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The Parmelia omphalodes (Ascomycetes) complex in Eastern Fennoscandia

Chemical and morphological variation

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Wide chemical variation was shown by *Parmelia omphalodes* (L.) Ach., especially when minor and accessory phenolic compounds were included. Three subspecies are recognized within *P. omphalodes*, viz. subsp. *omphalodes*, subsp. *pinnatifida* (Kurok.) Skult, comb. nova, and subsp. *discordans* (Nyl.) Skult, comb. nova. A fourth subspecies may possibly be separated in the arctic regions. Although the subspecies are usually clearly distinguishable, in certain areas where their ranges overlap specimens can be found which are intermediate in chemistry and/or morphology. The populations of *P. omphalodes* in the southwest of Finland are particularly variable, since all three subspecies meet in that region. The distribution of each subspecies in Eastern Fennoscandia is mapped.

Key words: lichen, *Parmelia*, chemical variation, phenols, Eastern Fennoscandia

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I. INTRODUCTION

For many years lichen chemistry has played a major role in solving taxonomic problems. Good examples of such lichenological studies in the genus *Parmelia* are W.L. Culberson's (1973) work on the *Parmelia perforata* group and Esslinger's (1977) study on the brown *Parmeliae.*

The lichen-forming ascomycete *Parmelia omphalodes* (L.) Ach. is a widespread saxicolous species in the northern hemisphere. Its morphological variability was noted as early as 1803 by Acharius, when he recognized var. *panniformis* under it. Mainly on chemical grounds, Nylander (in Brenner 1886) separated a new species, *P. discordans* Nyl., from the *P. omphalodes* complex. W.L. Culberson (1970) accepts this species, whereas several other taxonomists, e.g. Magnusson (1919, 1929), Hillmann (1936), Poelt (1969), Krog (1971), Dahl & Krog (1973) and Krog et al. (1980), merely treat *P. discordans* as a variety of

Parmelia omphalodes. Recently, Kurokawa (1976) proposed that *P. omphalodes* be split into three species: *P. omphalodes* s. str., *P. pinnatifida* Kurok. and *P. discordans* Nyl. However, Kurokawa left some questions unanswered, e.g. to what extent is the delimitation of these new species supported by discontinuities in the chemical variation of the group, and are the diagnostic morphological characters really constant?

Attention will be paid here to the following points:

1. The occurrence and relative abundance of the chemical constituents (chiefly secondary phenolic compounds).
2. The frequencies of the different constituent classes in different regions of Eastern Fennoscandia (mainly Finland).
3. The chemical strains and their distribution.
4. Possible correlations between the chemistry and morphology.
5. Taxonomic and nomenclatural considerations.

II. MATERIAL AND METHODS

The study is mainly based on herbarium specimens, complemented with new samples from about 70 localities (collected by the author). The material is from the following herbaria (for the symbols, see Holmgren et al. 1981): H (incl. H-ACH, H-NYL), TUR, TURA, OULU and UPS. About 1 000 specimens were examined. Of these 490 were used for morphological measurements, and small pieces were taken from 670 for chemical analysis. Beside these specimens from Eastern Fennoscandia, samples were studied from Scandinavia, Western and Central Europe, Siberia, Central Asia, Japan, Madeira and North America.

Chemistry

The methods used were the standard techniques for thin-layer chromatography (TLC) presented by Culberson & Kristinsson (1970), Culberson (1972, 1974), and Culberson & Amman (1979).In solvent B benzene was replaced by toluene. The TLC analyses were first (33% of samples analysed) performed with the standard solutions A, B, C, later with the solutions B, C and G (in some instances with B and G only). For separation of some low-Rf compounds the two-dimensional TLC method, outlined by Culberson & Johnson (1976), and Culberson et al. (1981), was used. The solution G used in the last-named study, was thus also used here for one-dimensional analyses. Microextraction was performed upon thallus fragments using warm acetone (+45 ±4 °C) for three 10-min. periods. The acetone extracts were collected in small Petri dishes, and applied to the plates with graded micropipettes. The plates (Merck Silica Gel F 254 precoated glass plates) were examined before and after development (10% H_2SO_4 and +110 °C) under long- and short-wave UV light.

