The liverworts (Bryophyta) of the Julmat Lammet Nature Reserve, central Finland

Rikkinen, Jouko

1992

Rikkinen , J 1992 , ' The liverworts (Bryophyta) of the Julmat Lammet Nature Reserve, central Finland ' , Memoranda Societatis pro Fauna et Flora Fennica , vol. 1992 , no. 68 , pp. 33-45 .

http://hdl.handle.net/10138/309685

unspecified
publishedVersion

Memoranda Soc. Fauna Flora Fennica 68:33-45. 1992

The liverworts (Bryophyta) of the Julmat Lammet Nature Reserve, Central Finland

Jouko Rikkinen

Rikkinen J., Department of Botany, University of Helsinki, Unioninkatu 44, SF-00170 Helsinki, Finland

Received 17 June 1991, accepted 29 August 1991

The liverworts reported from the Julmat Lammet Nature Reserve and its immediate vicinity in Saarijärvi, Central Finland, represent 18 families, 34 genera and 85 species. The diversity of the flora of the 2 km^2 study area is paralleled by the variety of substrates and ecological conditions. The rugged topography of the area, in places descending to the groundwater table, offers many ecological gradients relating to elevation, exposure and moisture. It appears that the chief factor responsible for the local richness of the present liverwort flora is the availability of microhabitats serving as refuges for a large number of species. Most of the hepatic species found in the area have a holoarctic, circumpolar distribution. Species new to the biogeographical province of North Häme (Tavastia borealis) are *Barbilophozia atlantica*, *Cephaloziella hampeana*, *Cephaloziella rubella*, *Cephaloziella subdentata*, *Diplophyllum obtusifolium*, *Harpantus scutatus*, *Geocalyx graveolens*, *Lophozia laxa*, *Lophozia obtusa* and *Marsupella sprucei*.

1. Introduction

The general features of the hepatic flora of Finland are fairly well known, but detailed studies are still lacking for most of the country. As a result, the distribution and ecology of many hepatic species within Finland is not very well understood (cf. Isoviita & Koponen 1967). The biogeographical province of North Häme (Tavastia borealis) is one area for which information is particularly scarce. Much of the province has been only superficially collected and additions to its hepatic flora can be expected as bryological exploration intensifies.

The bryophyte and lichen flora of the Julmat Lammet Nature Reserve and adjacent areas were studied in the summers of 1987–1990. The aim of this paper is to list the liverwort species recorded, to indicate their local frequency and to describe the habitats where they were most often found. Some historical factors possibly affecting the present day flora are briefly discussed. In the discussion special attention is given to some rare or rarely collected species. Similar studies on the moss and lichen floras will be published later.

2. Study area and its inventory

The area studied comprises the Julmat Lammet Nature Reserve (size 8 ha) and adjacent areas. It is about 2 km^2 in extent and is situated in the northern part of the commune of Saarijärvi (62° 46'N, 25° 09'E) in Central Finland (Fig. 1). Only a brief outline of the geomorphology and vegetation of the area will be given here. Readers requiring more details should consult Rikkinen (1988, 1989a, 1989b).

The area comprises a glacial connecting channel containing glaciofluvial material and featuring springwater ponds and extensive rock outcrops. The formation developed when a glacial river found its way into a bedrock fault as it circled round the supra-aquatic hill of Kelkkamäki (Rikkinen 1988). The fault assumes the proportions of a canyon in the middle part, and the glaciofluvial material which has accumulated on the valley floor provides a terrain of small-scale landforms. The glaciofluvial material varies in amount and grain size from one part of the valley to another, and the lowest parts of the valley extend down to the groundwater table, so that a number of ponds and mires have developed in them. The water which flowed through the valley at one time exposed the bedrock surface over extensive areas, so that there are now islands of exposed bedrock with steep walls of varying height and large accumulations of rocks and boulders in places (Figs. 1b and 2).

The fragmented terrain of the Julmat Lammet area offers a wide variety of habitats for vegetation. Thus the vegetation forms a diverse mosaic, in which can be found all the forest site types typical of Central Finland and many mire types. Some rich vegetation types which are otherwise rare in Saarijärvi (e.g. sloping grass-herb forests and eutrophic mires and fens) occur in the area. For a more detailed description and a map of the vegetation, see Rikkinen (1989a, 1989b).

The following list of species is based on field work done in the summers of 1987–1990. The local frequency of each species is mainly based upon subjective observations in the field. About 2000 specimens were checked microscopically. Seven frequency categories are used:

very rare (1–2 finds)
rare (3–10 finds)
occasional (11–20 finds)
frequent (21–40 finds)
fairly common (41–80 finds)
common (81–160 finds)
very common (more than 160 finds)

Several specimens of each taxon will be deposited in the Botanical Museum of the University of Helsinki (H). One representative specimen of each taxon is cited in the list. The collection numbers are those of the author.

The arrangement and nomenclature of families, genera and species follows Grolle, (1983) except for the genus *Chiloscyphus*, in which they follow Järvinen (1983). The nomenclature of intraspecific categories follows Koponen et al. (1977). The nomenclature of vascular plants follows Hämet-Ahti et al. (1986).

3. The list of species

Marchantiaceae

Marchantia polymorpha L. var. *polymorpha* — Occasional, but locally abundant on moist peat and soil in disturbed sites (7023).

M. polymorpha L. var. *aquatica* Nees – Rare, but locally abundant in some springs and streams. Various substrates, often partly submerged (7217).

Aneuraceae

Aneura pinguis (L.) Dum. — Frequent on and among *Sphagnum* in bogs and on peaty soil in various wet habitats. Abundant on a rich pine fen, on mud and among *Sphagnum* (7171).

Riccardia chamedryfolia (With.) Grolle — Occasional in permanently wet habitats, especially on the marshy shores of ponds where growing on the bases of culms of sedges and mud, usually submerged (8238).

R. latifrons (Lindb.) Lindb. — Fairly common on peat and rotten wood in damp to wet habitats, especially by springs and in bogs. Often along paths on compact, peaty soil which holds water well (7183).

R. palmata (Hedw.) Carruth. — Occasional on wet rotten logs, especially on the periodically flooded shores of ponds (9235).

