

# Notes on the chemical and morphological variation of the lichen *Ophioparma ventosa* in East Fennoscandia

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The chemical compounds in 275 specimens of *Ophioparma ventosa* s. lat. from East Fennoscandia were analysed, resulting in three major chemotypes. They are: (I) thamnolic–divaricatic–usnic acid, (II) hypothamnolic–divaricatic–usnic acid, and (III) divaricatic–usnic acid. Chemotypes I and II are characterised by long, multiseptate spores, whereas chemotype III occurs as two morphotypes: (A) with long, multiseptate spores, and (B) with short, non-septate or 1-septate spores. The chemotypes with long, multiseptate spores represent the species *O. ventosa* (L.) Norman s. str., whereas *O. lapponica* (Räsänen) Hafellner & R. W. Rogers is the correct name for specimens of chemotype III-morphotype B. A tendency to a higher usnic acid-content and to more yellow thalli occurs especially in *O. lapponica* and in chemotypes II and III of *O. ventosa* growing in northernmost latitudes and at high altitudes. The distribution of *O. lapponica* and the chemotypes of *O. ventosa* in Finland is mapped.

Key words: chemotypes, East Fennoscandia, lichen, *Ophioparma*

## INTRODUCTION

Rogers and Hafellner (1988) reinstated the genus *Ophioparma* Norman, segregating it from *Haematomma* A. Massal. They recognized two species of *Ophioparma* in northern Europe, viz. *O. ventosa* (L.) Norman and *O. lapponica* (Räsänen) Hafellner & R. W. Rogers. Though the generic segregation has generally been accepted, there is considerable disagreement about the status of the species *O. lapponica*. The particular purpose of this paper is to study the variability of the *O. ventosa* complex in Finland, an area of considerable interest since *O. lapponica* was originally described from northern Finland.

Räsänen (1931: 67, 1933) recognised *Haematomma lapponicum* primarily on a chemical basis: its medulla is K<sup>-</sup> (i.e., it does not react in a spot test with KOH), while *O. ventosa* reacts K<sup>+</sup> yellow. The same difference can be observed with PD (p-phenylenediamine). Räsänen (1933) added a third variant, *H. lapponicum* var. *violascens* Räsänen (K<sup>+</sup> violet in the upper part of the medulla), to the complex. Räsänen also indicated a difference in spore size and structure, but Degelius (1937) could not detect any such difference in mature spores. James and Brightman in Purvis *et al.* (1992) again reported a difference in spore size, however. Most authors have distinguished *Ophioparma ventosa* and *O. lapponica* solely on a

chemical basis. The chemical compounds of these taxa have been identified and discussed by Solberg (1957), Thomson (1968, North American material), Hawksworth (1970, British Isles), Leuckert and Meinel (1981) and Kalb and Staiger (1995). Leuckert and Meinel (1981) analysed a large number of mainly European specimens (13 from East Fennoscandia) with several methods. Their results mainly confirmed the data obtained earlier: usnic, divaricatic, thamnolic and decarboxythamnolic acids but, as new compounds, hypothamnolic and psoromic acids were recorded. Decarboxythamnolic acid occurs as a minor satellite with thamnolic acid, whereas stenoporic or 4-0-demethyldivaricatic acids occur as minor satellites with divaricatic acid. They did not find barbatic acid and zeorin, reported by Thomson (1968). The K+ violet reaction, observed by Räsänen (1933) and Degelius (1937), is caused by hypothamnolic acid according to Asahina and Shibata (1954: 107) and Leuckert and Meinel (1981: 480). In the hymenium of apothecia and sometimes in adjacent areas of the medulla there occurs a red pigment, called haemoventosin (a naphthoquinone; Kalb & Staiger 1995). This conspicuous pigment, soluble in acetone, is diagnostic for the genus *Ophioparma* according to Rogers and Hafellner (1988).

