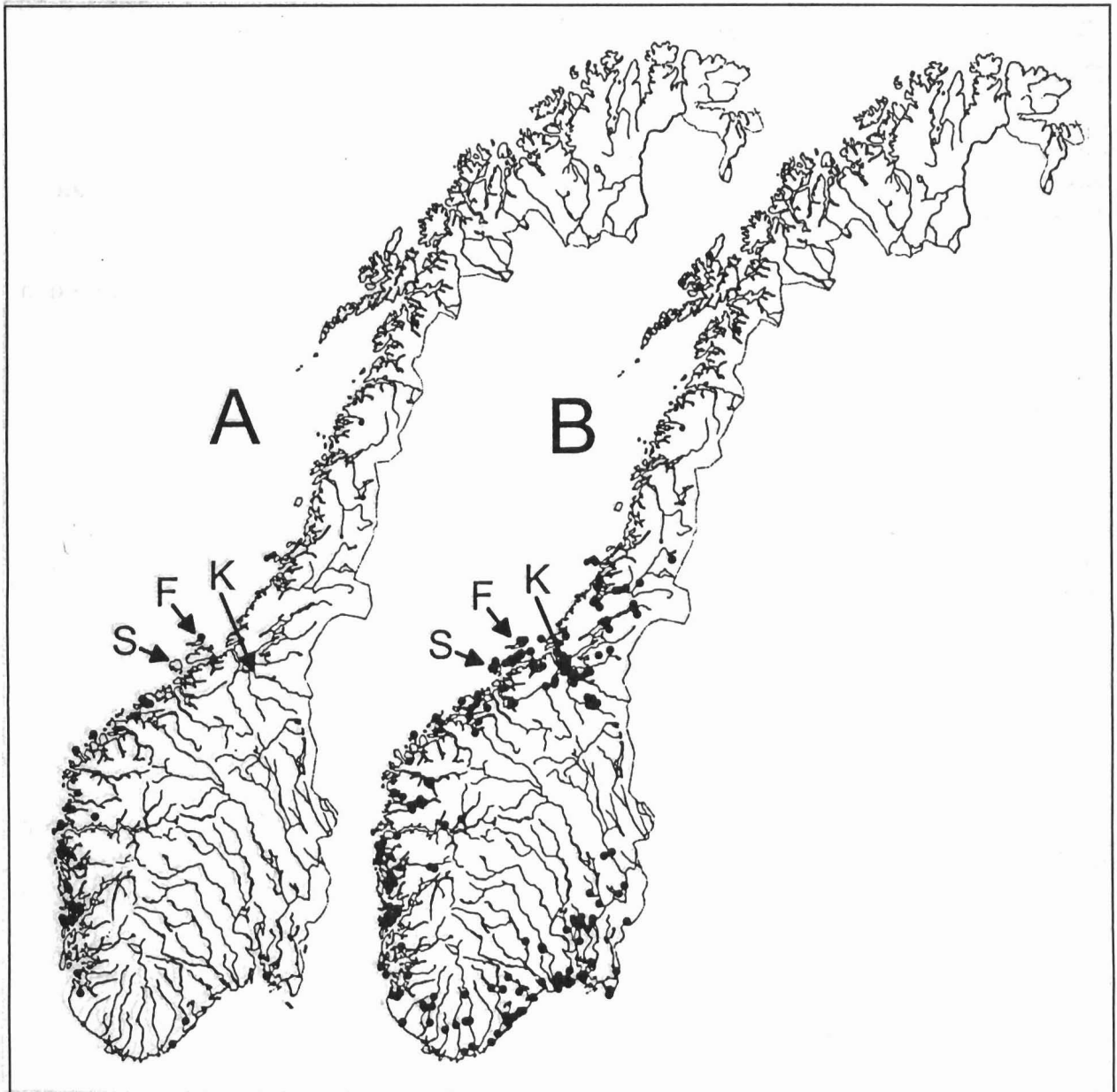


Figure 1. Distribution of *Sphagnum viride* (A) and *S. cuspidatum* (B) in Norway (from Flatberg 1988). The localities where material was collected are Klæbu (K), Frøya (F) and Smøla (S). Both species were present at all localities except *S. viride* at Klæbu.

The results of the genetic analysis will be used to measure the genetic variation (percentage of polymorphic loci, mean number of alleles per locus, number of multilocus genotypes and expected heterozygosity per locus) and of genetic distance (Nei 1972, 1973). A summary will be made of the allelic variation in a dendrogram, and UPGMA cluster method will be used. Multivariate methods will be used to see if there is some kind of correlation between the genetics and the morphology.

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Characters useful in the taxonomy of *Philonotis* (Bartramiaceae)

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The genus *Philonotis* Brid. is the largest genus of the family Bartramiaceae, having ca. 220 accepted species (Wijk et al. 1959-69, Crosby et al. 1992, Crosby & Magill 1994). The genus has been considered one of the taxonomically most difficult genera. This may be partly due to its habitats; species of *Philonotis* often grow on wet soil or trickling cliffs or even in water, and this may cause considerable variation in characters. Another feature of many tropical *Philonotis* which causes practical difficulties is the small size of the plants.

Philonotis was monographed worldwide by Brotherus (1924). Kabiersch (1938) revised East Asian taxa, and Ochi (1962, 1963) those of Japan and adjacent areas. Ochi (1967, 1970) continued revising Asian species in several papers. Zales (1973) monographed *Philonotis* for North America, but his research was not published. Griffin & Buck (1989) dealt with the generic taxonomy of Bartramiaceae.

The Koponen & Norris (1996; see Koponen 1993, 1995) study of Western Melanesian species synonymized ca. 30 names described from the Pacific and Melanesia. In connection with this revision I went through many Australian and some continental Asian collections, a task necessary when trying to establish a constant nomenclature. I also tried to find previously neglected characters useful in identification and classification of *Philonotis*. This paper is based on these observations, some of which are preliminary.

Growth habit; sexual differentiation

A generic characteristic of the species of *Philonotis* is that they are branched below the perichaetium and perigonium. This is the

characteristic habit of mature *Philonotis* plants. One or several of these innovations may continue the growth of the plant as a new main stem. On the basis of preliminary observations the branching pattern, or the possibility to branch, is different in *Philonotis* from that of, for instance, *Mnium* and its relatives which have a "dormant bud" at every leaf axil. In *Philonotis* this is not the case; there are leaf axils without a bud. This character must be studied further as well as the rhizoid topography, which is connected with it. In *Philonotis*, macronemata (and macronematous initials) seem to be the type of rhizoids developing on the stem, and they are situated in rows laterally above the leaf axils. Correns had in 1899 already found the regularities and differences in the branching potentialities in mosses (Correns 1899).

In some species, such as *P. hastata* (Duby) Wijk & Marg., the shape of stem leaves and the structure of their costa may be rather different from the characters of the branch leaves. In some other species the branch leaves are similar to stem leaves, or are slightly narrower than stem leaves. There are other minor characters varying between the species, such as the length of the leaves and the strength of the costa. Leaves in some species are tightly imbricate and in some others distant so that the red stem is visible. Several species have leaves in distinct rows on the stem. These characters give a characteristic habit for some species.

Little attention has been paid to the possibility that sterile male and female plants may have a different morphology. This is true in some species of the family Plagiomniaceae where the leaf shapes, cell sizes and the teeth of the leaf margin and leaf decurrencies may differ between the sexes.

Sexual differences in *Philonotis* include differences in the structure of the perigonium and in the shape and size of perichaetial and perigonal leaves. The special morphology of the male plants of *Philonotis fontana* has even been used as a key character. Sterile male plants cannot be separated from female plants; their leaf shapes and cellular details are similar. The perigonia develop on the top of specialized branches, on which the leaves are inhibited in growth so that they consist only of a broad basal part with wide leaf cells and a short, acute apical part where the leaf cells are narrow. Innovations below the perigonium may continue as in normal plants with long arcuate leaf apices.

Capsule

Capsule shape and peristome. The separation of the genus *Bartramidula* B.S.G. from *Philonotis* is largely based on the smooth and erect, globose to subglobose capsule and reduced peristome of the former genus. I have not yet found gametophytic characters which would match with these characters of the sporophyte. Griffin & Buck (1989) proposed that these genera are congeneric, and I agree.

Striae of the capsule. In addition to the shape and size of the capsule, differences exist also in the exothecium. This is obviously related to dispersal of the spores. In many species of *Philonotis* the dispersal mechanism is the constriction of the capsule which we see as striations on it. In some species the exothecial cells are about equal in size, more or less isodiametric. In the places where the striae are formed the cell walls of exothecial cells are thinner than between the striae. The striation takes place when these thin-walled cells collapse, and the thick-walled cells retain their original size. This kind of mechanism operates in *P. runcinata* Aongst. In *P. yezoana* Besch. & Card. the cells forming the striae also have a different size and shape, being narrower and longer than the isodiametric cells between them. Differences occur in the number and location of the

striae. In some species the striae are formed along the whole length of the capsule, whereas in some others they are present on the upper part of the capsule, but the lower part joining the neck remains smooth. In *P. yezoana* the striae are formed only on the dorsal side of the capsule where rows of narrow thin-walled cells are present. The ventral side of the capsule remains smooth.