Pelliaceae

Pellia epiphylla (L.) Corda — Found occasionally with *P. neesiana* on moist soil. Sterile,

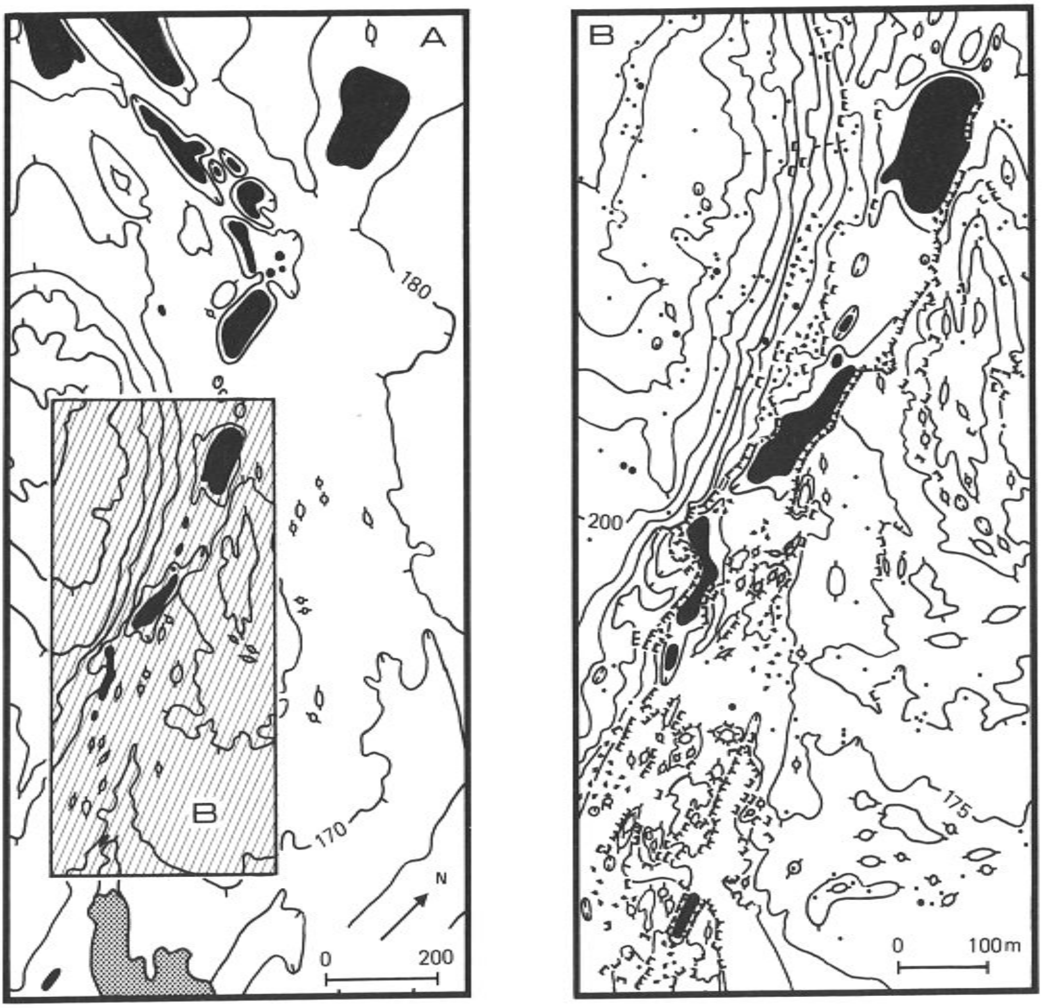

Fig. 1. General features of the study area. A. Major landforms of the study area. B. A more detailed map of the Julmat Lammet fault (only major cliffs and boulders are presented). C. The location of the study area. – Illustrations by the author.

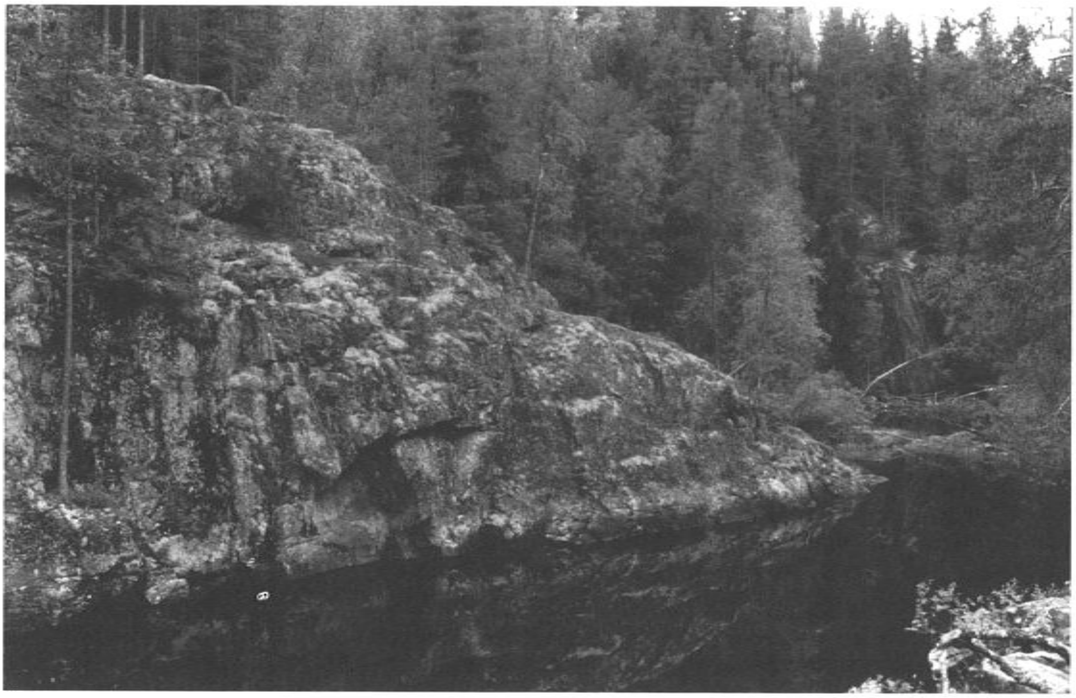

Fig. 2. High cliffs descending to water provide stable "refuges" for many liverwort species in the Julmat Lammet area. The open rock face in the foreground is suitable for a number of northern species, such as *Lophozia sudetica*, *L. wenzelii* and *Marsupella sprucei*. The more sheltered cliff in the background provides a habitat for many species that have a generally more southern distribution in Finland (e.g. *Geocalyx graveolens*, *Lejeunea cavifolia* and *Radula complanata*).

indeterminable plants of *Pellia* are common in the study area (7094).