To indicate the quantity of each substance on the TLC plates the approximative scale 0–5 was used (the degree was determined from spot size and colour intensity): 1 = faint traces, 2 = traces, 3 = rather scarce, 4 = moderate, 5 = abundant.

Morphology

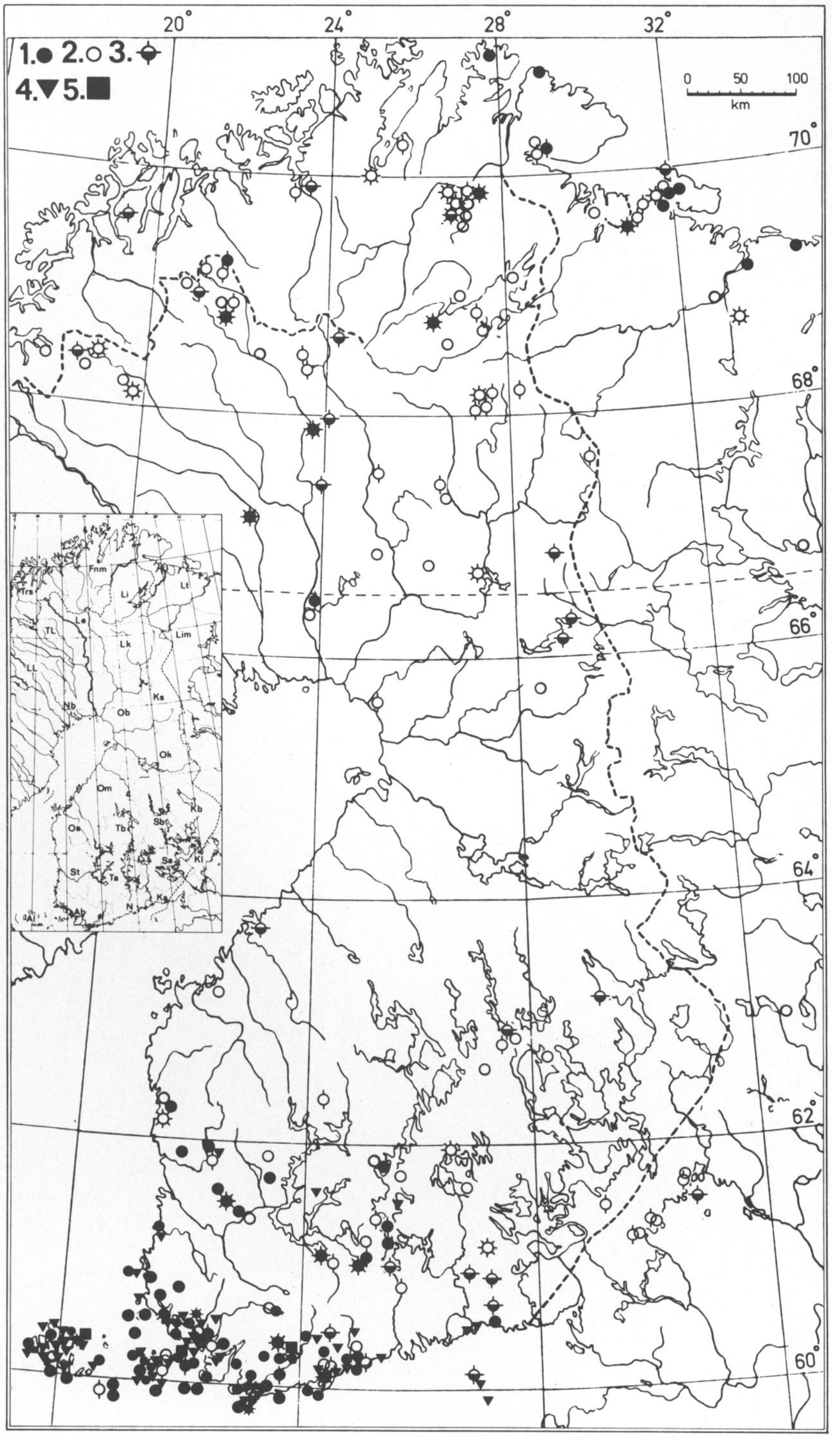
Measurements and observations of morphological characters of potential taxonomic value were made on individuals collected from four regions of Eastern Fennoscandia (Figs. 1 and 8). The following characters were chiefly scored: maximum and minimum lobe width, dominant lobe width, profile of upper cortex (convex/ concave), upper cortex glossy or dull (periphery/ central parts), pseudocyphellae laminal and/or marginal (abundant/sparse/absent), apothecia (present/absent), pycnidia (present/absent). The morphological characters were scored independently of the chemical ones to avoid introducting a bias into the data.