## MATERIAL AND METHODS

Chemical and morphological studies were performed on approx. 285 herbarium specimens (275 from East Fennoscandia).

scandia). These were obtained from the Finnish herbaria H, OULU, TUR and TURA. The chemistry, i.e. the occurrence of secondary phenolic compounds, was analysed with one-directional and, in a few cases, two-directional thin-layer chromatography (Culberson 1972, Culberson & Johnson 1976, 1982, Skult 1984). The morphology was studied by microscope, emphasising general structure, colour of the upper cortex and type and dimensions of the ascospores. The general characters of *Ophioparma ventosa* s. lat. are adequately given by James and Brightman in Purvis *et al.* (1992: 416). Before spore measurements the apothecia were placed in KOH-solution.

## CHEMISTRY

My TLC-analyses are in full accordance with the very thorough investigation by Leuckert and Meinel (1981). The results of my TLC-analyses are briefly presented in Table 1.

The depside divaricatic acid is a constant substance in all specimens, accompanied by small quantities of some satellite compounds, such as stenoporic or 4-0-demethyldivaricatic acid (cf. Culberson *et al.* 1977, Culberson & Culberson 1976, Leuckert & Meinel 1981). The depside thamnolic acid is a constant compound in chemotype I. Decarboxythamnolic acid often occurs as a satellite compound with thamnolic acid, whereas it is lacking in specimens of chemotype II. Hypothamnolic acid occurs instead of thamnolic acid as a constant compound in chemotype II. The close chemical relationship between thamnolic and hypothamnolic acid has been pointed out by Leuckert and

Table 1. The compound combinations of the three major chemotypes of *Ophioparma ventosa* s. lat. in East Fennoscandia. Th. = thamnolic acid, Hyth. = hypothamnolic acid, Div. = divaricatic acid, Us. = usnic acid, Ps. = psoromic acid, At. = atranorin.

Compound combination	Number of samples	Major chemotype	% of total
Th.-Div.-Us.	132	I	67
Th.-Div.-Us.-At.	43		
Th.-Div.-Us.-Ps.	4		
Th.-Div.-Us.-Ps.-At.	1		
Th.-Div.	1		
Hyth.-Div.-Us.	21	II	8
Hyth.-Div.-Us.-Ps.	1		
Div.-Us.	57	III	26
Div.-Us.-At.	11		
Div.-Us.-Ps.-At.	3		
Div.-Us.-Ps.	1		

Meinel (1981), for instance; in the former there is an aldehyde group in the 3' position, in the latter a methyl group. Usnic acid in this material is a practically constant compound (totally absent from one specimen only, but often found in small quantities). This fact is in accordance with observations made by Leuckert and Meinel (1981: 478), who found only one specimen (from Sweden) without usnic acid, whereas the usnic acid quantities were sometimes extremely low (depending upon changes in the environment?). Also Hawksworth (1970) reported a chemotype lacking usnic acid in the British Isles. The depsidone psoromic acid was found in a small number of specimens in Finland, always as a minor compound and is therefore regarded as being without taxonomic value.

A rather unexpected compound in this taxon is atranorin, which according to Rogers and Hafellner (1988: 167–174) is diagnostic for the genus *Haematomma*, in contrast to *Ophioparma*. The presence of atranorin is perhaps caused by contamination (e.g., in the thick prothallus). In some specimens norstictic acid was also detected, probably likewise a result of contamination. The red pigment haemoventosin was observed in all fertile specimens. On the TLC-plates small spots of unidentified substances, including aliphatic acids, were also frequently observed. A compound of this group with low Rf-value occurs sometimes in all three chemotypes. In *Ophioparma handelii* (Zahlbr.) Printzen & Rambold, Printzen and Rambold (1996) reported the aliphatic compounds constipatic, protoconstipatic and dehydroconstipatic acids.

## MORPHOLOGY

Microscopical screening of the samples showed that the appearance of the thallus, independent of variety or chemotype, varies to some extent as a consequence of the kind of substratum. On hard rock with an even surface the thallus is frequently very discontinuous and often exhibits a thin prothallus. When growing on more porous rock the thallus is often rather compact, with a thick prothallus.