P. neesiana (Gott.) Limpr. — Common on moist substrates in densly wooded habitats, especially by ditch and stream banks and around springs (7262).

Blasiaceae

Blasia pusilla L. — Occasional on clayey or sandy soils along shaded roadside banks and other disturbed sites. Especially abundant on compact clayey soil on the bottom of a large gravel pit in the southern part of the study area (8283).

Codoniaceae

Fossombronia foveolata Lindb. — Occasional, but locally abundant on the periodically flooded shores of ponds, where growing on peat, mineral soil and well-decayed wood (9159).

Lophoziaceae

Anastrophyllum hellerianum (Nees ex Lindenb.) Schust. — Occasional, but locally abundant on decorticated conifer logs and stumps in shaded and humid habitats (9049).

A. minutum (Schreb.) Schust. — Common on shady, intermittently dry rock faces and boulders, where growing on rock and in crevices filled by soil (7150).

A. saxicola (Schrad.) Schust. — Common on partly shaded, often dry cliffs and bolders, where growing on rock. Also on the rocky soil of steep talus slopes (7114).

Barbilophozia atlantica (Kaal.) K. Müll. — Very rare. On rotten wood on the occasionally flooded bank of a pond (9013).

B. attenuata (Mart.) Loeske — Common in sheltered sites with a reasonably constant, but not necessarily high moisture supply, such as on thin humus covering rocks and on decaying wood (7033).

B. barbata (Schmid. ex Schreb.) Loeske — Common on more or less shady stones and boulders. Also among other bryophytes on the ground in fresh heath forests and thin peat spruce mires (7045).

B. hatcheri (Evans) Loeske — Occasional in rather xeric, exposed places such as rock outcrops and gravel pits, where growing on rock and sandy soil (9131).

B. kunzeana (Hüb.) K. Müll. — Fairly common in moist places, mostly on peat or among other bryophytes in mires and around springs. Also on peaty soil covering seepage-moist cliffs (8043).

B. lycopodioides (Wallr.) Loeske — Fairly common in mesic, at least partly shaded sites, especially at the foot of cliffs and on steep, densely wooded slopes. Also among other bryophytes on the ground in fresh heath forests and spruce mires (8209).

Gymnocolea inflata (Huds.) Dum. — Very common on oligotrophic mires, especially in the flarks of wet fens, on *Sphagnum* and mud. Also in other habitats, such as along forest paths, on peat, mineral soil and rock (7037).

Lophozia ascendens (Warnst.) Schust. — Rare. Found only on decaying conifer wood in shaded and humid habitats (9023).

L. bicrenata (Hoffm.) Dum. — Common on dry clayey or sandy soil in more or less xeric, exposed situations such as on rock face terraces, forest paths, gravel pits (8221).

L. excisa (Dicks.) Dum. — Very rare. On clayey soil on an exposed roadside bank in the southern part of the study area (9077).

L. heterocolpos (Hartm.) Howe — Rare, but locally abundant on a steep, shady and moist slope in the central part of the study area. It grows among other bryophytes on wet peaty soil and seepage-moist rock (9148).

.*L. incisa* (Schrad.) Dum. — Occasional in shady and moist habitats, forming small, often pure carpets on rotten wood and on peat banks (7168)

L. laxa (Lindb.) Grolle — Very rare, but locally abundant on living *Sphagnum* on a pond shore fen in the northern part of the study area (9029).

L. longidens (Lindb.) Macoun — A frequent species on partly shaded to well-insolated, more or less dry cliffs (7249).

L. longiflora (Nees) Schiffn. — Frequent on decaying conifer wood. Much less common on other substrates such as peaty soil on cliff ledges (7004).

L. obtusa (Lindb.) Evans — Rare. Found a few times growing among other bryophytes on the ground in thin peat spruce mires (8034).

L. sudetica (Hüb.) Grolle — Fairly common on large, partly shaded rock faces. Growing on thin soil covering rock, often invading adjacent rock from crevices filled by soil (8152).

L. ventricosa (Dicks.) Dum. var. *silvicola* Buch — Common in various shady and mesic habitats, on thin humus covering rock, peaty soil and decaying wood (7072).

L. ventricosa (Dicks.) Dum. var. *ventricosa* — Not as common as var. *silvicola.* In similar habitats, most frequent on shady rock faces (7189).

L. wenzelii (Nees) Steph. — Frequent on open, well-insolated, but not too xeric rock faces in the central part of the study area (7023).

Tetralophozia setiformis (Ehrh.) Schljak. — Rare. On some boulders in the southern part of the study area, growing with lichens on bare rock and on thin humus covering rock in rather dry and strongly insolated sites (9037).

Tritomaria exsectiformis (Breidl.) Loeske — Very rare. Found growing on moist, well-decayed wood on a steep woody slope (8293).

T. quinquedentata (Huds.) Buch — Common on shady, moist cliffs and boulders, on rock or thin soil covering rock (8087).

Jungermanniaceae

Jungermannia caespitica Lindenb. — Occasional on clayey, sandy soil on ditch banks, on paths and other disturbed sites (9294).

J. leiantha Grolle — Occasional, but locally abundant on seepage-moist cliffs and adjacent peat banks in the central part of the study area. Also on decaying wood and peaty soil on the shores of a springwater pond (7141).

J. pumila With. — Very rare. On the side of a wet rock by a stream which runs through a small *Alnus glutinosa* mire (9053).

J. sphaerocarpa Hook. — Rare. On a peaty bank of a small springwater pool and on moist, clayey soil along shady forest paths (9057).