Leaf characters

Papilosity. In *Philonotis* special attention must be paid to the presence or absence of papilosity on leaf cells, and to the distribution of papillose cells on the leaf. In addition, the position of the papillae on the cell and the structure of the papillae seem to be significant characters. In the majority of species the papilla or mamillae is at the upper end of the leaf cell, or at both ends. If there are two papillae on a cell, one is on the upper end of the cell on the ventral surface, and the other on the lower end on the dorsal surface. This kind of distribution of papillae on the cells is a rather constant character. In the species related to *P. fontana* the papillae is on the lower end of the leaf cell, but there is variation. Commonly scattered leaf cells on which the papillae is in the middle of the cell exist in *P. seriata* Mitt., and this I have observed in *P. fontana* and *P. tomentella* Mol. To some extent this depends on the length of the cell; in short and broad cells the papillae tends to be central. Moreover, there are several species which always have a central papilla or mamilla on the cell. There may be large papillae on the costa, or the costa may be smooth.

The structure of papillae or mamillae and their situation on the cell is useful, although not easy to observe. The papillae often look merely like dots under the light microscope, but SEM discovers papillae which are straight or turned sickle-like backwards (Fig. 1), or which even branch.

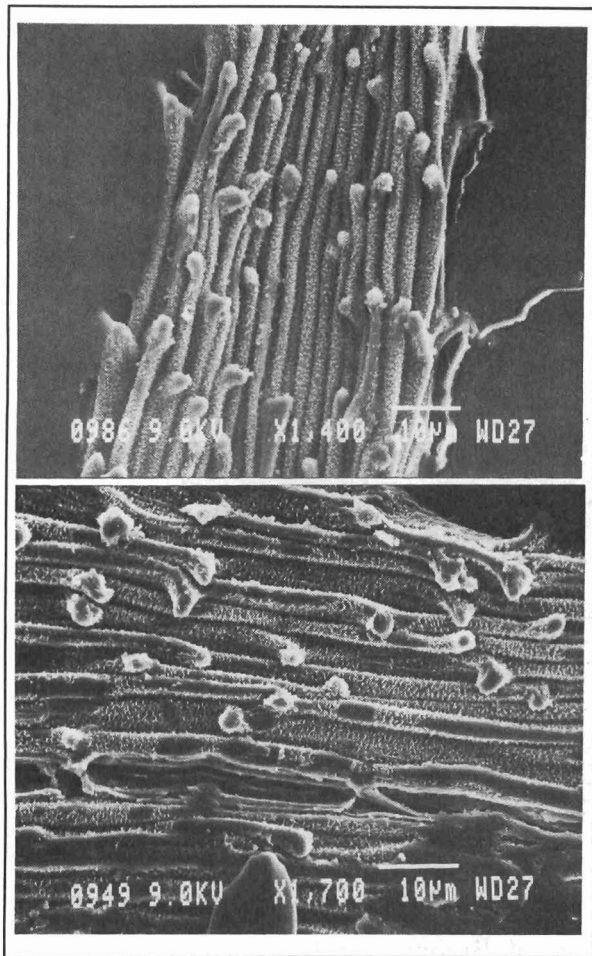


Fig. 1. SEM photographs of dorsal leaf surfaces of *Philonotis runcinata* Aongstr. (above) and *P. secunda* (Dozy & Molk.) Bosch & Sande Lac. (below).

Areolation. Papillosity is connected with the size of the leaf cells. Many species exhibit an area of large basal leaf cells which is more translucent than the apical area of narrower cells. This difference in transparency is caused both by the density of cell walls (walls near to each other) and by the papillae which in the apical area are often taller than in basal cells. The basal cells may be nearly smooth, or there may be a bulging mammilla at the cell end. Accordingly, these two characters, the transparency and the breadth of the cells and the mammilla/papilla are associated with each other. This character is useful in identification. The leaves with dense areolation down to the leaf base look very different from those with a translucent basal part. The transition from translucent base to dense upper leaf may be gradual, or the basal part may extend straight across the leaf (e.g.

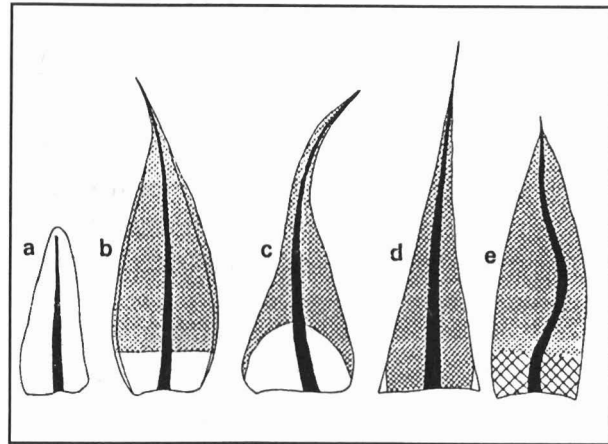


Fig. 2. Leaf shapes and areolation types in *Philonotis* (schematic). Dense areolation indicated by hatching. a: Areolation translucent (e.g. branch leaves of *P. hastata* (Duby) Wijk & Marg.); b: Basal leaf translucent with \pm sharp line of demarcation; leaf border re-curved (e.g. *Philonotis thwaitesii* Mitt.); c: Translucent area of basal leaf's turned u-shape form (e.g. *P. fontana* (Hedw.) Brid.); d: Most of the leaf with dense areolation, only angular cells thin-walled (e.g. *P. turneriana* (Schwaegr.) Mitt.); e: Transition between translucent basal area and dense area gradual; leaf strongly carinate (e.g. *P. falcata* (Hook.) Mitt.).

in *Philonotis thwaitesii* Mitt.) or may form a structure which I call the "turned u-shape form", present in *P. fontana* and its relatives (Fig. 2).

Leaf shapes. The general leaf shapes used in separating taxa are useful in many cases. For instance, it is rather easy to decide between straight leaves (e.g. *Philonotis thwaitesii*) and flexuose leaves (e.g. in *P. secunda* (Dozy & Molk.) Bosch & Sande Lac.). The broadest point of the leaf is also useful: some species have leaves distinctly ovate and the others have triangular leaves with straight sides (Fig. 2). The leaf shapes and sizes, however, vary even on the same stem and especially the juvenile plants are problematic.

Leaf margin. Structure of the leaf border and leaf margin in different parts of the leaf is very useful in identification. The basal margin in many species is different from that in the middle of the leaf, and the apical border may be still something else. For instance, the basal marginal cells may be smooth, cells

at mid-leaf biserrate, and apical marginal cells uniserrate; or the border may be uniserrate from base to apex. This may be in connection with the curvature of the border; in plants with a recurved border the teeth seem to be more regularly biserrate, though this is not a general rule. The marginal teeth may be large and sharp, or merely protruding cell corners. Species of *Philonotis* with a more or less distinct group of alar cells have been seen.

Other characters. Differences also occur in the anatomical structure of stem and costa. Such a character as hyalodermis has been reported in some species, but I have not yet made any thorough study of it.

Conclusion

Specific characters exist both in the sporophytes and the gametophytes of *Philonotis*. I have tried to identify my material on the basis of the gametophytes, and the keys I have made are based mainly on gametophytic characters, since most of the specimens have no sporophytes. The observations reported above are based on material from southeast Asia, the Pacific and Australasia. My aim is to test these character sets against material from Africa and South America. If they prove useful for these other continents, the specific identification of *Philonotis* may become easier than it has been up to now.

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On Western Melanesian *Breutelia* (Bartramiaceae, Musci)

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The genus *Breutelia* (B. S. G.) Schimp. has ca. 125 species worldwide. However, no recent revision exists. Western Melanesian (West Irian, Papua New Guinea and the Solomon Islands) taxa were revised in connection with current studies on bryoflora of New Guinea (Virtanen 1996). Six species occur in the area: *Breutelia arundinifolia* (Dub.) Fleisch., *B. crassicaulis* C. Müll., *B. aristifolia* Zanten, *B. longi-capsularis* Dix., *B. roemeri* Fleisch., and *B. papuensis* Virtanen. *B. crassicaulis* is newly reported for New

Guinea. *B. aristifolia* Zanten, *B. longi-capsularis* Dix., *B. roemeri* Fleisch., and *B. papuensis* Virtanen are endemic for Western Melanesia. *B. arundinifolia* has a wide range in southeast Asia and *B. crassicaulis* is reported in addition to New Guinea only from Hawaii.

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The genus *Schistidium* in northern Europe. An overview

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The taxonomy of the *Schistidium* taxa occurring in the Nordic countries is well known through the recent revision by Blom (1996, and in prep.). This new treatment differs significantly from that of Bremer (1980a, b) as shown in Table 1.

The distribution of the taxa is fairly well known except for the Baltic countries and a large part of the forest areas in northern Sweden. The flora is richest in countries with major mountain ranges, but also remarkably rich in the arctic archipelago of Svalbard (figur 1). The greatest species richness is found in areas with a humid but subcontinental climate. The main ecogeographical diversification occurs along the alti-

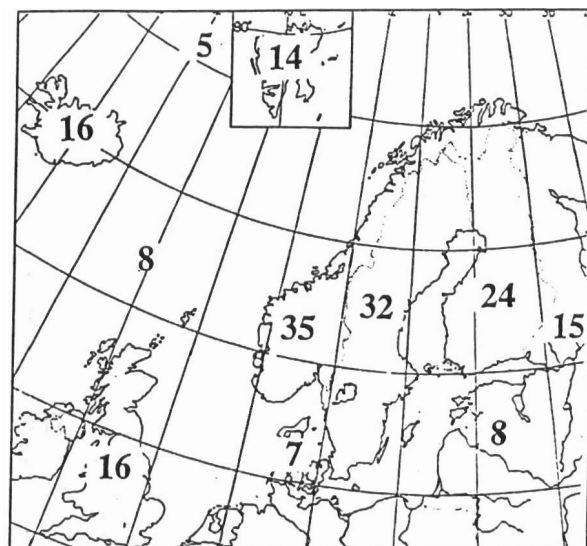


Figure 1. Number of known *Schistidium* species in Nordic countries and major areas.