Attempts were made to seek relations between the chemotypes and four thallus colour categories: grey, grey with a yellowish tinge, yellow with a greyish (greyish green) tinge, and intensely yellow upper cortex (Table 2). Some data on approximate usnic acid contents are also given. I found that 45.2% of the chemotype I (*Ophioparma ventosa* s. str.) specimens are grey, and that no specimens fall into the category intensely yellow. In chemotype II (“*violascens*”) 57.9% are yellow with a grey tinge, whereas both other categories of yellow colour are represented by 15.8%. Chemotype IIIA (part of “*lapponica*”) exhibits specimens of all colour categories, but with the main point in the two middle ones. Of type IIIA, viz. the specimens mainly originating from Lapland, 11.5% are intensely yellow. Chemotype IIIB (the rest of “*lapponica*”) exhibits a high percentage, 69%, in the category intensely yellow, and no specimens in the category grey. A feature common to specimens with a markedly yellow colour is that they have largely been collected in the northernmost parts of East Fennoscandia. In these

Table 2. Colour and approximate usnic acid contents in thalli of chemotypes examined with regard to chemistry and spore type. The colour is estimated by eye in dried herbarium specimens (old specimens are omitted because changes of colour possible with age). Us = Usnic acid, scale 1–5 (averages). N = Number of specimens checked.

Colour	Chemotype			
	I (N = 42) <sup>1</sup>	II (N = 19) <sup>1</sup>	IIIA (N = 26) <sup>1</sup>	IIIB (N = 29) <sup>2</sup>
Grey	45.2%/Us 3.2	10.5%/Us 3.5	15.4%/Us 3.0	– / –
Grey with yellow tinge	26.2%/Us 3.5	15.8%/Us 2.7	34.6%/Us 3.3	3.4%/Us 2.0
Yellow with grey tinge	28.6%/Us 3.4	57.9%/Us 4.1	38.5%/Us 3.8	27.6%/Us 4.1
Intensely yellow	– / –	15.8%/Us 3.0	11.5%/Us 4.7	69.0%/Us 4.3

<sup>1</sup> Long-spored specimens.

<sup>2</sup> Short-spored specimens.

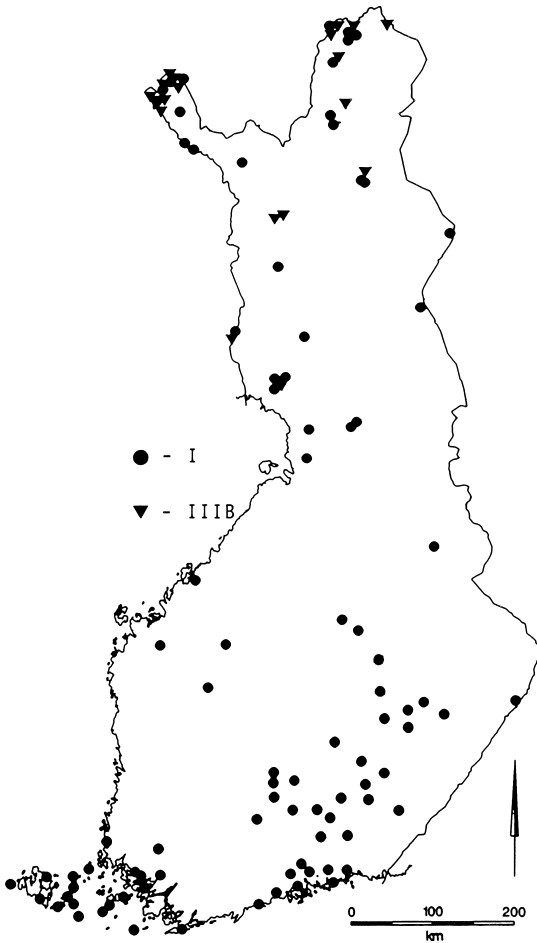


Fig. 1. The distribution of *Ophioparma ventosa* s. str. (chemotype I) and *O. lapponica* (Räsänen) Hafellner & R. W. Rogers (chemotype III B) in Finland, according to specimens examined.

specimens the usnic acid content is frequently rather high. However, even in Lapland there are grey thalli, but they probably do not belong to chemotype III B.