Mylia anomala (Hook.) S. Gray — Common in mires, especially on mire paths and high, fairly dry hummocks in poor bogs and fens. Growing mainly on and among *Sphagnum*, but also on bare peat (7129).

Nardia geoscyphus (De Not.) Lindb. — Occasional on shady forest paths and other disturbed sites, on damp clayey or sandy soil (9004).

Gymnomitriaceae

Gymnomitrion obtusum Lindb. — Very rare, but locally abundant on the basal part of a high cliff in the central part of the study area. On bare rock on a well insolated, fairly dry rock face near the shore of a pond (8340).

Marsupella emarginata (Ehrh.) Dum. — Frequent on rocks and cliffs descending into water, especially in periodically flooded rock crevices close to the average waterline (8840).

M. sparsifolia (Lindb.) Dum. — Rare. On steep, moist cliffs and rocks descending into water in the northern part of the study area (9029).

M. sphacelata (Lindenb.) Dum. — Very rare. On a steep and moist cliff descending into water in the northern part of the study area (9055).

M. sprucei (Limpr.) H. Bern. — Rare. On the upper parts of a high cliff in the central part of the study area. Limited to xeric, exposed rock and thin sandy soil covering rock. Forms minute patches or grows intermingled with *Andreaea rupestris* (8902).

Plagiochilaceae

Plagiochila asplenioides (Tayl.) Dum. — Rare. On soil and litter in the fresh deciduous forests in the northern part of the study area (8131).

P. porelloides (Nees) Lindenb. — Fairly common on shady, seepage-moist rock faces. Growing on rock and talus, often forming extensive, dense carpets (8382).

Geocalycaceae

Chiloschyphus polyanthos (L.) Corda var. *polyanthos* — Frequent in various moist habitats such as paludified forests, stream sides and wet ditches. On moist soil and litter (7203).

C. polyanthos (L.) Corda var. *fragilis* (A. Roth) K. Müll. — Very rare, but locally rather abundant in a spring and springwater stream running to a pond. Growing submerged or floating in water (7247).

Geocalyx graveolens (Schrad.) Nees — Occasional in shady moist places, especially on the occasionally flooded banks of a springwater pond. On peaty soil and decaying wood. Also on humus-covered ledges and among other bryophytes on shady, seepage-moist cliffs (8531).

Harpanthus flotovianus (Nees) Nees – Rare, but locally abundant on the banks of a springwater pond. On wet soil and peat, often partly submerged (7010).

H. scutatus (Web. & Mohr) Spruce — Very rare. On a large rotten log on a shady shore of a pond. Also in a thin peat spruce heath forest, where growing on the ground among other bryophytes (9014).

Lophocolea heterophylla (Schrad.) Dum. — Common in moist forests, especially in the northern part of the area. On decaying wood, among ground litter, on moist soil (7241).

L. minor Nees — Very rare. On a decorticated stump in a fresh deciduous forest in the northern part of the study area (8912).

Scapaniaceae

Diplophyllum obtusifolium (Hook.) Dum. — Occasional on forest paths and other disturbed sites, on sandy or peaty soil (9340).

D. taxifolium (Wahlenb.) Dum. — Occasional on partly shaded cliffs, often on thin layers of soil covering small ledges and crevices. Also on compact mineral soil along paths in rocky terrain (8122).

Scapania apiculata Spruce — Rare, but locally fairly abundant on the shady shores of four ponds. Restricted to rather large rotten logs subject to periodical flooding (9340).

S. curta (Mart.) Dum. — Rare, but locally abundant on compact, damp soil on the bottom of a large gravel pit in the southern part of the study area (9382).

S. irrigua (Nees) Nees — Fairly common in various wet habitats such as along streams, in swamps and on the peaty shores of ponds. Mostly on peaty soil and rotten wood (7138).

S. paludicola Loeske & K. Müll. — Occasional in wet swamps, where growing among *Sphagnum* and other mosses. Also on the occasionally flooded shores of ponds, on peaty soil (8461).

S. scandica (H. Arn. & Buch) Macv. — Very rare. Found on the shady base of a large boulder, where growing on bare rock (9063).

S. subalpina (Lindenb.) Dum. — Occasional in swiftly running streams and ditches. Often submerged, attached to rocks, tree roots or rotten wood (8340).

S. umbrosa (Schrad.) Dum. — Frequent on and along shady forest paths, on compact, peaty soil with high water retention. Also on decaying wood (8531).

S. undulata (L.) Dum. — Common in places similar to those of *S. subalpina*, but also in various other wet habitats such as mires and peaty shores (7158).

Cephaloziellaceae

Cephaloziella divaricata (Sm.) Schiffn. — Very common in a wide range of dryish to arid habitats, but also in mires. On peat, sandy or clayey soil, soil-covered rock, rotten wood and among other bryophytes (8461).

C. hampeana (Nees) Schiffn. — Occasional on moist decaying wood especially in mires and marshes. Also among other bryophytes on small humus-covered ledges of a shady, moist cliff (9311).

C. rubella (Nees) Warnst. — Fairly common in a wide range of moist to dryish habitats. On peat, soil, soil-covered rock and rotten wood (9254).

C. subdentata Warnst. — Rare. Among *Sphagnum* and other mosses on hummocks in pine bogs. Also on bare peat and rotten wood in similar habitats (9033).

Cephaloziaceae

Cephalozia bicuspidata (L.) Dum. — Very common in a wide range of mesic sites, such as shady forest paths, peat banks and mires. On moist peaty soil, decaying wood and among other bryophytes (7027).

C. connivens (Dicks.) Lindb. — Frequent on peaty hummocks and *Sphagnum* in mires, but also on peaty soil covering moist cliffs, on rotten wood and among other bryophytes (8280).

C. leucantha Spruce — Occasional, but locally abundant on the shady banks of ponds and in mires, on moist, decaying wood and peaty soil (9382).

C. loitlesbergeri Schiffn. — Occasional in mires, where growing among *Sphagnum*. Also on wet, rotten wood in similar habitats (9241).

C. lunulifolia (Dum.) Dum. — Very common on peaty soil, peat banks and decaying wood in moist habitats. Especially abundant on the compact peaty soil of shady forest and mire paths (8129).