Observations were made partly under an Olympus dissecting microscope, partly under a Wild M 5 dissecting microscope. Photomicrographs were taken with a Nikkormat camera, adapted to Wild M 5. Observations of the ultrastructure were made with an ISI Mini-SEM electron microscope.

Cluster analysis

Several procedures for numerical classification are now available (Sneath & Sokal 1973). The use of such classification has been tested in similar work, e.g. the studies by Sheard (1978a, 1978b) on the *Ramalina siliquosa* species aggregate. The computer program used in the present study was that for cluster analysis of cases (BMD/P2M), designed by Engelman (1979). P2M forms clusters based on the Euclidean distance (the square root of the sum of squares of the difference between the values of the variables for two cases), and joins cases and/or clusters of cases in a stepwise process until all cases are combined into one cluster. The outputs, in the form of dendrograms, give a picture of the existing chemical combinations and their relations to each other. The data work was done on a UNIVAC 1100 computer at Åbo Akademi.

Fig. 1. The distribution of *Parmelia omphalodes* s. lat. in Eastern Fennoscandia, according to samples analysed. 1: subsp. *omphalodes*, 2: subsp. *pinnatifida*, 3: intermed. of 1 & 2, 4: subsp. *discordans*, 5: intermed. of 1 & 4.—Symbols: 1, 1b, 1c = Sa-, Lo-, PL-rich specimens; 2, 2b, 2c = Sa-rich, Lo-lacking specimens; 3 = intermed. of 1 & 2; 4 = Pr-rich specimens; 5 = intermed. of 1 & 4. For further explanations, see the text. The biogeographic provinces (abbreviated) in the inset. →



(*Fig. 1*)

Study area

The material studied is mainly from Eastern Fennoscandia, especially Finland. For cluster analysis the material was grouped into the following four regions (those in Finland without indication of the country):

1 = Al (Alandia)
2 = Ab (Regio aboensis), N (Nylandia), Ka (Karelia australis, partly in the U.S.S.R.), St (Satakunta)
3 = Ta (Tavastia australis), Sa (Savonia australis), Kl (Karelia ladogensis, the main part in the U.S.S.R.), Oa (Ostrobottnia australis), Tb (Tavastia borealis), Sb (Savonia borealis), Kb (Karelia borealis), Kon (Karelia onegensis, U.S.S.R.), Om (Ostrobottnia media)
4 = Ok (Ostrobottnia kajanensis), Ob (Ostrobottnia borealis), Ks (Regio kuusamoensis), Lk (Lapponia kemensis), Lim (Lapponia imandrae, U.S.S.R.), Le (Lapponia enontekiensis), Li (Lapponia inarensis), Lt (incl. Lps; Lapponia tulomensis, U.S.S.R.), Lm (Lapponia murmanica, U.S.S.R.), Nrd (Nordland, Norway), Fnm (Finnmark, Norway)

Samples from the following provinces were mapped, but excluded from cluster analysis: Trs (Troms, Norway), Nb (Norrbotten, Sweden), LL (Lule Lappmark, Sweden), TL (Torne Lappmark, Sweden). The provinces are given on the map in Fig. 1, the regions in Fig. 8.