Spore dimension measurements were taken of selected specimens from several parts of the region, on the basis of chemical data obtained with TLC. The data from these measurements are grouped according to the chemotypes. I found that long, multiseptate spores are predominant in the East Fennoscandian material examined. Chemotypes I and II are totally lacking spores of the short, frequently aseptate type, whereas chemotype III exhibits spores of both types, but never in the same specimen (Table 3). These measurements correspond rather well to the data on specimen packets given by V. Räsänen on some specimens later analysed by me:

*Haematomma ventosum* (= chemotype I):  $41 \times 3 \mu\text{m}$ , septate. *H. lapponicum* var. *violascens* (= chemotype II):  $32\text{--}53 \times 4 \mu\text{m}$ , and  $46\text{--}49 \times 4.3\text{--}4.4 \mu\text{m}$ , 5-septate. *H. lapponicum*, chemotype IIIA:  $38\text{--}55 \times 4\text{--}6.5 \mu\text{m}$ , 5-septate, chemotype IIIB:  $12\text{--}21 \times 3.5\text{--}5.5 \mu\text{m}$ , simple.

A picture of the long multiseptate spore-type by *Ophioparma ventosa* s. str. is given by Rogers and Hafellner (1988: fig. 2), whereas the short, frequently aseptate spore-type is pictured by May (1997). An interesting fact: aseptate and  $\pm$  ellipsoid spores of chemotype IIIB show similarity to spores of the East Asian species *O. handelii* and *O. pseudohandelii* (Asahina) Printzen & Rambold (see Printzen & Rambold 1996).

#### GEOGRAPHICAL DISTRIBUTION IN EAST FENNOSCANDIA

The samples investigated were mapped according to the results obtained by TLC and spore measurements. Some data on the distribution of these taxa in Finland were earlier published by Leuckert and Meinel (1981: 486). My maps (Figs. 1 and 2)

Table 3. Spore dimensions of the chemotypes of *Ophioparma ventosa* s. lat. in East Fennoscandia. *N* = Number of specimens checked.

Chemotype	<i>N</i>	Spore dimensions, $\mu\text{m}$	Morphotype
I	33	(32)40–50(58) $\times$ 4.1–4.4	Multiseptate <sup>1</sup>
II	20	(32)41–52(58) $\times$ 3–4.4	Multiseptate <sup>1</sup>
IIIA	34	(31)40–55(60) $\times$ 3.5–5.8	Multiseptate <sup>1</sup>
IIIB	36	(12)14–20(26) $\times$ 3.5–4.5	Short, nonseptate to 1-septate <sup>2</sup>

<sup>1</sup> Spirally packed in ascus, when immature, spores with “tail”.

<sup>2</sup> Not spirally packed, spores without “tail”.

include only the locations in the Finnish part of East Fennoscandia. A few specimens from the Russian part were taken into consideration in the investigation but not mapped. The material mapped has been collected over a long period by a number of botanists. Despite that, large white regions can be seen on these maps. In some regions that reflects the real absence of *Ophioparma ventosa* s. lat., whereas in other areas field records are lacking. Chemotype I is distributed mainly in the SW, S, SE and northern areas (Fig. 1). Chemotype IIIB (with short spores) is restricted to the northern, arctic parts of Finland and adjacent regions in the east and west. Chemotype IIIA exhibits a geographical distribution rather similar to chemotype I, but with a lower number of locations (Fig. 2). Chemotype II (with hypothamnolic acid) is rare, and distributed in the N and W.