C. pleniceps (Aust.) Lindb. — Rare. Among *Sphagnum* and other bryophytes in mires. Also on the wet, peaty banks of a pond (8079).

Cladopodiella fluitans (Nees) Buch — Occasional in wet, oligotrophic mires, where growing among *Sphagnum* and other bryophytes (8123).

Odontoschisma elongatum (Lindb.) Evans — Frequent on the shady shores of ponds, among other bryophytes on peaty soil and rotten wood (9158).

Lepidoziaceae

Lepidozia reptans (L.) Dum. — Common in various mesic habitats. On peaty soil, decaying wood and seepage-moist rock walls, often in rather deep shade (7049).

Calypogeiaceae

Calypogeia intergristipula Steph. — Common in a wide range of mesic habitats. Growing on moist soil, peat and decaying wood. Also in rock crevices and at the bases of boulders and rocks, often in deep shade (7053).

C. mulleriana (Schiffn.) K. Müll. — Very rare. On rotten wood in a swiftly running stream (8144).

C. neesiana (Mass. & Carest.) K. Müll. — Fairly common in shady habitats, on moist peaty soil, decaying wood and among other bryophytes (7185).

C. sphagnicola (H. Arn. & J. Perss.) Warnst. & Loeske — Fairly common in oligotrophic mires, where growing on *Sphagnum*, peat and wet rotten wood (8622).

Pseudolepicoleaceae

Blepharostoma trichophyllum (L.) Dum. — Very common in various shady habitats. On moist soil, decaying wood and on rock. Often among other bryophytes or sometimes forming small, pure patches (7223).

Ptilidiaceae

Ptilidium ciliare (L.) Hampe — Very common in a wide range of well-insolated and often fairly xeric sites. Among other bryophytes and lichens on rocks, decaying logs and sandy soil in dry to moderately dry heath forests (7238).

P. pulcherrimum (G. Web.) Vainio — Very common, especially in moist and shady habitats. On decaying wood and as an epiphyte on the trunk bases of *Betula pendula* and other trees. Also on bare rock (7236).

Radulaceae

Radula complanata (L.) Dum. — Rare, but locally abundant on some smooth, shady cliffs with considerable seepage. Also as an epiphyte on the trunk bases of two large *Populus tremula* trees in an old spruce forest (9392).

Lejeuneaceae

Lejeunea cavifolia (Ehrh.) Lindb. — Occasional on the large, seepage-moist rock faces in the central part of the study area. On smooth, wet rock and among other bryophytes (9374).

4. Some general remarks on the flora

The hepatic flora of the study area is largely composed of holoarctic, circumpolar species. This is readily understood in view of its location on the boundary between the southern boreal and middle boreal vegetation zones (Ahti et al. 1968). The flora includes 85 species, some of which are widespread and some of which are more restricted.

The main members of the hepatic flora are common forest and epilithic species, which are widespread throughout Finland as well as adjacent areas (e.g. *Blepharostoma trichophyllum*, *Cephalozia bicuspidata* and many species of the Lophoziaceae). However, a number of species, such as *Lophozia sudetica* and *Tetralophozia setiformis*, represent a distinctly northern element. On the other hand, species such as *Diplophyllum obtusifolium*, *Geocalyx graveolens* and *Riccardia chamedryfolia* have a generally southern distribution in Finland. The communities most diverse in northern species occur in rather extreme habitats, such as high rock walls and boulder outcrops of glaciofluvial origin. The southern element is best represented on moist, shaded cliffs and on shores and mire habitats.

Even when all habitats are taken together, hardly any hepatic species makes a significant contribution to the ground layer vegetation on a landscape scale. Most of the species do not grow in major landscape habitats; or if they do they grow in special microsites such as rocks and boulders or decaying logs. Hepatics are poorly represented in the ground layer of all forest site types in the study area. On the other hand, they do well in unstable and temporary habitats, where they may have a competitive advantage over vascular plants and forest mosses (cf. Studlar 1980). The semi-cultural grass-herb forests in the northern part of the study area are remarkably poor in hepatic species. Insufficient light together with abundant leaf litter may limit hepatic growth under dense vascular communities, although bare soil and sufficient moisture are present. *Lophocolea heterophylla* and *Plagiochila asplenioides*, however, seem to be specialists of this habitat.

Major disturbances of soil, for example by road widenings and gravel pits, creates suitable habitats for a number of ruderal species (e.g. *Blasia pusilla*, *Cephaloziella divaricata*, *Lophozia bicrenata*, *Marchantia polymorpha*). Some of these species associated with evidence of a high level of disturbance can also be found on forest paths, a major habitat for other low-growing "weedy" hepatic species in the study area (e.g. *Cephalozia bicuspidata*, *C. lunulifolia*, *Nardia geoscyphus*, *Scapania umbrosa*).

The high cliffs along the southern part of the Julmat Lammet fault are places of special interest. They show the greatest relief in the area (Figs. 1b and 2). Rugged topography offers a wide variety of environmental gradients relating to elevation, moisture and exposure. This in turn creates a high potential for a rich hepatic flora. A number of species grow in rather extreme habitats such as open, well-insolated rock faces and boulders. The flora is most diverse, however, on and around shaded, seepage-moist rock walls. Species diversity and total hepatic abundance both seem to be strongly correlated with slope steepness, moisture and ground-level light intensity, the latter two determined primarily by exposure together with vascular plant density and height. Because of their lack of soil, the rock walls generally support few vascular plants, but surrounding trees give some walls considerable shading. Many rock walls produce seepage, which keeps them moist during dry weather. In addition evaporation is reduced, since the walls are shaded by each other and by trees and other vascular plants. This shelter produces a microclimate which is cooler and moister in the summer than the surrounding areas. Most of the rock available for saxicolous hepatics in the area is granite or quartz porphyry and porphyrite (Wilkman 1938), bedrock elements which are not particularly favourable for demanding hepatic species. However, some of the seepage has at least slight mineral enrichment, which can be determined by the presence of meso-eutrophic species such as *Lophozia heterocolpos*.