Key to the symbols used for specimens in dendrograms and other figures (see Fig. 6):

1 = *P. omphalodes* subsp. *omphalodes*: typical specimen, 1b = specimen with one to a few 'pinnatifida' characters, 1c = specimen with a greater number of such characters.
2 = *P. omphalodes* subsp. *pinnatifida*: typical specimen, 2b = specimen with one to a few 'omphalodes' characters, 2c = specimen with a greater number of such characters.
3 = Specimen 'intermediate' between subsp. *omphalodes* and subsp. *pinnatifida* (e.g., *pinnatifida* in morphological sense, but *omphalodes* in chemical sense).
4 = *P. omphalodes* subsp. *discordans.*
5 = Specimen 'intermediate' between subsp. *omphalodes* and subsp. *discordans* (especially with respect to the compounds salazinic and protocetraric acid: observed in approx. equivalent amounts).

Abbreviations used in text, tables and figures:
At = atranorin
CN = connorstictic acid
Csa = consalazinic acid
Fa-2 = unknown fatty acid '2'
Fa-3 = unknown fatty acid '3'
Fu = fumarprotocetraric acid
Ga = galbinic acid
Lo = lobaric acid
L = laminal pseudocyphellae
M = marginal pseudocyphellae
N = norstictic acid
omp-1 = unknown yellow-brown compound
omp-2 = unknown orange (-yellow) compound
omp-3 = unknown pink compound
PL = protolichesterinic acid
Pr = protocetraric acid
Sa = salazinic acid
Ufa = unknown fatty acids in general (incl. Fa-2 and Fa-3)

Table 1. *TLC data for compounds found in the Parmelia omphalodes complex.* The number preceding the virgule (/) is the Rf × 100 value of the compound; those after the virgule are the Rf × 100 values of control substances Fu (in G only), N and At on the same plate. Fa-2, Fa-3 = unknown fatty acids, omp-1, omp-2, omp-3 = unknown phenolic compounds. Numbers after Protocetraric ac. (Pr)

Rf classes				Compound and usual abundance		RF × 100 values				Average spot colour after H_2SO_4 and heat
A	B	C	G			A	B	C	G	
2	2	2	2	Salazinic ac. (Sa)	5(0)	13/46,84	8/29,71	4/29,85	29/63,93	orange-yellow
2	3	2	2	Protocetraric ac. (Pr)	1–2(5)	5/47,83	19/29,81	6/28,85	32/63,93	dark grey-lilac
3	5	5	3(4)	Lobaric acid (Lo)	3–5(0)	39/47,83	44/29,71	45/28,85	59/63,93	pale green
3	5	5	3(4)	Protolichesterinic acid (PL)	3–5(0)	43/49,87	44/29,71	44/28,85	59/63,93	opaque (H_2O)
4	5	5	3	Fa-2	3–4(0)	47/49,87	49/34,71	48/28,85	55/63,93	—"—
5	6	5–6	5	Fa-3	3(0)	51/49,87	56/34,71	59/28,85	62/63,93	—"—
7	7	7	7	Atranorin (At)	3–5(0?)	-	-	-	-	orange-yellow
1			2	Consalazinic ac. (Csa)	2(0)	4/47,86			8/44,63,92	yellow-orange
	3	2–3	3	Galbinic acid (Ga)	1–2(0)		5/29,71	15/28,86	53/44,64,92	yellow
1–2	3	2	2	Fumarprotocetraric acid (Fu)	2(0)	4/33,61	25/28,71	9/27,84	35/35,60,92	dark grey-lilac
	2		2	omp-1	2(0)		7/39,74		13/44,63,93	yellow-brown
3	5	3	3	omp-2	2(0)	29/47,83	36/31,72	23/28,84	52/34,60,92	orange(-yellow)
			2	omp-3	2(0)				20/44,62,92	pink