*Representative specimens examined.* — *Ophioparma ventosa* (L.) Norman: Chemotype I. **Finland.** *Alandia.* Brändö, Åva, 1988 *Alava* (TUR 49322); Eckerö, Signildskär, 1951 *Nordström* (H); Kumlinge, Seglinge, 1991 *Skytén* (H). *Regio aboensis.* Korppoo, Lohm, 1962 *Kärenlampi* (TUR 16366); Hiittinen, Vänö, Stubbö, 1963 *Ravanko* (TUR 16351). *Nylandia.* Pyttis, Mogenpörtö, 1941 *Fagerström* (H); Sipoo, Träskby, 1971 *Vänskä* (H); Askola, Rahikko, 1992 *Haikonen* (H). *Tavastia australis.* Kuhmoinen, Päijälä, 1991 *Haikonen* (H); Hollola, Luhdantausta, 1989 *Haikonen* (H); Anttola, Hiidenmaa, 1983 *Vitikainen* (H); Taipalsaari, Kuhala, 1964 *Vitikainen* (H). *Savonia borealis.* Leppävirta, Laitilanniemi, 1990 *Haikonen* (H). *Ostrobottnia media.* Alajärvi, Käärme kallio, 1907 *Backman* (H). *Ostrobottnia borealis ultima.* Kemi, Kivalot, Ylipenikka, 1945 *Räsänen* (H); Simo, Kivalot, Alapenikka, 1924 *Räsänen* (H); Ylitornio, Alkkula, Aavasaksa, 1915 *Räsänen* (H); Rovaniemi, Ounasvaara, 1920 *Räsänen* (H). *Laponia kittilensis.* Kittilä, Lohiniva, 1995 *Väre & Halonen* (OULU). *Laponia enontekiensis.* Maunu, Vikkurinvaara, 1939 *Roivainen* (H); Porojärvet, Toskalharji, 1955 *Henssen* (H); Kilpisjärvi, Ailagavaara, 1967 *Vänskä* (H). *Laponia inarensis.* Utsjoki, "Kevonjoenlaakson pohjoisin osa", 1965 *Laine* (TUR 16336), SW of Nuvvos-Ailigas, N part of Rusjokoalgi, 1990 *Mäkinen* (TUR 46061); Inari, Seävnulvaara, 1970 *Vitikainen* (H), Laanila, Laaninselkä, 1967 *Vitikainen* (H). **Russia.** *Laponia petsamoensis.* Maattivuono, Petrinpahta, 1939 *Räsänen* (H), Porovaara, 1931 *Räsänen* (H), Peuravuono, 1931 *Räsänen* (H). *Laponia Imandrae.* Porya Guba, 1861 *Selin* (H). *Exsiccata.* Lichenoth. Fenn. 886 (H), 173 (OULU, TUR), 472 (OULU, TUR).

**Chemotype II. Finland.** *Satakunta.* Kankaanpää, Venesjärvi, 1935 *Laurila* (H, TUR 16359). *Ostrobottnia australis.* Lapua, Simsiö, 1920 *Räsänen* (H). *Laponia sompiensis.* Savukoski, 1994 *Soppela* (OULU). *Laponia enontekiensis.* Kilpisjärvi, W-Saana, 1947 *Huuskonen* (OULU, TUR 16374); S-Haltia, 1948 *Huuskonen* (H); Porojärvet,

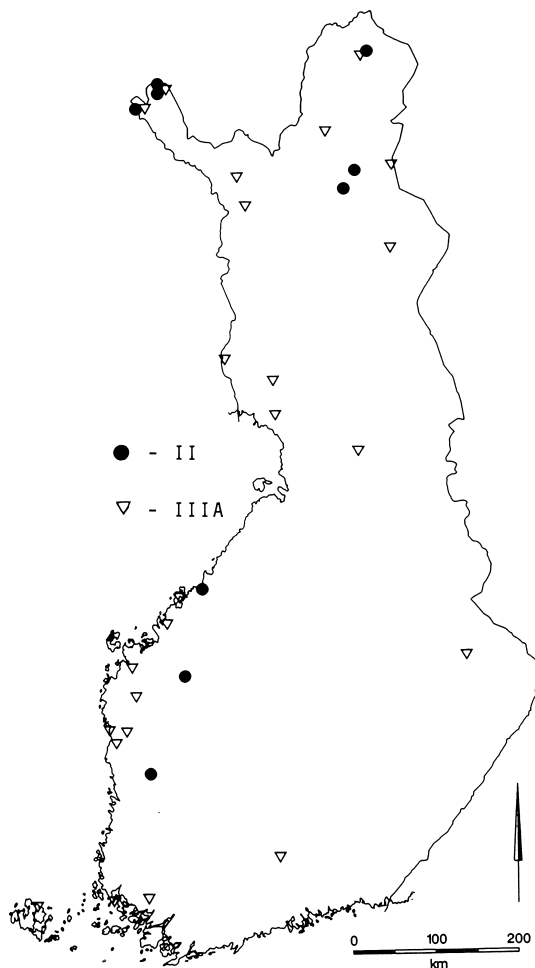


Fig. 2. The distribution of *Ophioparma ventosa*, chemotype II (hypothamnolic) and chemotype IIIA (thamnolic lacking) in Finland.