With its 85 species, the hepatic flora of the Julmat Lammet area includes 40% of the Finnish flora (212 species in Koponen et al.1977). Many of the species now collected are either rare or have not been collected frequently. To the author's knowledge, the following ten have not been reported previously in the literature from the province of North Häme:

Barbilophozia atlantica
Cephaloziella hampeana
Cephaloziella rubella
Cephaloziella subdentata
Diplophyllum obtusifolium
Harpantus scutatus
Geocalyx graveolens
Lophozia laxa
Lophozia obtusa
Marsupella sprucei

Some others have been reported only once or twice (e.g. *Gymnomitrion obtusum*, *Scapania apiculata*, *Tritomaria exectiformis*). Some of these records are expected range extensions, which fill voids suggested by the presence of the species in neighbouring provinces (e.g. *Cephaloziella rubella*, *Lophozia obtusa*). The "rarity" of liverworts such as *Cephaloziella subdentata* and *Marsupella sprucei* is probably mainly due to undercollecting. These species have been largely overlooked because of their minute size. *Scapania apiculata*, however, is without a doubt a rare liverwort in Finland. In spite of some effort (S. Laaka, pers. comm.), it has previously been found only from three locations in the southern and central part of the country: Noormarkku Paasjärvi (St) 1937, Tampere Teisko (Ta) 1962 and Jyväskylä Koski (Tb) 1921 (Rassi et al. 1985).

The presence of *Barbilophozia atlantica* and *Lophozia laxa* in the study area marks a notable range extension for these species, as they generally represent a clearly coastal element in the hepatic flora of Southern Finland. *Barbilophozia atlantica* occurs mainly on the southern coast and in Lapland (Al–Ka, Om and Lk, Le, Li according to Buch 1936 and Arnell 1956). *Lophozia laxa* has previously been found in the provinces of Al, Nyl, Om and Le (Rassi et al. 1985).

5. Discussion

Several aspects of the occurrence of hepatics in such quantity in the study area, especially rare or rarely collected species, deserve discussion. The single most important factor explaining the high number of species is undoubtedly the geomorphological and physiographical diversity of the area. It includes many varied habitats and the hepatic flora is a reflection of this diversity of environments. Two features, however, are known to characterize all natural plant communities, they are dynamic and spatially heterogeneous in any scale of resolution (Söderström 1987). Population structures and the relative abundance of species change with time and local extinctions are common (e.g. Söderström 1987, 1990). Many of the hepatic species marked as being rare in the study area are species which are considered to be rare in other parts of Central Finland as well. Even within the study area they are often represented only by restricted local clones. Their restricted distributions suggest subtlety in microclimatic or other habitat requirements. As they exist only in small and scattered populations, their persistence would seem precarious. Small populations are known to be relatively sensitive to stochastic extinctions (e.g. Leigh 1981, Söderström 1987). They could easily disappear as a result of some environmental change. Against this background 85 species of liverworts occuring simultaneously in a 2 km^2 study area would seem somewhat peculiar.

The occurrence of a flora with many distinct elements within a very restricted geographical area suggests that a historical component should be sought as an explanation for this diversity. How does the present flora relate to post-glacial plant succession? Are some of the species recent arrivals, or are some of them relicts of a formerly more widespread flora? Past dispersal and disturbance could, indeed, be major factors explaining the species diversity and the present distribution pattern of some hepatic species in the area.

The persistence of relict species in the present-day flora would require refugia with unusually stable ecological conditions, e.g. microclimates similar to those of the past. In the Julmat Lammet area the high, steep rock walls facing open water have probably undergone the least climatic and vegetational change since deglaciation. Most of these cliffs are atleast partly supra-aquatic, in other words they have not been under water since the retreat of the continental ice sheet (Fig. 1b & 3). The uppermost shoreline in the general area has the present height of about 170 m above sea level. It was laid down around 9600 B.P. and marks the level of the Yoldia Sea immediately following the retreat of the ice sheet (Aartolahti 1972, Ristaniemi 1985, Rikkinen 1988). During the process of deglaciation, however, a local ice lake developed to the north of the Julmat Lammet area. For a short time it emptied its waters through the Julmat Lammet fault to the Yoldia Sea, located just south of the study area. At that time the water level in the fault reached the present height of 180 m or more (Rikkinen 1988). After the ice sheet had retreated further, the water level dropped and the flow through the channel stopped (Fig. 3). Since then most of the cliffs have been located above water. Not even a significant rise in the groundwater table in the moist Atlantic period (7500–4500 B.P.) can have flooded them. A rise of less than two metres in the water level would open a channel in the southern part of the fault through which water would flow out of the area (Fig. 3). In summary, it may be said that the cliffs in the Julmat Lammet area have been available for colonizing hepatics since the Preboreal period. This stretch of ca. 9500 years is a very long time by the standards of post-glacial Central Finland. Some northern, saxicolous liverworts, such as *Lophozia sudetica* and *Tetralophozia setiformis* may be expected to have colonized the cliffs soon after deglaciation. Since then, these early post-glacial immigrants may well have survived forest fires and other environmental changes in the refuge provided by high, vertical cliffs descending into water (Fig. 2).

Gymnomitrion obtusum has a southern distribution in Finland (Haapasaari 1966). This hepatic together with other southern species may have reached the Julmat Lammet area much later than the northern species. The only population of *G. obtusum* in the area is located on a high rock wall facing open water. There this species grows abundantly on an area of a few square metres. This very restricted distribution could be the result of a single event of diaspore immigration. Near its geographical distribution limits, *G. obtusum* is probably very narrow in its ecological demands. As a result it may have been unable to disperse further from the single location where its requirements are met. *Racomitrium lanuginosum* is another coastal bryophyte species whose distribution pattern in the study area is similar to that of *G. obtusum*. The question whether these restrictions in the present distribution are actually due to narrow ecological demands, coupled with an inability to disperse or compete with other species in suboptimal habitats, cannot be conclusively determined without autecological studies of the species in question.