Table 1. Comparison between the treatment of *Schistidium* in Bremer (1980a, b) and Blom (1996).

Bremer 1980a, b	Blom 1996
<i>S. apocarpum</i>	28 species
<i>S. trichodon</i>	<i>S. trichodon</i> + 1 variety
<i>S. flaccidum</i>	<i>S. flaccidum</i>
<i>S. maritimum</i>	<i>S. maritimum</i>
<i>ssp. piliferum</i>	<i>ssp. piliferum</i>
<i>S. agassizii</i>	<i>S. agassizii</i>
<i>S. rivulare</i>	<i>S. rivulare</i>
<i>ssp. latifolium</i>	2 species and 1 subspecies
<i>S. holmenianum</i>	<i>S. holmenianum</i>

Table 2. Geographic elements among the Nordic *Schistidium* taxa.

Geographic element	No. of taxa
Alpine	8
Western	4
Northern (circumarctic)	5
Weakly northern (circumboreal)	4
Southern	6
Southeastern	4
Eastern	3
Widespread	4

tudinal and edaphical gradients. The *Schistidium* flora of the Nordic countries can be divided into eight geographical elements (Table 2).

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Population biology of *Plagiomnium undulatum* in Finland

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The world distribution of *Plagiomnium undulatum* is centred in Europe. In Finland it is at the northern extreme of its range. In the south-western part of Finland *P. undulatum* grows on rich forest soil but towards the north it favours spring areas as habitats. The spring water areas are favourable sites for many temperate species in boreal regions because springs lower the annual fluctuation of temperature and flowing water improves the

availability of nutrients.

Plagiomnium undulatum is a dioecious moss in which the male inflorescences have rarely been recorded. It has been shown that the induction of male and female inflorescences require different ecological conditions. This leads to spatial disparity of antheridia and archegonia in a population and this again to the absence of sporophytes. Consequently

asexual reproduction is more important in *P. undulatum* than sexual.

My interests are in the effects of spring water on plants. I am going to compare the growth and reproductive biology of *P. undulatum* in different habitats at different latitudes. As the first step of my study I will compile a distribution map based on museum specimens. From the specimens I will also look for suitable study areas.

Interesting questions concerning the population biology of *P. undulatum* in Finland are: What are the known localities of the

moss in Finland? What is the distribution of suitable habitats where *P. undulatum* is not found? If the present populations towards the north are isolated, what is the degree of morphological differentiation between those peripheral and those southern, more central populations? Is there an advantage concerning the annual biomass production of the moss because the growth season may begin earlier in a spring area? Or is there no advantage at all because of the constant coolness of water? What is the reproductive capability of the moss at the extreme of its distribution?

Diaspore bank and germination ability of an expanding species

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My main objective is to try to achieve a better understanding of the distribution ecology of the species *Pogonatum dentatum*. To do this I need to obtain information about:

- 1) the germination ability of spores
- 2) the existence/range of the diaspore bank

At the beginning of this century *P. dentatum* was a species exclusively found in the higher parts of Sweden. Today it has spread east to the coast and as far south as to areas around Stockholm (Fig. 1). The mean path of the distribution is believed to follow forest roads, where it establishes on open soil. My study area is in the area of Dorotea and Åsele (dot with circle around, Fig. 1).

The germination ability of spores at the laboratorium and in the field

- 1) In the laboratory I have sown out spores from capsules collected in the field, in petri dishes with an agar gel containing nutrient in order to find the percentage of spores per capsule that germinate.

- 2) In the field I have sown out spores along a new forest road, where *P. dentatum* is absent. I have fifty quadrates (10 × 10 cm) with 0, ½, 1 or 2 capsules sown out in each of them in order to find the germination ability of spores in field.

The existence/range of a diaspore bank

To investigate the diaspore bank I have taken soil samples along:

- 1) a new road, where *P. dentatum* was absent
- 2) a 3-4 year old road, with *P. dentatum* present
- 3) an old road, with *P. dentatum* present

I have taken soil samples at distances of 5 cm, 25 cm, 1 m, 10 m and 50 m away from the edge of the colonies. The soil samples have been put in pots and placed in a green-house, where the samples can germinate and grow. In order to find the frequency of *P. dentatum* in the diaspore bank I will compare it with the occurrence of *P. urnigerum*, which is an old and common species in the study area.

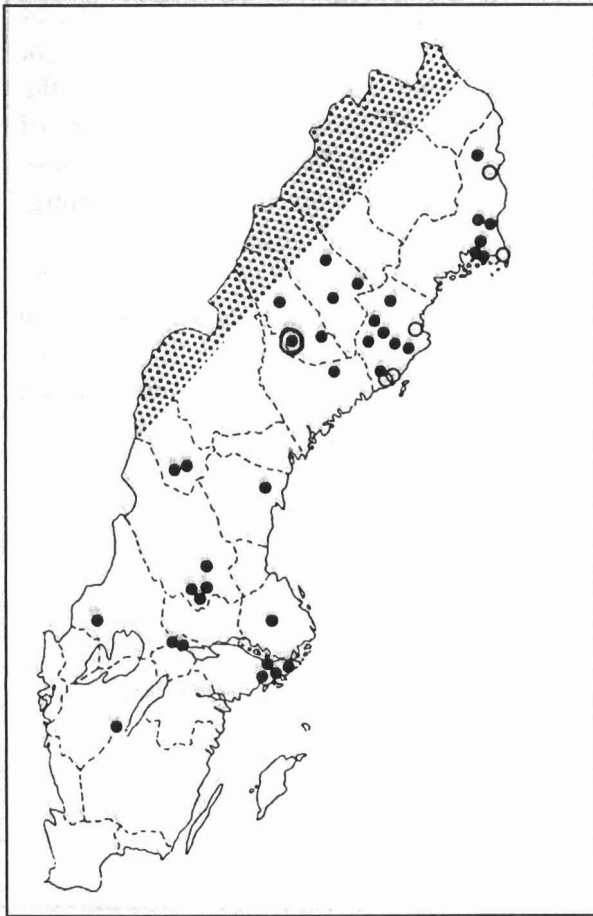


Figure 1. The distribution of *P. dentatum* in Sweden, open circles = before 1900 and filled circles = after 1900 (after Söderström 1992 with additional localities).

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Survival ability of bryophyte diaspores

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Bryophytes have been observed to disperse along rivers, and an important question in this context is whether diaspores disperse with the water or along the shore.

If the diaspores are to succeed in dispersing by being transported in water, it is crucial that the diaspores tolerate "drowning" as long as they are being transported.

In this project diaspores (fragments and spo-

res) of different species will be collected; the diaspores will be kept in water for different time intervals, and will then be grown on agar with Knop's solution in the laboratory. The frequency of germination will be registered.

Diaspores that have not been in water, and have been kept dry for the same time intervals as the diaspores kept in water, will also be grown, and their germination fre-

cuencies will be registered. By comparing the germination frequencies of diaspores kept in water and of diaspores kept dry, the effect of water on diaspores can be estimated.

Depending on the results, one can say something about the likeliness or at least the possibility of diaspore dispersal in water, and one can also say something about the diffe-

rences in survival ability between types of diaspores.

Both species living by running water and species that live at dry sites will be sampled. This is to test if there is any reason to assume that any ability to survive drowning is an adaptation for dispersal by the species living by running waters.

Interactions in bryophyte carpets. The influence of density and environmental factors on plant growth and competition

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Ongoing studies at the Norwegian University of Science and Technology in Trondheim, on interactions in bryophyte carpets, were briefly presented. Through experiments, descriptive and theoretical studies, a concept of understanding interactions within and between species is sought established.

Research is focused on the influence of density, humidity and light on the competition and coexistence of species. Mechanisms

for interactions are investigated at scales ranging from the individual shoot and shoot segment to the populations and communities of the species.

Studies are concentrated on six common and co-occurring bryophyte species: Dicranum majus, Plagiochila asplenoides, Ptilium crista-castrensis, Sphagnum girgensohnii, Rhytidia-delphus loreus and Hylocomium splendens in a boreal spruce forest.

Bryophyte - vascular plant interactions in a sea shore meadow

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A study on the effect of bryophytes on emergence and seedling establishment of *Plantago maritima* L. was conducted in a Baltic seashore meadow at Tullgarn ca. 45 km SW of Stockholm. The meadow which is used for cattle grazing shows a vegetational

zonation in relation to sea level. At a distance of ca. 80 m from the shore, in the zones dominated by *Juncus gerardii* Lois. and *Festuca rubra* L. s.l., three neighbouring areas (ca. 5 m²) with different abundances of bryophytes in the ground layer, but similar

regarding topography and vascular plant vegetation, were selected. In the first, the surface was completely covered by a dense, several cm thick moss carpet (mainly *Bryum intermedium* (Brid.) Bland. and *Calliergonella cuspidata* (Hedw.) Loeske); in the second, mats of the same species were less dense and interrupted by bare soil; and in the third, finally, bryophytes were lacking except in a few spots (closely intermingled *Desmatodon heimii* (Hedw.) Mitt., *Bryum intermedium* and *Campylium polygamum* (B.S.G.) Lange & Jens.).

Six plots of a size of 12 x 12 cm were placed in the areas with no and with an intermediate moss cover, and twelve within that with a dense moss cover. The bryophyte layer was partly removed in six of the latter, chosen at random, to obtain a patchy cover. Seeds of two genotypes (male-sterile and hermaphrodite) of *Plantago maritima* from inflorescences collected at the same locality in 1994 were sown into four subunits of each plot. The number of seeds applied (25 per subplot) corresponds to a density known to occur under natural conditions of seed dispersal (Jerling, pers. comm.).