III. RESULTS AND DISCUSSION

Chemistry

The main results regarding the chemical compounds found (with TLC) in *Parmelia omphalodes* s. lat. in the present study are summarized in Table 1. According to C. Culberson (1969), some of the major compounds of this taxon were observed a long time ago; lobaric acid was reported by Asahina (1938), salazinic acid by Schindler (1936; from C. Culberson 1969), atranorin by Asahina (1951), protocetraric acid by C. Culberson (1970), protolichesterinic acid by Krog et al. (1980). For more details, see C. Culberson (1969, 1970), Culberson et al. (1977), Dahl & Krog (1973) and Krog et al. (1980). In a specimen collected in France (Vezda 1980: no. 1740) A. Johnson and C. Culberson reported consalazinic acid and a trace of galbinic acid.

Some compounds occur as 'satellites' with distinct major constituents: consalazinic acid (an orange-yellow pigment, abundance 1–2) only with salazinic acid (abundance 4–5). The new unknown pigment omp-3 (abundance 1–2) occurs only in connection with salazinic acid, whereas the compound omp-1 (abundance 1–2) occurs in connection with protocetraric acid (abundance 4–5). These satellite substances probably belong to the β-orcinol depsidones (see Culberson et al. 1981). Attempts to identify them by two-dimensional TLC, e.g. by using extracts from *Parmelia crinita* Ach., *P. squamans* Stizenb., *Ramalina farinacea* (L.) Ach., *R. implectens* Nyl. (constictic acid, hypoprotocetraric acid, hyposalazinic acid?) for comparison, were not successful. Fumarprotocetraric acid occurs sporadically as an accessory compound, scored in c. 7 % of the 670 specimens (control extracts from *Cladonia symphycarpa* (Ach.) Fr.: At, N; *Cladonia gracilis* (L.) Willd. subsp. *gracilis*: Fu, *Parmelia olivacea* (L.) Ach.: Fu). Fu was also tested with two-dimensional TLC. The corresponding frequencies in that material for galbinic acid were 57 % and for omp-2 35 %. In the case of some small speci-

Table 2. *Survey of different constituent classes found in the Eastern Fennoscandian material of Parmelia omphalodes s.lat.* The values given for each class are the percentages of the total number of samples in the region. Atranorin (regularly present) and several minor and accessory compounds are excluded.

Constituent class	Region 1 (N=77)	Region 2 (N=272)	Region 3 (N=46)	Region 4 (N=86)
Sa + Lo + PL	37.6	56.6	13.0	14.9
Sa + Lo + PL + Ufa	2.6	10.4	17.4	14.9
Sa + Lo + Ufa	-	1.8	4.4	8.1
Sa + Lo	-	1.8	-	-
Σ %	40.3	70.6	34.8	38.4
Sa + PL + Ufa	-	1.1	17.4	9.2
Sa + Ufa	3.9	3.7	43.5	49.4
Sa	-	-	-	2.3
Σ %	3.9	4.8	60.9	61.6
Pr + Lo + PL	18.2	6.2	4.3	-
Pr + Lo + PL + Ufa	35.1	17.3	-	-
Pr + Lo	-	0.37	-	-
Σ %	53.2	23.9	4.3	-
Sa + Pr + Lo + PL + Ufa	2.6	0.7	-	-
Frequency of Pr as minor compound in the Sa-rich material:	97	97	75	80

mens, only a tiny fragment was used for TLC and for this reason the results obtained were sometimes misleading, especially for minor compounds. This could explain the absence of omp-1 from some specimens rich in protocetraric acid and that of consalazinic acid from specimens rich in salazinic acid.