There is no reason to belive that the location where *G. obtusum* grows, a sheltered but well-illuminated rock wall facing a springwater pond, has undergone any major climatic or vegetational change since the Atlantic period. At that time the climate in Central Finland would have been more suitable for the dispersal of southern and suboceanic bryophyte species. The majority of

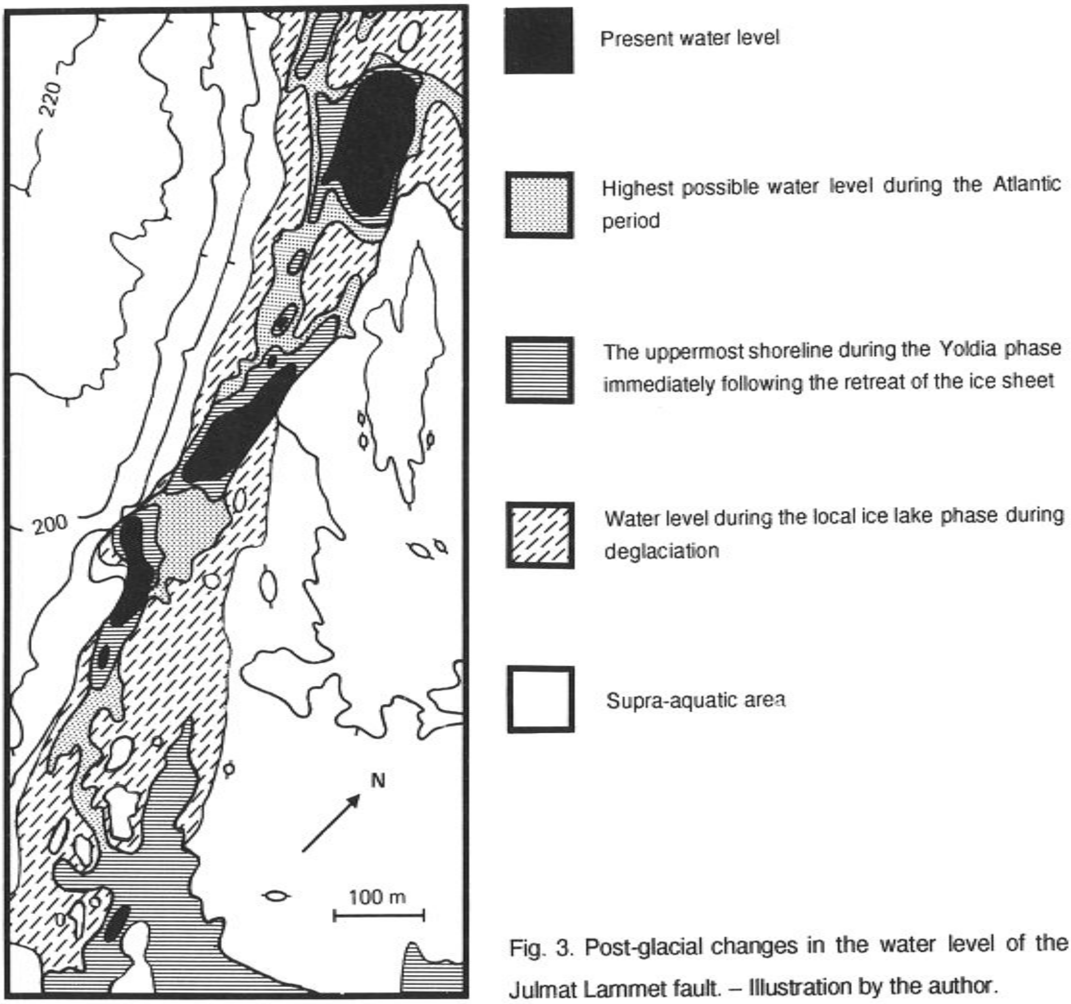

Fig. 3. Post-glacial changes in the water level of the Julmat Lammet fault. – Illustration by the author.

the other southern saxicolous, terricolous and muscicolous hepatics found in the Julmat Lammet area prefer shady cliffs with considerable seepage. These humid habitats support patches of azonal vegetation, and are known to be suitable for many northern bryophyte and lichen species as well (e.g. Laaka 1989).

The "relict" species growing on vertical rock walls can be said to occupy a relatively stable habitat. Many other hepatics are found in specialized, much less stable, habitats. In the study area *Cephaloziella hampeana*, *Harpanthus scutatus*, *Lophozia ascendens*, *Tritomaria exectiformis*, *Riccardia palmata*, *Scapania apiculata* and many more common species are mainly confined to decaying wood. The crucial factor affecting the local richness and abundance of epixylic hepatics is the availability of suitable decaying logs in a permanently moist and sheltered habitat (e.g. Söderström 1988a, 1988b). Many of these species have probably had their ranges greatly reduced by extensive logging, which has eliminated most of the moist, cool habitats in mature forests that they require. Previously, these mesic forest species may have been very sensitive to forest fires. In any restricted, homogeneous forest, they may have been easily eliminated by fire.

The Julmat Lammet area as a whole is not particularly rich in decaying logs. Most of the logs (and rare epixylics) are confined to two rather special habitats: steep hill slopes and periodically flooded shores of ponds. This leads one to suspect that the geomorphological processes active at these sites could be major factors explaining the large amount of decaying wood and the diversity of epixylic species found there. On steep slopes, particulate or mass movements will regularly lead to the fall of trees. In the study area this can be clearly seen around seepage-moist cliffs, where water probably plays a major role in dislocating trees. Most of the trees seem to fall in spring, which indicates that thawing of frozen ground could trigger many of these incidents. It is probable that the slopes in the Julmat Lammet area have provided a fairly constant supply of fallen logs in the past as well. On these unstable slopes the frequency of such incidents has probably been much higher than in neighbouring forests on level ground.

On the shores of ponds fluctuating water levels are probably the main cause of falling trees. The Julmat Lammet ponds show the present groundwater table in the area. Seasonal changes in groundwater levels can be seen as fluctuating levels in the ponds as well. Fairly regular flooding subjects trees growing close to the waterline to shore processes and a high risk of falling. In spite of their small area, some of the ponds are rather deep, e.g. the depth of the largest pond shown in Fig. 3 is 12 meters. There is no reason to believe that it has been dry at any time after deglaciation. Its shores have presumably provided a reasonably constant supply of fallen logs for hundreds or thousands of years. The large number of fallen logs on the bottoms of the ponds also point in this direction. A dendrochronological study of these submerged logs could offer valuable information on the availability of substrate for epixylics over a long time span (cf. Koutaniemi & Sillanpää 1985, Eronen & Kankainen 1986).