The emergence and fate of plantain seedlings was followed during one growing season using a Pentograph which allows the survey of individual plants. The length of the longest leaf of each seedling was recorded at the end of the season as an estimate of their productivity.

The questions addressed in the present study are how the bryophyte cover influences the germination, establishment and survival of *Plantago maritima* in a shore meadow, and in particular, if there are differences in response between hermaphrodite and male-sterile plants.

Only three seedlings emerged in the plots selected in the area with intermediate cover, a phenomenon not fully understood yet, and which will require further consideration. At

the moment, however, these plots had to be excluded, since the low number does not allow any statistical treatment.

A preliminary data evaluation revealed the following results:

- The total number of emerging seedlings was highest in the plots lacking a bryophyte layer and lowest in those with a dense moss carpet, suggesting a negative impact of the bryophyte cover on the emergence of the plantains.
- The mortality was generally high (53 to 80 %) and turned out to be significantly lower in the plots with a manipulated (patchy) bryophyte cover as compared with those with dense or no bryophyte vegetation, respectively.
- Productivity in terms of leaf length differed between the juveniles (excluding late seedlings, i.e. those that had germinated after the middle of July) growing in plots with different bryophyte cover: Plantains in the plots with manipulated moss carpets had produced significantly shorter leaves than those in the other plots.
- No distinct differences in the performance of the two genotypes could be detected so far.

At present, the interpretation of these results causes some problems. Reduced seedling emergence rates in the presence of bryophytes have previously been reported for a number of other species (Keitzer et al. 1985, Johnson & Thomas 1978, Van Tooren 1988, 1990). In the case of *Plantago maritima*, this is presumably due to lower light availability within/under the bryophyte carpets. The success of juveniles of this species in a shore meadow was shown to be negatively affected by factors reducing light intensity (Jerling 1984). Shading by remaining moss cushions of a height of several cm could also be responsible for the shorter leaves of the

plants in the plots with the patchy bryophyte cover. On the other hand, it is possible that the manipulations in these plots had created micro-environmental conditions favouring the establishment and hence increasing the survival of juveniles (e.g. disturbance of the soil surface allowing a deeper rooting). Unfortunately, no other 'productivity estimates' (e.g., the number of leaves) were recorded. Two factors may, at least partly, account for the enhanced overall-mortality: the pronounced drought in summer 1995, and the fact that the study sites were selected in an area with a low density of adults of *Plantago maritima* (to avoid emergence from naturally dispersed seeds) which may indeed be the result of unsuitable recruitment conditions.

I intend to perform a number of comparative experiments in the greenhouse in order to clarify the impact of a bryophytes on the establishment phases of *Plantago maritima* and to obtain a better understanding of the results obtained in the field. In addition, I plan to continue the survey of the recruited

plants in the coming year.

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A quantitative study of the niche relationships of *Andreaea* in western Norway. An extended abstract

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In the summer of 1994 a field study of the saxicolous genus *Andreaea* was undertaken. The study area was located in western Norway, mainly in the counties of Rogaland and Hordaland. A total of 568 sites supporting one or more *Andreaea* taxa were visited. This fieldwork was the basis for my Cand. scient. thesis at the Botanical Institute, University of Bergen. The main aim of my study was to analyse quantitatively the niche relationships of the *Andreaea* taxa, namely to interpret the response of each taxon to its environment, and to detect the environmental relationships between taxa.

There is a great heterogeneity of climate at all scales within the study area. In the west the climate is oceanic with high precipitation, cool summers, and mild winters, whereas in the eastern part of the area there is a more continental climate, with low precipitation, hot summers, and cold winters. The fjords, which stretch in an west - east direction, create local differences between the warmer and drier south-facing hillsides and the more humid, cooler north-facing slopes. Along the whole of the east-west gradient there is a large altitudinal range over short distances. In addition to the climatic variation, the geology of western Norway is

also rather diverse, although acidic bedrocks, mainly gneiss and granite, predominate (Sigmond et al. 1984). On the basis of Murray's (1988) monograph, this oceanic to sub-continental, lowland to alpine area was expected to support a great variety of *Andreaea* taxa.

Bryophytes are, in general, regarded as responding to environmental fluctuations at a micro spatial-scale (Hedderson & Brassard 1990, Alpert 1985, 1991). Thus a sample unit of 10 by 10 cm was found to be appropriate. A square of this size was drawn onto transparent paper and used in the field to obtain the abundance of the plants occurring within the sampling unit. One m² sites including *Andreaea* were selected in the field, and within this square metre a sample unit was placed to obtain the maximum abundance of *Andreaea* taxa. Sites were at least five metres apart or differed in at least two environmental variables. This reduced over-sampling of certain environmental combinations, and reduced the effect of spatial autocorrelation. The environment on rocks is known to be harsh, and species occurring in such habitats must withstand stress for prolonged periods. Most rupestral mosses, such as *Andreaea*, endure stress in a dry state, and a compact growth form reduces the influence of stress (Mägdefrau 1982). Their water relationships are a crucial factor for survival in such an environment, and to obtain an adequate estimate of the moisture level of a site, environmental factors most likely to control moisture were measured: degree of flushing, degree of shelter, number of cracks, and topography. In addition, the potential solar radiation was calculated from the slope and aspect (Okê 1987). Altitude was also considered, and for areas at higher altitudes a factor estimation of snow-cover was obtained. Snow-cover influences the moisture level at the sites as well as the length of the growing-season.

Andreaea has mostly been observed on acidic rocks, but in the last decades many

observations of occurrences on mildly basic substrates have been reported (e.g. Birks & Birks 1974, Bates 1978, Murray 1987, 1988). The Ca-concentration and pH of the rock and of soil in cracks close to the samples were measured. The pH of water percolating from the sites was also measured. Unfortunately both soil and water samples were unavailable from many sites.

Within the study area all *Andreaea* taxa which had previously been reported from Norway were found. However, *A. crassinervia* Bruch, the only *Andreaea* taxon which is regarded as rare, was only observed once. The taxa could be divided into four altitudinal groups: low altitude, *A. rothii* Web. & Mohr ssp. 4, *A. rothii* spp. *falcata* (Schimp.) Lindb., *A. megistospora* Murr. ssp. *megistospora* and *A. alpina* Hedw.; intermediate altitude, *A. frigida* Hüb. and *A. crassinervia*; high altitude, *A. nivalis* Hook., *A. blyttii* Schimp., *A. rupestris* var. *papillosa* (Lindb.) Podp., *A. alpestris* (Thed.) Schimp. and *A. obovata* Thed.; and widespread occurrence, *A. rupestris* Hedw. var. *rupestris*. Information regarding *A. crassinervia* was obtained from herbarium specimens (BG, TROM, O, TRH).

The environmental relationship of each taxon was studied by regression analyses, generalized linear models (GLM, McCullagh & Nelder 1989), and generalized additive models (GAM, Hastie & Tibshirani 1987). The environmental relationships between taxa were explored by a combination of constrained ordination (canonical correspondence analysis, CCA; ter Braak 1990), which estimates the optimum for a species occurrence assuming a unimodal response to linear combinations of environmental variables (axes) (ter Braak & Verdonschot 1995), and a comparison of the regression results obtained for each taxon. The latter technique is more flexible in its estimation procedure, and a proper basis for interpretation is thus obtained by using a combination of different regression and ordination techniques.

During this study I found that the environmental factor that differentiated most between the realized niches of the *Andreaea* taxa was moisture (Heegaard 1997). However, the taxa were widely spread along the altitudinal gradient, which is an indirect gradient (sensu Austin & Smith 1989). The altitude gradient correlates with moisture, temperature, and length of growing season. The distribution of *Andreaea* taxa along the altitudinal gradient is thus determined by the distribution of suitable micro-scale habitats, the dispersal ability of the taxa, and the history of both the taxa and the habitats. At high altitudes there was a strong gradient in relation to snow-persistence, which was negatively correlated with the degree of flushing. *A. blyttii*, which grows almost solely in late snow-beds, receives moisture from melting snow, whereas taxa not related to snow-beds (*A. nivalis*, *A. obovata*, and *A. rupestris* s.l.) mostly receive water from other sources. At lower altitudes *A. alpina* is the only taxon associated with high moisture levels. A general tendency within the genus in relation to moisture is an increase in the degree of shelter or the number of cracks or a decrease in potential radiation with a decrease in the degree of flushing.

All taxa are restricted to Ca-poor substrates, but some differentiation in relation to pH, i.e. soil pH, was detected. All the lowland taxa, except *A. alpina*, tolerate extremely low pH. The same is true for *A. blyttii*, whereas the measured pH is slightly higher for the other *Andreaea* taxa (Heegaard, in prep.). In addition at high altitudes, lithosol and phyllite are alternative substrates to acidic and other hard rock types, such as gneiss and granite.

In a summary, the distribution of *Andreaea* taxa is constrained by the occurrence of acidic rock although they can occur on mildly basic substrates, usually at higher altitudes. The main differential environmental gradients are moisture and soil pH. However, differentiation between pairs of taxa was also detected along other environ-

mental gradients (Heegaard 1997).

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Factors affecting bryophyte distribution patterns on siliceous boulders in deciduous forests

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This project aims at detecting the most important factors influencing the bryophyte flora on siliceous erratic boulders in deciduous forests. A main hypothesis is that the tree layer has a considerable impact on the bryophyte flora by reducing incoming light, changing chemistry and amount of precipitation in throughfall as well as quality and quantity of litterfall. These factors differ between tree species, which has been shown in several investigations, but the correlation with the bryophyte layer has not been tested previously.