Several fatty acids were observed; the most frequent was protolichesterinic acid (determined according to Rf values only; see C. Culberson 1972:118). Frequent were also two unknown fatty acids, Fa-2 and Fa-3, probably identical with the fatty acids Rf 0.41 and 0.52 in Kurokawa (1976). I found that one or both of them can occur with protolichesterinic acid and/or with some other fatty acids, or they can be the only fatty acids present. The presence or absence of fatty acids seems to be of limited value for attempts to separate infraspecific taxa within *Parmelia omphalodes* s. lat.

The majority of the diagnostic and accessory compounds in the specimens of *P. omphalodes* belong to the same 'chemosyndrome' (C. Culberson 1976, Elix 1982), i.e. β-orcinol depsidones. These compounds can, theoretically, be derived from each other by reduction or oxidation processes (C. Culberson 1967). According to Sheard (1978a), protocetraric acid could be a biosynthetic precursor of salazinic acid. For specimens of the *Ramalina siliquosa* complex he reported two discrete biosynthetic pathways. If one of these is realized here (phenolic precursors → protocetraric acid → salazinic acid), then the regular occurrence of trace amounts of protocetraric acid in salazinic acid-rich specimens would be understandable. A recent paper by Huovinen and Ahti (1982) on the chemistry in *Cladonia* presents more complicated biogenetic relationships. In that genus salazinic and protocetraric acids are suggested to be produced partly along separate pathways. The question of possibly intimate biogenetic relations in the synthesis of salazinic and protocetraric acid in the thalli of *Parmelia omphalodes* s. lat. remains unanswered. Protocetraric acid (as an accessory compound) is very frequent in salazinic acid-rich specimens (90 %; Table 2). Sheard (1978a) found a value of 78 % for the salazinic acid-rich strain of *Ramalina siliquosa.* Bowler and Rundel (1978) reported simultaneous occasional occurrence of Sa and Pr in the same thallus of *Ramalina farinacea* s. lat.

As many as 80 different combinations of

Table 3. *The occurrence of some minor and accessory compounds in different constituent classes in Parmelia omphalodes s. lat.* The frequencies are the percentages of the total number of specimens analysed in the constituent class and region. The values for consalazinic acid are too low for technical reasons (Csa adequately detected only with solution G, which was not used at the beginning).

Region and constituent class		Csa	Ga	omp-2	Fu	omp-1
Region 1 (N = 77)						
Sa + Lo	(31)	100	100	29	3.2	-
Sa	(3)	100	66.7	66.7	-	-
Pr + Lo	(41)	-	53.7	58.5	24.4	97.6
Sa + Pr + Lo	(2)	-	-	-	-	100
Region 2 (N = 272)						
Sa + Lo	(92)	96.2	92.2	29.2	4.7	-
Sa	(13)	100	69.2	46.2	38.5	-
Pr + Lo	(65)	-	32.3	29.2	6.2	98.5
Sa + Pr + Lo	(2)	-	50	-	-	100
Region 3 (N = 46)						
Sa + Lo	(16)	92.3	100	18.8	37.5	-
Sa	(28)	100	64.3	42.9	17.9	-
Pr + Lo	(2)	-	100	-	-	50
Region 4 (N = 86)						
Sa + Lo	(33)	100	66.7	78.8	3.0	-
Sa	(53)	93.9	73.6	64.1	13.2	-