In summary, it may de said that due to its rugged terrain with many steep slopes, together with fluctuating water levels, the Julmat Lammet area has provided an unusually constant and reliable supply of the decaying logs required by epixylic hepatic species. At the same time, its dissected topography with its many ponds and mires has probably functioned as a natural fire break, providing many small refuges from local extinction during periods of treelessness.

6. Conclusions

It appears that within the region, the Julmat Lammet area may have acted as a "species trap" receiving different species at different times. The initial postglacial development of its hepatic communities depended on the immigration of propagules. It is generally accepted that hepatic spores and fragments can be carried long distances by wind. Accordingly, it can be assumed that the peripheral populations of some species, such as *Lophozia laxa*, could have migrated to the region from their main areas of distribution. However, there is no reason why the Julmat Lammet area should have been a more favourable target for dispersal than any other location in the region. The crucial reason for the local richness and abundance of its present-day flora would seem to be its ability to provide stable microhabitats serving as refuges for a number of demanding hepatic species. At the same time, it has provided an unusually constant supply of temporary habitats, such as decaying logs for epixylic species. The Julmat Lammet area represents a geographically fairly isolated formation, but large rock outcrops and deep ravines throughout Central Finland may have acted in the same manner. Without a doubt, the rock faces, springwater ponds, mires and diverse forests of the Julmat Lammet area provide a valuable reserve for rare and threatened hepatic species.

Acknowledgements: I wish to thank Prof. Timo Koponen, who read the manuscript and made suggestions for its improvement. I also wish to thank Sanna Laaka, M. Sc., for many inspiring discussions on liverwort ecology. Financial assistance from Societas pro Fauna et Flora Fennica is gratefully acknowledged.

References

Aartolahti, T. 1972: On the deglaciation in southern and western Finland. — Fennia 114:1–84.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5:169–211.

Arnell, S. 1956: Illustrated moss flora of Fennoscandia. I. Hepaticae. 2nd ed. — Swedish Natural Science Research Council, Lund. 308 pp.

Buch, H. 1936: Suomen maksasammalet [The liverworts of Finland]. — Otava, Helsinki. 116 pp.

Eronen, M. & Kankainen, T. 1986: Radiohiili-ikien rinnastamisesta kalenterivuosiin — milloin mänty hukkui Niskalampeen? (Comparing radiocarbon ages with calendar years — when did the pine drown in Niskalampi?). — Terra 98:68–71.

Grolle, R. 1983: Hepatics of Europe including the Azores: an annotated list of species, with synonyms from recent literature. — J. Bryol. 12:403–459.

Haapasaari, M. 1966: The genus Gymnomitrion Corda in Finland. — Ann. Univ. Turku Ser. A. II, 36:211–235.

Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. (eds.) 1986: Retkeilykasvio [A field guide to the flora of Finland]. 3rd ed. — Suomen Luonnonsuojelun Tuki Oy, Helsinki. 598 pp.

Isoviita, P. & Koponen, T. 1967: Suomen sammalkasviston tutkimuksen nykyvaiheesta. (The present stage of study of the Finnish moss flora). — Luonnon Tutkija 71:78–84.

Järvinen, I. 1983: Taxonomy and distribution of the European taxa of the genus Chiloscyphus (Hepaticae, Geocalycaceae). — Ann. Bot. Fennici 20:87–99.

Koponen, T., Isoviita, P. & Lammes, T. 1977: The bryophytes of Finland: An annotated checklist. — Flora Fennica 6:1–77.

Koutaniemi, Leo & Sillanpää, A 1985: Hukkunut mänty — Niskalammen turvekerrostumien avaintodistaja (A relict scots pine as a key to the origin of submerged peat deposits in Niskalampi). — Terra 97:153–163.

Laaka, S. 1989: Conostomum tetragonum (Musci, Bartramiaceae) in Eastern Fennoscandia. — Memoranda Soc. Fauna Flora Fennica 65:141–144.

Leigh, E. G. 1981: The average lifetime of a population in a varying environment. — J. Theor. Biol. 90:213–239.

Rassi, P., Alanen, A., Kemppainen, E., Vickholm, M. & Väisänen, R. 1985: Uhanalaisten eläinten ja kasvien suojelutoimikunnan mietintö III. Suomen uhanalaiset kasvit. — Komiteamietintö 1985(43):1–431.

Rikkinen, J. 1988: Pinnanmuotojen, mikroilmaston ja kasvillisuuden väliset suhteet Kalmarin–Saarijärven harjujaksolla. — Master's Thesis, Department of Geography, University of Helsinki. 128 pp.

— 1989a: Maksasammalkasvisto ja maksasammalvaltainen kasvillisuus Julmien lampien alueella Saarijärvellä, Keski-Suomessa. — Master's Thesis, Department of Botany, University of Helsinki. 59 pp.

— 1989b: Relations between topography, microclimates and vegetation on the Kalmari–Saarijärvi esker chain, Central Finland. — Fennia 167:87–150.

Ristaniemi, O. 1985: Keski-Suomen muinaisrannat. — Keski-Suomen seutukaavaliitto B (73):1–38.

Studlar, S. M. 1980: Trampling effects on bryophytes: trail surveys and experiments. — Bryologist 83:301–313.

Söderström, L. 1987: The regulation of abundance and distribution patterns of bryophyte species on decaying logs in spruce forests. — Dissertation, Department of Ecological Botany, University of Umeå. 144 pp.

— 1988a: Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. — Nord. J. Bot. 8:89–97.

— 1988b: The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. — Biol. Conserv. 45:169–178.

— 1990: Dispersal and distribution patterns in patchy, temporary habitats. — In: Krahulec, F., Agnew, A. D. Q., Agnew, S. & Willems, J. H. (eds.), Spatial processes in plant communities: 99–109.

Wilkman, W. W. 1938: Explanation to the map of rocks — Geological map of Finland 1:100 000, sheet C3 Kuopio.