As the method to describe the bryophyte vegetation on boulders, a sample plot of 10 x 10 cm which is divided into 25 subplots is used. In the subplots records of presence/absence of living gametophytes, dead parts,

specialised asexual propagules and sporophytes are gathered. In the forest a certain number of each tree species are randomly selected for investigation. The boulders lying under each of these trees are used in the study. On the boulders sample plots are placed horizontally after each other at regular distances. This is repeated at regular 'levels' till the boulder is 'covered' with sample plots. The number of sample plots is therefore dependent on how large the boulder is.

For each sample plot measurements of slope, aspect and height above ground are made. For each boulder a larger amount of environmental parameters are measured and estimated, e.g. shadowing tree and shrub species, crown projection, basal area and slope and aspect of the ground.

Effects of detergents and ammonium nitrate on the morphology and growth of the aquatic mosses

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In late August 1995 there was an accidental detergent discharge from Hackman Havi Riihimaki factory to the River Vantaa. The detergent discharge caused the death of hundreds of fish and the bacterial populations of Riihimaki municipal water purifying plant also died immediately after contamination.

The accident was noticeable because the River Vantaa runs through the most densely populated area in Southern Finland and has its outlet in the City of Helsinki. The river is widely used for recreational purposes.

My MSc thesis is part of a larger project concentrating on research into the impacts of detergents (specially synthetic tensides) on the key organisms in the River Vantaa ecosystem. My first problem is to find the lethal concentration of detergent and if there are concentrations which have persisting effects on the growth and morphology of the aquatic mosses. The other question is the response of mosses to this type of environmental stress. How fast can mosses recover from contamination and are some species more resistant than others?

Material will be collected from the upper stream of the River Vantaa. After careful cleaning I will cultivate small tips of four moss species in pure macronutrient media (Basile 1975) to determine the most effective

concentrations of detergent by small pilot cultivation. Mosses will be cultivated for 14 days in ten different concentrations with ten replicates from each concentration. Temperature, light and light intensity will be according to Glime's (1987) study on the growth model for *Fontinalis duriaei*. In an other experiment mosses will be cultivated in the same concentrations of detergents for different time intervals and cultivation will be continued in pure media.

The first experiment analyses the lethal concentrations of detergents and the visible effects of sub-lethal doses of detergents. The second experiment measures the speed of changes in morphology and growth of the mosses in the different concentrations of detergents. The changes will be categorised according to their life ability (Benson-Evans & Williams 1976).

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Effects of flow regulation on bryophytes in north Swedish rivers

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We sampled bryophytes in 52 rapids in regulated and unregulated north Swedish rivers with the objective to quantify effects of flow regulation on taxonomic richness and abundance of bryophytes. Effects were quantified using predictive models based on conditions at unregulated sites. These models were used to predict richness and abundance at impacted sites and the residuals were used as a measure of the effect of regulation.

Taxonomic richness was significantly lower than predicted at impacted sites. The diffe-

rence was as reduction by 22% of the predicted richness at sites with reduced flow and 26% at sites with regulated but unreduced flow. The overall abundance of bryophytes was not significantly different from the predicted. However, an analysis of the five most abundant species showed that the abundance of two species, *Fontinalis antipyretica* and *F. dalecarlica*, was lower than predicted at sites with reduced flow, while the abundance of *Blindia acuta* and *Schistidium agassizii* was higher than predicted at sites with regulated but reduced flow.

Monitoring of bryophytes in boreal rain forests. Effects of forestry

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Introduction

This paper presents some examples of the conflict between conservation of forest bryophytes and forestry practices in Norway. Some components of a research project in boreal rain forest, including monitoring, are presented. The status of some interesting bryophyte species that are dealt with in the research project is reviewed.

Bryophyte conservation in Norway. In Norway 220 bryophytes are presently on the red list (Frisvoll & Blom 1992). About 18 % of these species are forest species, but an additional number of species are threatened by forestry activities. For instance bryophytes that grow in mires are exposed to drainage. Epilithic species that grow in forests or on

cliffs with forest beneath may be dependent on trees for shelter.

The conflict between conservation of rare and threatened species and forestry is due to the disability of combining logging activities and supplying substrates for tree- and wood-inhabiting species.

Practical solutions must be worked out for the topics

- where to take down trees
- how to take down trees
- which trees to take down
- what not to take down

Forest conservation and multiple forestry in Norway. A conservation plan for coniferous forests in Norway started in the mid

1980's, but has still not been completed. When the plan is finished, about 0.84% percent of the productive coniferous forests in Norway will be protected (Miljøvern-departementet 1995). The government has already admitted that the plan is insufficient and they have proposed an expansion of the forest conservation plan. Highly productive forest and lowland forests are under-represented in these conservation areas, whereas low-productive forests and mountainous forests are over represented. The expanded conservation plan will focus particularly on highly productive forest in general and lowland forests in particular. The government has acknowledged the boreal rain forest of central Norway as a forest type that Norway has particular responsibility for. This part of the lowland forests will be a focal forest type (Miljøverndepartementet 1995).

It is unlikely that viable populations of all rare and threatened species can be maintained within protected areas only. There is no Norwegian law that protects threatened species, like for instance the Endangered Species Act of the USA (e.g. Chadwick 1995). Hence, the way we manage localities of species outside the reserves will be decisive as to what extent we can maintain the biodiversity.

Forest managers in Norway must justify their activity according to the Norwegian Forest Act of 1965 (revised in 1976). This act gives priority to the forest production and harvesting, but the foresters are also encouraged to take actions that improve and maintain forests as a living place for plants and animals. The act is based on the principle "freedom subject to the consequences of the law", which means that apart from activities initiated by grant-in-aid (i.e., road construction, various subsidies), considerations that are necessary to maintain biological diversity to a large extent are voluntary considerations that each land owner is encouraged to apply. Last year a five-year research programme in "Forest ecology and multiple forestry" ended. One of the projects focused on effects of

management on bryophytes, lichens and fungi in coniferous forests in central and south-eastern Norway. This project stated the importance of highly productive forest stands in the conservation of biological diversity (Prestø 1994, Framstad et al. 1995). One of the products from the programme is a manual of sustainable forestry (Solbraa 1996), where all the programme participants have contributed.

The outline of considerations that should be taken into account by forest managers has been progressed during the programme (e.g. Solbraa 1996). Considerations that should be recognised and taken into account in modern multiple forestry include non-logging in old forest, forest along rivers and brooks, forest beneath cliffs, no drainage of mires or swampy forests, avoid logging in the vicinity of threatened species. Also, the biological importance of old and large trees, dead wood (decaying logs and snags of various decay stages and sizes, especially the importance of large decaying logs), highly productive forests, swampy forests, lowland forest (as main habitats for many threatened species) should be recognised and applied to modern forest management. The value of classifying the vegetation in addition to site classification based on production capacity is stressed in forest management planning.

Still, basic biological questions that have to be dealt with to secure a sustainable forestry include:

- Which species are threatened?
- Where do they grow? What are the general characteristics of the habitats?
- Can forest management be attained at or in the vicinity of the species, and if yes, what kind of management and what species?

A monitoring programme in boreal rain forests. Boreal rain forest was not included in "Forest ecology and multiple use", but as the value of the forest type has been commonly

accepted, an interdisciplinary project called "Management strategies for boreal rain forests in central Norway" could be started. The botanical part of this project is called "Monitoring of bryophytes and lichens in boreal rain forest".

The main objective of this new interdisciplinary project is to "...develop a strategy for combining economical forestry with conservation of biodiversity in boreal rain forest"

The botanical project aims to increase the basal knowledge of

- population biology of threatened bryophytes and lichens
- the ability of rare and threatened species to tolerate forestry activities
- the silvicultural alternatives in stands and forests with rare and threatened species

This involves three major approaches

- monitoring of rare and threatened species
- studies of the management requirements of communities
- studying the effects of logging operations

All three topics were listed as main priorities for bryological research in Europe by the European Committee for Conservation of Bryophytes (1995: 26).

Boreal rain forests?

Some aspects of rain forest ecology and phytogeography. Traditionally, the spruce forests of central Norway have been included in the boreal zone (e.g. Dahl et al. 1986). Hence, they constitute the westernmost part of the Eurasian taiga. Norwegian lichenologists have recently proposed that the most humid part of the taiga should be called boreal rain forest, mainly based on the exclusive epiphytic lichen flora (Holien & Tønsberg 1996). The term coastal spruce forest has also been applied to the same region (e.g. Directorate for Nature Management 1994). It has been known for a long time that the coastal spruce forests of central

Norway have a lichen flora unique in Europe (e.g. Ahlner 1948, Jørgensen 1978, Holien 1982, Tønsberg 1992, Holien & Tønsberg in press). This has now been recognised and accepted by most Norwegian botanists and many ecologists (e.g. Framstad et al. 1995), public administration (e.g. Nordisk Minister-råd 1994: 59) and forest land owners.

The conventional use of the term rain forest is a forest with high precipitation and high and stable humidity. This goes for some tropical and subtropical **deciduous** forests, but also highly humid temperate deciduous and **coniferous** forests (e.g. Whittaker 1975: 167). An overview of the ecosystems of the world was presented by Whittaker (1975) and later modified by Keddy (1994). Aune (1994) observed that the rain forests rather unmotivated ceased to appear when entering the taiga zone. He suggested that the most humid parts of the taiga could be termed rain forest (Figur 1). Aune (1994) said that high annual precipitation is typical to this zone, but also high frequency of precipitation and high frequency of fog and cloudy weather.