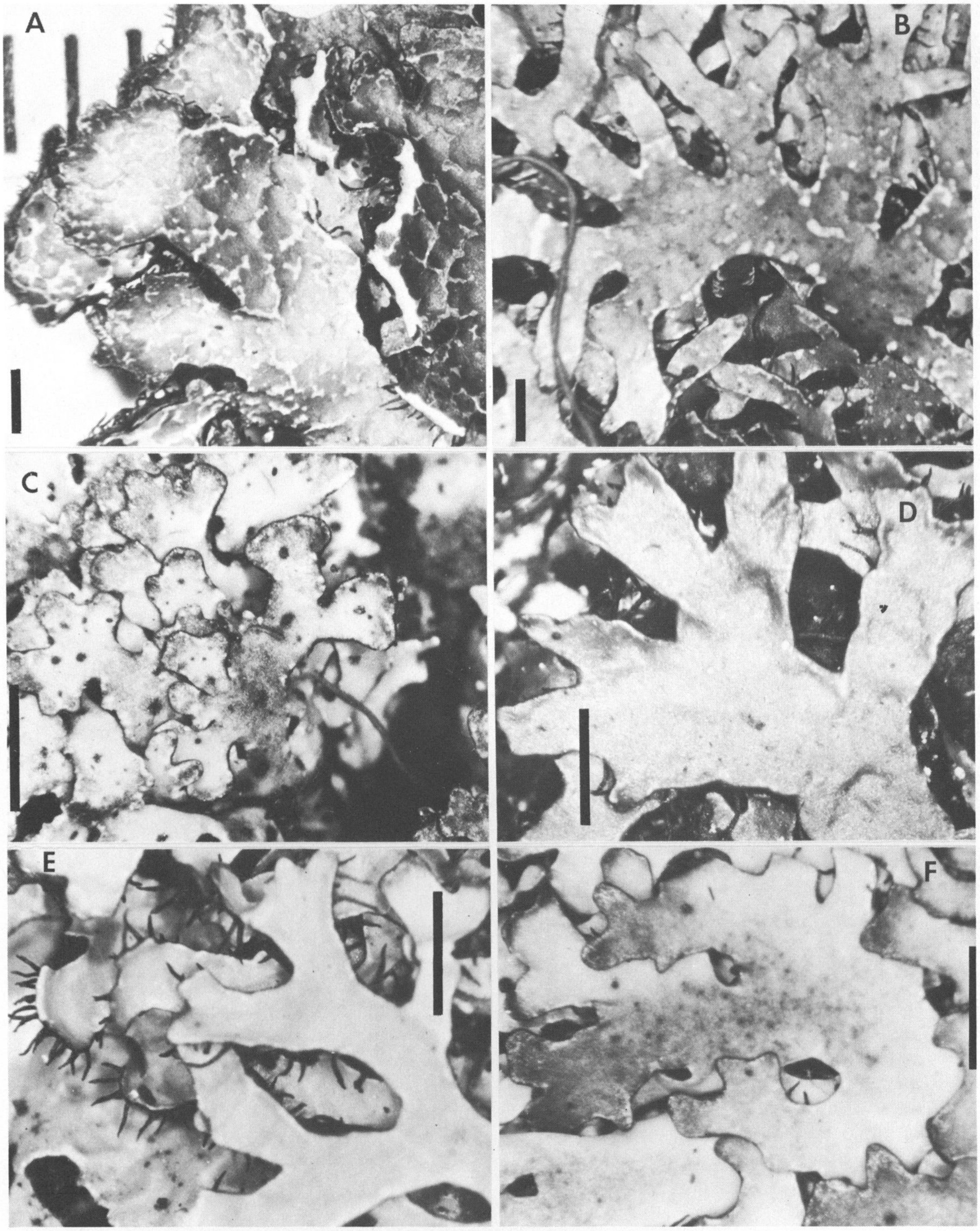


Fig. 2A–F. Lobes of different morphotypes in the *Parmelia omphalodes* complex. — A–C: subsp. *omphalodes*: A: Finland: N, Tvärminne 1912 Salmenlinna (H); B: Ab, Tenala 1939 Häyrén (H); C: U.S.S.R.: Lt(Lps), Porovaara 1931 Räsänen (H)); D: subsp. *discordans*: D: Finland: Al, Vårdö 1938 Häyrén (H); E–F: subsp. *pinnatifida*: E: Finland: Ab, Nagu 1874 Elfving (H), F: Li, Utsjoki 1964 Laine (TUR 1802). — Bar = 1 mm.

compounds (including accessory and minor substances) were scored in the present material. The diversity is greatest in regions 1 and 2. Eleven constituent classes can be distinguished. Only three of these: 'Sa + Lo + PL', 'Sa + Lo + PL + Ufa', and 'Sa + Ufa' are distributed in all four regions (Table 2). The constituent classes with salazinic and lobaric acids (usually including fatty acids) are well represented in all regions, with the highest frequency in region 2 (70 %). The classes containing salazinic acid, but lacking lobaric acid, are most frequent in the climatically cooler regions 3 and 4 (60 %). In the suboceanic southwest (region 1 and parts of region 2), the constituent classes rich in protocetraric acid are best represented (53 %).