Toskalharji, 1955 *Henssen* (H). *Laponia inarensis.* Utsjoki, "Akshunjunista SO-tunturi", 1958 *Kallio* (TUR 16339), Kuorboavi, 1960 *Kallio et al.* (TUR 16386). **Russia.** *Laponia petsamoensis.* Kalkuoavi, 1938 *Räsänen* (H); Salmijärvi, Kaulatunturi, 1931, 1938 *Räsänen* (H). *Laponia ponojensis.* Orlov, 1889 *Kihlman* (H). *Laponia Imandrae.* Porya Guba, 1861 *Selin* (H). *Exsiccata.* Lich. Fenn. Exs. 402 (H, TUR 16340).

**Chemotype IIIA. Finland.** *Alandia.* Saltvik, Orrdalsklint, 1909 *Florström* (TUR 16370). *Regio aboensis.* Lieto, "kirkon pohjoispuolella", 1963 *Kärenlampi* (TUR 16350); Merimasku, 1860 *Karsten* (H). *Ostrobottnia australis.* Lappfjärd, Pyhävuoren NW-pää, 1968 *Vitikainen* (H); Jurva, 1859 *Malmgren* (H); Mustasaari, sairaala, 1953 *Suominen* (H, TUR 16377); Kristinestad, vid gymnasiet, 1959 *Klingstedt* (H). *Ostrobottnia media.* Uusikarleppey mlk, Bonäs, 1968 *Vitikainen* (H); Luoto, Holm, 1959 *Ahti* (H). *Ostrobottnia borealis.* Pudasjärvi, Sotkajärvi, 1965 *Takala* (OULU);

Tervola, Kätkävaara, 1995 *Väre*, Halonen & Soppela (Oulu). *Karelia borealis*. Pielisjärvi, Koli, Ukko-Koli, 1948 *Leppälä* (TUR 5653). *Lapponia sompiensis*. Savukoski, Ortsavaara, 1961 *Ulvinen* (OULU); Muonio, Pallastunturi, 1991 *Väre* (OULU). *Lapponia enontekiensis*. Ounasvaara, Pyhäkero, 1936 *Räsänen* (H). *Lapponia inarensis*. Inari, N of Rajajooseppi, 1972 *Mäkinen* (TUR 37874); Utsjoki, Kuorboaivi, 1960 *Kallio et al.* (TUR 16386). **Russia**. *Lapponia petsamoensis*. Trifona, Isotunturi, 1931 *Räsänen* (H), Mattert, 1931 *Räsänen* (H), Maattivuono, 1931 *Räsänen* (H). *Exsiccata*. Lichenoth. Fenn. 395 (OULU).

*Ophioparma lapponica* (Räsänen) Hafellner & R. W. Rogers (= chemotype IIIB): **Finland**. *Lapponia enontekiensis*. Guonjorvoorri, 1951 *Huuskonen* (H); Haltia, 1948 *Huuskonen* (OULU); Marfivaari, 1956 *Huuskonen* (Oulu); Ridni, 1955, 1958 *Huuskonen* (OULU, TUR 16341, 16347); Saana, 1947, 1948 *Huuskonen* (H, OULU); Terbmisvaari, 1957 *Huuskonen* (OULU); Toskalharji, 1955 *Huuskonen* (OULU); Urtasvankka, 1955 *Huuskonen* (TUR 16343, 16345). *Lapponia inarensis*. Inari, Kaunispää, 1921 *Räsänen* (TUR 16384); Toarpumoaivi, 1880 *Hult* (H); Utsjoki, Njaggalpahtat, 1955 *Laine* (TUR 16383), Kistuskaidi, 1956 *Mäkinen* (TUR 16335, 16337, 16338), Loktavaara, 1961 *Parviainen* (TUR 16344), Paðos, Risnjarvarri, 1906 *Rancken* (H), Kultala, 1974 *Ahti* (H). *Lapponia kittilensis*. Kittilä, Levitunturi, 1936 *Räsänen* (H), Pyhätunturi, 1912 *Häyrén* (H). *Ostrobottia borealis ultima*. Ylitornio, Alkkula, Aavasaksa, 1915 *Räsänen* (H); Kemi, Kivalot, Ylipenikka, 1945 *Räsänen* (H). **Russia**. *Regio kuusamoensis*. Salla, Vuosnatunturi, 1937 *Lehtonen & Pankakoski* (H). *Lapponia Imandrae*. Umba, 1892 *Kihlman* (H). *Lapponia petsamoensis*. Trifona, 1931 *Räsänen* (H), Karapleka, 1938 *Räsänen* (H), Kaulatunturi, 1938 *Räsänen* (H), Kalkuoaivi, 1938 *Räsänen* (H). *Lapponia tulomensis*. Nuortijaur, 1883 *Hollmén* (H). *Exsiccata*. Lich. Fenn. Exs. 61 (H, TUR 16346), Lichenoth. Fenn. 473 (TUR), 1232 (TUR 16347).