According to the Directorate for Nature Management (1994) coastal coniferous forests with the characteristics of rain forest occur in the northern coast of both the Atlantic and the Pacific (see also Holien 1994, Holien et al. 1995). For a more detailed discussion of the distribution, definition and characterisation of boreal rain forests, see Holien & Tønsberg (1996). The boreal rain forests in Norway mainly consist of the coastal Norway spruce forests of central Norway (Figur 2, data from Directorate for Nature Management 1994, Holien 1994, Holien et al. 1995, but see also Holien & Tønsberg (1996).

A general overview of the differences between continental and coastal coniferous forests was presented by Aune (1994). Among the characteristics of coastal forests he mentioned that forest fires are rare, storm felling of trees is frequent, magnesium is

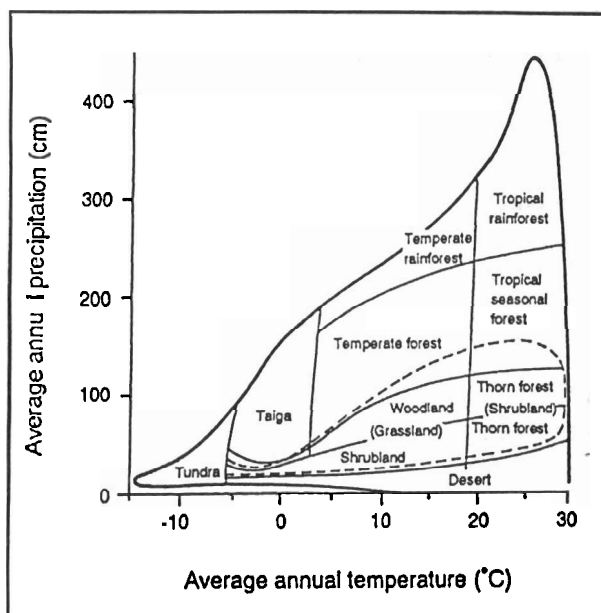


Figure 1. The world vegetation related to the major gradients temperature and precipitation according to Keddy (1994). Aune (1994) noted that rain forests rather unmotivated ceased to occur when entering the taiga zone. Boreal rain forests may occur in the most humid parts of the taiga zone.

supplied from the sea, soil leakage is strong due to high precipitation, cultural impact is strong (deforestation, grazing, logging, etc.) and wind speeds are often high. Holien (1994) added characteristics like copious networks of flowing water, varied topography with many small ravines, rarely dry episodes during summer, mild winters and cool summers.

A more detailed delimitation of a life zone termed boreal rain forest should imply comparison of for instance length of growing season, effective temperature sum, biotemperature, potential evapotranspiration, frost sum, continentality index and summer precipitation of central Norway and North America (see e.g. Tuhkanen 1984).

Supposing the use of the term boreal rain forest is reasonable, Norway has the only European boreal rain forests. Further, the only boreal rain forests in the world where the tree layer mainly consists of Norway spruce (*Picea abies* (L.) Karst.) is found in Norway. The international responsibility of



Figure 2. The major distribution area of boreal rain forests in Europe, redrawn from the Directorate for Nature Management (1994) on a vegetation section map (Moen & Odland 1993). Outposts of rain forest are found north and south of the main area. The vegetation sections ranges from O3 (strongly oceanic) to C1 (slightly continental); see also Ahti et al. (1968).

Norway to conserve this forest type is unquestionable (Directorate for Nature Management 1994, Holien et al. 1995).

Aune (1994) briefly dealt with the floristic and vegetation characteristics of the coastal forests. He mentioned that there are many oceanic and suboceanic species of vascular plants, bryophytes and lichens. He mentioned that hepatics are particularly frequent and abundant (both in species number and in cover). Lichens are rare in the forest floor.

Spruce is a recent invader in central Norway (Aune 1994, but see Hafsten 1992 for more details). In some of the boreal rain forests, spruce established almost 2000 years ago,

but in the westernmost parts of central Norway spruce established less than 800 years ago. It is reasonable to suggest that most species characterising boreal rain forest were present before spruce invaded. Spruce may still spread to new localities north and west of its present distribution area (Aune 1982).

The Directorate for Nature Management (1994), Holien (1994) and Holien & Prestø (1995a) presents examples of topographic types of boreal rain forests. Boreal rain forests are chiefly lowland forests (rarely above 200 m a.s.l.), in ravines, swampy forests, on marine glacial deposits, in slopes and cliffs exposed to north and north-east (potential storm and fire refuges) and in the spray zone of river falls (Holien & Prestø 1995b). The forest stands are mostly highly productive (Directorate for Nature Management 1994).

Biodiversity of boreal rain forest in central Norway. The boreal rain forests contain a large number of species and much variation within several plant and animal groups. Many rare and threatened species are found. Few fungi characterise boreal rain forest, but few studies have been conducted. Some exclusive tree-living saprophytes may occur (S. Sivertsen pers. comm.). Species richness of birds and invertebrates seems to be rather high (Tømmerås & Breistein 1995).

Our project mainly deals with epiphytic lichens and epixylic bryophytes. These species groups contain species that are unique to and characterise the boreal rain forests and include species that are rare and threatened in Norway and Europe. The boreal rain forests of central Norway are mostly known for their rich epiphytic lichen flora (e.g. Jørgensen 1990, Directorate for Nature Management 1994, Holien 1994, Holien et al. 1995, Holien & Tønsberg 1996, Tønsberg et al. 1996).

Among the epiphytic lichens we find species that (see e.g. Holien & Tønsberg 1996,

Tønsberg et al. 1996)

- are regarded as threatened (red listed species) in Norway and Europe
- have their only European occurrences in boreal rain forests
- have their main European distribution in boreal rain forests
- have their northernmost European occurrences in boreal rain forests

Among the epixylic bryophytes we find species that

- are regarded as threatened (red listed species) in Norway and other European countries
- have their northernmost European occurrences in boreal rain forest
- possibly have their major Norwegian populations in boreal rain forest

The red listed bryophyte species dealt with are *Anastrophyllum hellerianum*, *Calypogeia suecica*, *Cephalozia catenulata*, *Lophozia ascendens* and *Lophozia longiflora*. Frisvoll & Blom (1992) regarded all these species as **requiring consideration**, but considering the results of Prestø (1994) *Lophozia ascendens* possibly should be treated as a vulnerable species.

Species which have their northernmost European occurrences in boreal rain forest in central Norway are *Anastrophyllum michauxii*, *Nowellia curvifolia* and *Cephalozia catenulata*. Studies of populations at the margin of their distribution are considered important in conservation biology (e.g. Holten & Carey 1992, Maurer 1994).

Bryophyte monitoring in boreal rain forest in central Norway. The dynamics of the rare and threatened species in central Norway is unknown. We do not know how the populations fluctuate, establish, disappear, reappear, and, if reappearing, where have they been in the meantime. We only have information on where the species have been recorded.

To maintain viable populations of these species we must get more detailed information about these species demands on their environment. What considerations should be taken into account? Some of the above-mentioned species are found in protected areas, but the number of areas and the population sizes varies much. Should the localities be protected by using the law of Nature Conservation? Are the common (chiefly voluntary) considerations taken into account by modern multiple use forestry sufficient (i.e., non-logging of old growth forest, forest along rivers and brooks, forest beneath cliffs, no drainage of mires). Can we evolve logging practices that combine conservation of the species and forestry activity in the same stands or the same localities, and if so, how can we do this?

Nevertheless, no special consideration strategy has been developed that determines more exactly what considerations may/must be taken to safeguard populations of plant species in general. Through this project, we hope to gain more detailed knowledge of what considerations must be taken to fulfil the requirements of some rare and threatened species of bryophytes and lichens.

Like all other species the species we focus on in the boreal rain forest have ecological demands that must be fulfilled. Two major ecological demands of the interesting epixylic and epiphytic species that, as far as we know, must be fulfilled are

- a continuous supply of substrate
- a stable micro-climate

A continuous supply of substrate means old deciduous trees with rich bark and old spruce trees (old trees often also means large) for the epiphytic species and large decaying logs in various decay stages (large often means old) for the epixylic species. More specific knowledge of the relation between size and age will be obtained during the current project.

A stable micro-climate means stable and high humidity besides a minimum supply of light and temperature. Studies of the micro-meteorological conditions in the sites of the species in consideration will be conducted throughout the project.

To summarise: we know where the boreal rain forests are. The forest stand size and its variation is known. Many localities of many rare and threatened species are known. Vegetation and topographical types are known. All stands with threatened species have previously been managed, but to a various extent. Grazing has been extensive in many localities. Many localities have been lost the last 50 years due to logging, cultivation, settling and other technical encroachments.