## DISCUSSION

The material in this study is rather homogeneous in a morphological sense. The main part represents samples with long, multiseptate spores (*ventosa*-type). In the northern parts of East Fennoscandia another type with short, aseptate or 1-septate spores (*lapponica*-type, according to P. F. May, pers. comm.) is also found. Three chemotypes are distinguished: (I) Thamnolic–divaricatic–usnic acid chemotype (corresponding *Ophioparma ventosa* s. str.), (II) Hypothamnolic–divaricatic–usnic acid chemotype (“*violascens*”), and (III) Divaricatic–usnic acid chemotype (= *Haematomma lapponicum* Räsänen s. orig.). These chemotypes seem to have very similar requirements with respect to the environment, sometimes grow-

ing side by side on exposed siliceous rocks at elevations from approx. 15 m to approx. 1 000 m.

The question concerning the “true” spore type or types of *Ophioparma lapponica* has until now been unclear. The reports by Räsänen in his papers (1931, 1933) and on his herbarium labels are somewhat contradictory. Through new findings and studies by P. F. May (pers. comm.) the problem is being solved. May reports some 10 specimens of the short-spore type from northern Fennoscandia. I have examined about 30 specimens of this type from Finnish Lapland and adjacent areas in Russia. The traditional *O. lapponica* in fact encompasses two morphotypes with similar chemistry (divaricatic–usnic acid): a multiseptate, long-spored, and an aseptate to 1-septate short-spored type. According to May (1997), specimens of the latter type represent *Ophioparma lapponica* s. str.

This study has shown that the question about the real character of var. *violascens* (= chemotype II) was already solved by Leuckert and Meinel (1981) through their finding that hypothamnolic acid in this taxon occurs as a diagnostic compound instead of thamnolic acid. Räsänen (1933) placed var. *violascens* under *Haematomma lapponicum* and Santesson (1993) also synonymised *violascens* with *O. ventosa* “var. *lapponica* (Räs.)”. But on morphological grounds, from the fact that var. *violascens* exhibits spores of the *ventosa*-type only (observations made by May as well as me) this taxon belongs to *O. ventosa* rather than to *O. lapponica* (= chemotype IIIB).

The close chemical relationships between thamnolic and hypothamnolic acids are shown by Huovinen and Ahti (1992: fig. 5). But it seems difficult to decide whether the thamnolic acid chemotype (I) is older in an evolutionary sense than the hypothamnolic acid chemotype (II), or vice versa. An explanation could be that chemotype II through a small mutation was produced from chemotype I, separately in several locations. In view of the fact that the number of known locations for chemotype II in East Fennoscandia is very low, compared with the high frequency for chemotype I, my opinion is that chemotype II represents a secondary strain.

Santesson (1993) synonymised v. *subfestivum* (Nyl. ex Cromb.) Zahlbr. with *Ophioparma ventosa* (L.) Norman, an opinion confirmed by me through spore analyses of two specimens in H-

NYL (no. 24231: Scotia, 1868 Crombie, type, and no. 24226: *Lapponia orientalis*, 1861 Selin). These specimens exhibit multiseptate, long spores of the ventosa-type and a "ventosa-chemistry".

In my opinion, the species *Ophioparma ventosa* is morphologically a homogeneous taxon, comprising three major chemotypes. They all share long, multiseptate spores of the ventosa-type and some degree of variability of the thallus structure (related to the substratum) and colour (possibly related to climatic factors).

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