What we do not know is for instance

- the spatial and temporal dynamics of the forest type or its species
- the magnitude and frequency of natural disturbance of the trees
- the magnitude and frequency of the substrates living and dead trees
- how all these factors influence the population dynamics of the species
- which features of population dynamics are crucial to local and regional maintenance of the rare and threatened species
- which features of natural forest dynamics are crucial to maintenance of the rare and threatened species
- how present forest management practices influence population dynamics of the species
- whether there are alternative forest management practices that can be combined with maintaining viable populations of the species

Interesting features of the population dynamics of rare and threatened epixylic bryophytes include:

- frequency and abundance of asexual production (incl. gemmae and branching)
- consequences of different systems for sexual reproduction

- frequency and abundance of capsules, perianths and antheridia
- co-occurrence of several species within a genus
- dynamics between patches of the same species on decaying log
- dynamics between various species on decaying logs
- dynamics between logs in a forest stand
- dynamics between logs in adjacent stands
- dynamics between logs in spatially separated stands

These features will be studied by monitoring populations of rare and threatened species in forests with the following status:

- forests not managed during the last decades
- large and small clear-cuttings
- old growth forests adjacent to large and small clear-cuttings
- young forests, to record possible establishing populations
- small-scale experimental logging operations

In each forest type bryophytes are recorded on the following scales

- permanently marked plots of 10 x 10 cm with 25 micro-plots (4 cm²) on logs selected by a restricted random sampling
- an overall recording of bryophytes on the logs with permanent plots
- an overall recording of selected bryophyte species on all logs in some forest stands, together with a total recording of the size and decay stage of all decaying logs in the stand
- resampling is planned each spring and autumn during the project

The floristic data will be supplemented by ecological habitat and substrate variables, and to some extent also by micro-meteorological measurements.

Status of some central Norwegian rare and threatened epixylic bryophytes

Anastrophyllum hellerianum. *A. hellerianum* prefers rather large logs of early or

intermediate decay stages, but it is also present on small logs and is sometimes present on old logs (Prestø 1994, Holien & Prestø 1995a). In central Norway *A. hellerianum* is recorded on bark of decaying logs, on naked wood and recently also as epiphyte on spruce in central Norway (only in boreal rain forest). *A. hellerianum* is distributed throughout Fennoscandia and the northern hemisphere (Schuster 1969, Konstantinova et al. 1992, Söderström 1995). It is rather frequent in central Norway, but less frequent in other regions (Jørgensen 1934, Frisvoll & Blom 1992, Prestø 1994). In central Norway *A. hellerianum* is also recorded on clear-cuttings that are 5-7 years old, but these may be spontaneous occurrences that easily disappear (Prestø 1994).

A. hellerianum alternates between sexual and asexual reproduction, including gemmae. It seems to reproduce sexually in humid, mature spruce forests, but more often by gemmae in drier forests and if stress is brought upon the individuals. Hence, humid forests most probably are crucial to regional persistence of the species. Capsules and gemmae are produced regularly, but rarely on the same plants or on the same logs.

Anastrophyllum michauxii. *A. michauxii* primarily grows on rather large logs of intermediate or late decay stages (Holien & Prestø 1995a). Wet cliffs in central Norway may be a suboptimal substrate. *A. michauxii* has a southern distribution in Fennoscandia as in Norway (Jørgensen 1934, Söderström 1995). The populations of central Norway and northern Sweden are the northernmost European populations, and possibly in the world (but see Schuster 1969, and Konstantinova et al. 1992).

A. michauxii reproduces both sexually and asexually. Gemmae are produced regularly, and most abundantly in suboptimal localities (Holien & Prestø 1995a). An overview of sex and reproduction in material collected in central Norway is shown in Table 1 and 2.

Table 1. *Anastrophyllum michauxii* in central Norway except the Åfjord district. The sexual state and reproduction of the populations are given.

Municipality	Locality	Collector/ year	Male plants	Female plants	Sterile plants	Perianth	Gemmae
Flatanger	Gaupdalen	Prestø 1990	yes	yes	yes	some	no
Flatanger	E of Trollengelva	Prestø 1990	yes	no	yes	no	some
Flatanger	E of Trollengelva	Prestø 1990	yes	yes	yes	many	no
Frosta	Åsen, Mossing	Hagen 1910	yes	no	yes	no	no
Namdalseid	Furudalshøgda	Prestø 1990	no	yes	yes	few	no
Namsos	E of Flåbekktjørna	Prestø 1990	no	no	all	no	many
Stjørdal	Forra bridge	Bryhn 1892	no	yes	yes	few	some
Stjørdal	Forbordfjell	Bryhn 1892	yes	yes	yes	many	no
Stjørdal	Fornes	Bryhn 1892	yes	yes	yes	some	no
Stjørdal	Grøthammeren	Bryhn 1892	yes	yes	yes	some	no
Stjørdal	Grøthammeren by Hegra	Bryhn 1892	yes	yes	yes	many	no
Malvik	Hommelvik, S of Mårstokkmyra	Blom 1985	no	yes	yes	some	no
Meldal	S of Sjursåstjørnan	Prestø 1993	no	no	all	no	some
Meldal	N of Vidmyra	Prestø 1992	no	no	all	no	some
Orkdal	N of Haugåsen	Prestø 1993	yes	yes	yes	many	some
Selbu	Rolset	Hagen 1909	?	yes	?	yes	?
Skaun	S of Mellingsætra	Prestø 1993	yes	yes	yes	some	few
Trondheim	Tiller	Hagen 1897	yes	yes	yes	many	no

Calypogeia suecica. *C. suecica* almost exclusively occurs on large, strongly decomposed logs. It is rather widely distributed in Fennoscandia and Norway (Söderström 1995), but it becomes more and more rare. Its distribution in the northern hemisphere is indicated by Schuster (1969) and Konstantinova et al. (1992). Its major Norwegian population may be that in central Norwegian spruce forest (Frisvoll & Blom 1992, Prestø 1994). It is rather frequent in mature stands of boreal rain forest (Holien & Prestø 1995a). *C. suecica* prefers highly productive spruce forest stands. Gemmae-production is neither frequent nor abundant. Gemmae seem to be most abundant in late autumn. Perianths and capsules are also rare.

Cephalozia catenulata. *C. catenulata* grows almost exclusively on rather large decaying logs of intermediate decay stages (Holien & Prestø 1995a). It has a southern distribution in Fennoscandia (Söderström 1995). The populations in central Norway are the northernmost in the world (Schuster 1974,

Konstantinova et al. 1992). The report from northern Finland is doubtful, as are those from Spitsbergen and Amur (Schuster 1974). *C. catenulata* is rather frequent in some parts of western Norway (Jørgensen 1934). It often grows together with *Nowellia curvifolia*. In central Norway all but one locality is in boreal rain forest (Jørgensen 1934).

Lophozia ascendens. *L. ascendens* prefers large logs in intermediate decay stages (Prestø 1994). According to Söderström (1995) it is only recorded in three Norwegian counties, but collections are few and no modern revision exists. Jørgensen (1934) recognised *L. ascendens* as *Lophozia longidens* fo. *lignicola*. The fact that he recognised the taxon may indicate that it is rare. In central Norway *L. ascendens* is most abundant in humid, large fern or small fern spruce forest (Prestø 1994). It is distributed throughout Sweden and Finland and rather widespread in the northern hemisphere (Schuster 1969, Konstantinova et al. 1992, Söderström 1995). *L. ascendens* is the only

Table 2. *Anastrophyllum michauxii* in Åfjord district, central Norway. Localities A to J refer to Holien & Prestø (1995a). Sexual state and reproductive state is presented.

Locality	Male	Female	Sterile	Perianth	Gemmae
Kringlathølen SW	no	no	all	no	many
Kringlathølen SW	no	some	yes	some	no
Kringlathølen SW	some	some	yes	many	no
Kringlathølen SW	few	no	yes	no	no
Kringlathølen SW	some	no	yes	no	some
NE of Jofjellet	no	no	yes	no	no
NE of Jofjellet	no	no	yes	no	no
NE of Jofjellet	some	some	yes	some	some
NE of Jofjellet	no	some	yes	some	no
NE of Jofjellet	some	some	yes	few	some
NE of Jofjellet	some	some	yes	no	many
Rogndalsbekken	no	some	yes	some	no
Rogndalsbekken	no	no	all	no	many
Inner Stakkengholet	no	no	all	no	some
Inner Stakkengholet	many	no	yes	no	no
Inner Stakkengholet	no	no	all	no	no
Inner Stakkengholet	many	many	yes	some	no
W of Melasætra	no	no	all	no	no
W of Melasætra	no	no	all	no	no
W of Melasætra	no	some	yes	few	no
W of Melasætra	some	many	yes	no	no
W of Melasætra	some	many	yes	many	no
W of Melasætra	no	no	all	no	some
Fjøsdaalen	no	no	all	no	no
Fjøsdaalen	yes?	no	yes	no	no
Fjøsdaalen	some	many	yes	some	few
Fjøsdaalen	no	no	yes	no	no
Fjøsdaalen	some	many	yes	some	some
NW Arnevikvatnet	many	some	yes	few	no
NW Arnevikvatnet	no	many	yes	many	no
NW Arnevikvatnet	no	no	all	no	many
NW Arnevikvatnet	some	many	yes	some	no
NW Arnevikvatnet	no	no	all	no	no
NW Arnevikvatnet	no	no	all	no	no

species dealt with in this study that is included in the European Red List (European Committee for Conservation of Bryophytes 1995). *L. ascendens* is red listed in Norway, Austria, Bulgaria, Czech Republic, Finland, France, Germany, Hungary, Italy, Kazakhstan, Liechtenstein, Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland and Ukraine (European Committee for Conservation of Bryophytes 1995). Based on Prestø

(1994) *L. ascendens* should perhaps be treated as a vulnerable species in Norway

In central Norway *L. ascendens* mainly reproduces asexually. Gemmae are always present. Sporophytes were recorded for the first time in Norway in 1995, and that was in boreal rain forests in central Norway. Unlike *Anastrophyllum hellerianum* (see above), *L. ascendens* grows almost exclusively on naked wood.

Lophozia longiflora. In central Norway *L. longiflora* prefers rather large logs of intermediate or late decay stages (Prestø 1994). It usually grows on naked wood. *L. longiflora* is most abundant in highly productive spruce forests (e.g. large fern forests). *L. longiflora* is distributed throughout Fennoscandia and the Holarctic region (Schuster 1969, Konstantinova et al. 1992, Söderström 1995). A modern revision of Norwegian species in *Lophozia* subgenus *Lophozia* is needed because Jørgensen's (1934) treatment of the subgenus is outdated. species dealt with in this study that is included in the European Red List (European Committee for Conservation of Bryophytes 1995). *L. ascendens* is red listed in Norway, Austria, Bulgaria, Czech Republic, Finland, France, Germany, Hungary, Italy, Kazakhstan, Liechtenstein, Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland and Ukraine (European Committee for Conservation of Bryophytes 1995). Based on Prestø (1994) *L. ascendens* should perhaps be treated as a vulnerable species in Norway

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regularly, but neither seem to be produced in high abundance (Prestø 1994).

Nowellia curvifolia. *N. curvifolia* prefers rather large logs of intermediate decay stages (Holien & Prestø 1995a). It has a southern distribution in Fennoscandia (Söderström 1995). The localities in central Norway are the northernmost occurrences in the world for this widely distributed species (Schuster 1974). Most localities in central Norway are in boreal rain forest, but some are from very humid forests outside this district (Jørgensen 1934, Holien & Prestø 1995a).

Gemmae and capsules occur regularly in *N. curvifolia*. Both dioicous and autoicous specimens are recorded in central Norway.

Activity plan

More details on the study can be found in Holien & Prestø (1995a) and Prestø & Holien (1996). At present the research programme has funding until 1998. We have launched supplementary studies of lichens in the upper crown canopies and a landscape ecological analysis of boreal rainforestry. A crown canopy study of lichens will evaluate what we can say about the lichen species from the ground level compared to what actually grows further up in the tree crowns. By comparing old aerial photographs and old maps with recent information, we will estimate how much of the boreal rain forest has been lost during the last 40 years or so and what has happened to old known localities of boreal rain forest and model future changes.

We also plan co-operation with a forest history project at the Norwegian Forest Research Institute and the Agricultural University of Norway. Based on local pollen deposition this will hopefully reveal for how long spruce have been the major tree species in some boreal rain forests, and to what extent they have been managed. A project dealing with logging engineering and effi-

ciency analyses is planned in co-operation with the Norwegian Forest Research Institute and the Norwegian Institute for Nature Research.

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Rare and endangered bryophytes of Europe

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In the five years since its formation, the European Committee for the Conservation of Bryophytes (ECCB) has been working to-

wards publication of a Red Data Book of bryophytes in Europe. The work, with a geographical coverage including Macaronesia and

the northern slopes of Caucasus, is in three parts. The first part is an introduction to threatened bryophytes in Europe, including a synopsis of the main bryophyte habitats and a background to legislation for the conservation of bryophytes in Europe. The second part of the book consists of the European bryophyte Red Data List, with detailed accounts of endangered, vulnerable and extinct species. The final part lists a selection of important bryophyte sites in Europe.

The book reveals that about 24% of the European bryophyte flora can be considered threatened. About 73% of the threatened species are represented in sites listed in part 3. Perhaps the most startling aspect of this

publication is to highlight just how little is known about threatened bryophytes in Europe.

We hope that this publication will serve as an important background for conservationists and that they will be able to take same steps towards protection of the rare bryophytes in Europe. Naturally, species status is changing constantly as our knowledge increases and this publication represents nothing more than a snapshot of our knowledge of threatened species at a particular moment in time. It is therefore our hope that we, in collaboration with bryologists all over Europe, will be able to improve knowledge of the rare species in our region.

Some ideas about peat stratigraphy or what possibilities the peat bulk density method gives us

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The constant peat bulk density method (CPBD) for dating the peat layers was first introduced by M. Ilomets in 1980. In the present work the method is being used for investigating the Ruunasoo bog in southwest Estonia. The area of the bog is 249 hectares. 42 peat cores have been drilled and about 2400 peat samples are collected. The CPBD method enables us to date all the distinguishable peat layers in the core, if the humification % and the content of dry matter (%) for each layer is known. For all the bog area only some C^{14} dating is needed to calculate the accumulation value ($g/cm \times y$).

The different structural levels of the bog (bog system, bog type, microsite) have a cyclical growth, which may be the cause of the

differences in the short-term and long-term accumulation of the organic matter. Due to this the speed of the anaerobic decay processes and the emission of methane might be significantly less than estimated before.

The aim of the work is to 1) determine the age of all the peat layers and restore the bog growth pattern, 2) make macro fossil analyses for all the peat samples and restore the dynamics and successions of the plant communities in Ruunasoo bog, 3) describe the relationships between the development of the plant communities and the peat accumulation, 4) find the causes of the changes in the peat accumulation, 5) describe the dynamics of the C accumulation in the peat.

Harsh bryophyte environments - 100 000 years ago

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In 1982, Robert Lagerbäck initiated a study of the glacial geology in northernmost Sweden in order to find new evidence of deglaciations and ice-free conditions that could possibly have occurred between the glaciations (Lagerbäck 1988a, Lagerbäck & Robertsson 1988). During the course of these studies, subfossil organic material in primary positions was found under later glacial deposits at several sites in the province Norrbotten (66°20'-67°40'N, 20°30'-23°30'E), especially in kettle holes and Veiki moraines. Based on lithostratigraphy, radiocarbon dating and biostratigraphical correlations, the organic deposits could be referred to two interstadials during the last glacial, the Peräpohjola and Tärendö interstadials (c. 105 000-93 000 and 85 000-75 000 years BP, respectively). During the course of the time these deposits have been investigated for their pollen (Lagerbäck & Robertsson 1988, Robertsson unpubl.), vascular plant macro material (Aronsson et al. unpubl.), bryophytes (Hedenäs 1995) and insect remains (Lemdahl, unpubl.), and a rather complete picture of the conditions during these interstadials has resulted. The climate was significantly colder than at present. The beetle fauna indicates temperatures around or below 10 °C during the warmest month of the year and temperatures slightly above (Peräpohjola) or below (Tärendö) -20 °C during the coldest. This can be compared with present day temperatures of 15 to 16 °C during the warmest month of the year and -11 to -12 °C during the coldest. The occurrence of fossil ice wedges and non-sorted polygons in the Tärendö interstadial deposits suggests a mean annual temperature of -5 to -6 °C, compared with 0.5 to 1.5 °C at present. The Tärendö interstadial had a harsher climate than the Peräpohjola interstadial, as indicated by both geological, entomological and bryo-

phyte vegetation data. Periglacial phenomena were common, as shown by fossil ice-wedges and non-sorted polygons during the Tärendö interstadial (Lagerbäck 1988b), but also by frequent occurrences of bryophyte species of late snow-bed environments or other unstable habitats, and by frequent occurrences of the fungus *Cenococcum geophilum* in limnic sediments. The latter occurs in raw humus rich soil and its occurrence in the limnic environment is best explained by strong erosion of the uppermost soil layers in the surroundings of the lake environments. The bryophyte flora in general suggests relatively mineral-rich conditions, despite the rare occurrences of calcareous or other mineral-rich rocks or soils in the area. Although pollen data indicate tree forming birches during the optima of the interstadials, vascular plant macro material and bryophytes show that tree-forming birches cannot have been very common. Instead, the landscape was open, and probably tundra or steppe vegetation dominated. All biological remains taken together tell us that despite the harsh climate, a large number of species and habitats existed in the area during the interstadials. Lakes, running waters, different kinds of mires (often spring-influenced, but few of mineral-poorer kinds), late snow-bed vegetation and drier unstable habitats as well as some more stable habitats with a more closed vegetation (especially during Peräpohjola), belong to the habitats identified during the present study.

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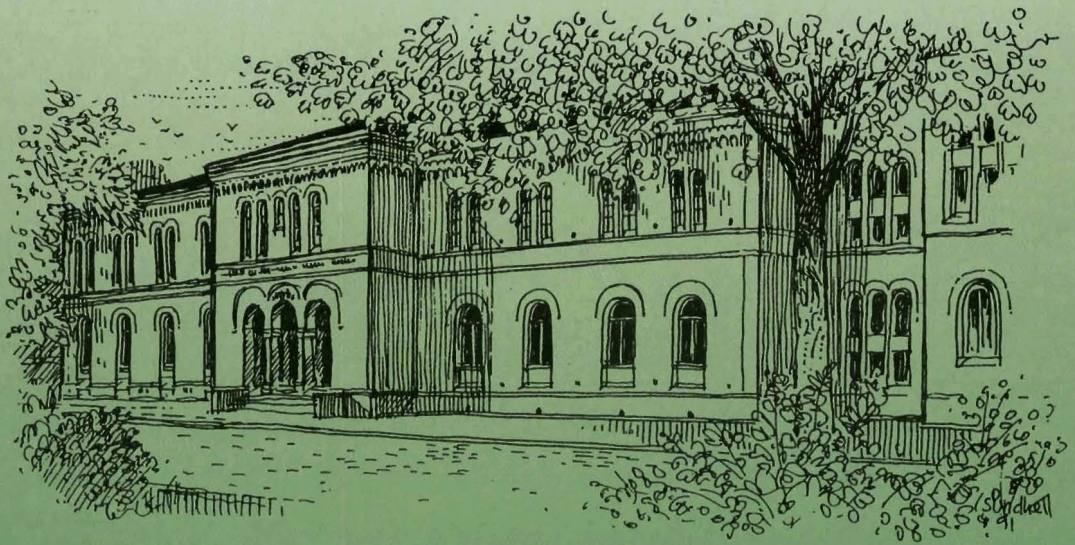
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