In the 'Sa classes' especially, consalazinic and galbinic acids occur with high frequencies (Table 3). The former is totally absent from Pr-rich specimens, where it is replaced by omp-1. Fumarprotocetraric acid and omp-2 are found in samples from all four regions. They are not clearly bound to any particular constituent class. Their frequency shows some regional differences: omp-2 is best represented in region 4 (70 % of the samples) and Fu in region 3 (24 % of the samples).

Morphology

Lobes

Shape. — Considerable variation was found in the shape of the repeatedly branching and ± imbricate lobes of the thalli of the three taxa proposed by Kurokawa (1976) and recognized below as infraspecific taxa of *P. omphalodes*. Some morphotypes are presented in Fig. 2. In the strain *omphalodes* the lobe diameter is mostly 0.16–3.1 mm, whereas in *pinnatifida* it is 0.13–2.9 mm and in *discordans* 0.13–2.8 mm. The dominant lobe diameter in thalli of *omphalodes* varies from narrow to broad, in *discordans* mostly from narrow to intermediate or sometimes broad, and in *pinnatifida* from narrow to intermediate. For more details, see Table 4. The lobe shape, seen in cross-section, is the same for *omphalodes* and *pinnatifida*: the lobes are mostly concave, or concave and convex lobes occur side by side in the same individual. In thalli of *discordans* convex lobes are more usual, frequently occurring together with concave ones (Table 4). The oldest, ± degenerating central parts of the thallus sometimes develop several new lobuli, a phenomenon observed by Beltman (1978: fig. 5 F) in *Parmelia sulcata*.

Surface structure. — Hale (1973) found that the cortex in *Parmelia omphalodes* was epicorticate and nonpored. The surface of the upper cortex in the present material is never smooth, but weakly undulating or nodulated. Elevated ridges are frequent, running in several directions (Fig. 4 A). The distance between adjacent ridges was found to be 80–400 μm. Specimens collected from extreme habitats (in all these strains), such as exposed sites at higher altitudes, fairly frequently had a bluish grey or bluish lilac pruina composed of crystals ("f. *caesia*", "f. *caesiopruinosa*").

Pseudocyphellae. — Pseudocyphellae occur in all three strains. They are linear, forming a ± reticulate pattern, especially in *omphalodes* (Fig. 2A). In this strain both marginal and laminal pseudocyphellae occur, being found on small, young lobes as well. In thalli of *discordans* and the combination strain 1+3 (Sa + Pr; Table 9), the pseudocyphellae are not usually as abundant as in the thalli of *omphalodes*; in young lobes they are generally sparse (Fig. 3A) and mostly marginal, whereas in older lobes they are more scattered and both marginal and laminal. In thalli of the strain *pinnatifida* the pseudocyphellae were found by Kurokawa (1976) to be mostly marginal. A similar tendency was observed in the present material, especially in specimens from the northern regions. The young, small lobes are most typical in this respect (Fig. 3B); in older parts of the thallus some laminal pseudocyphellae can occur as well. When young pseudocyphellae are studied in detail, separate rounded components can be observed. Typically such a "pore" has a supporting ring c. 0.5 μm in diameter (probably built up of epicortical matter) around the aperture (Fig. 3C). In older pseudocyphellae these structures are ruptured, and long cracks are formed (Fig. 3D). The main branching pattern in the central part of the thallus is partly determined by the radial lines of the pseudocyphellae. Slowly but continuously rupturing occurs along these lines, and new branch segments are formed. In the vicinity of the pseudocyphellae the epicortex is often

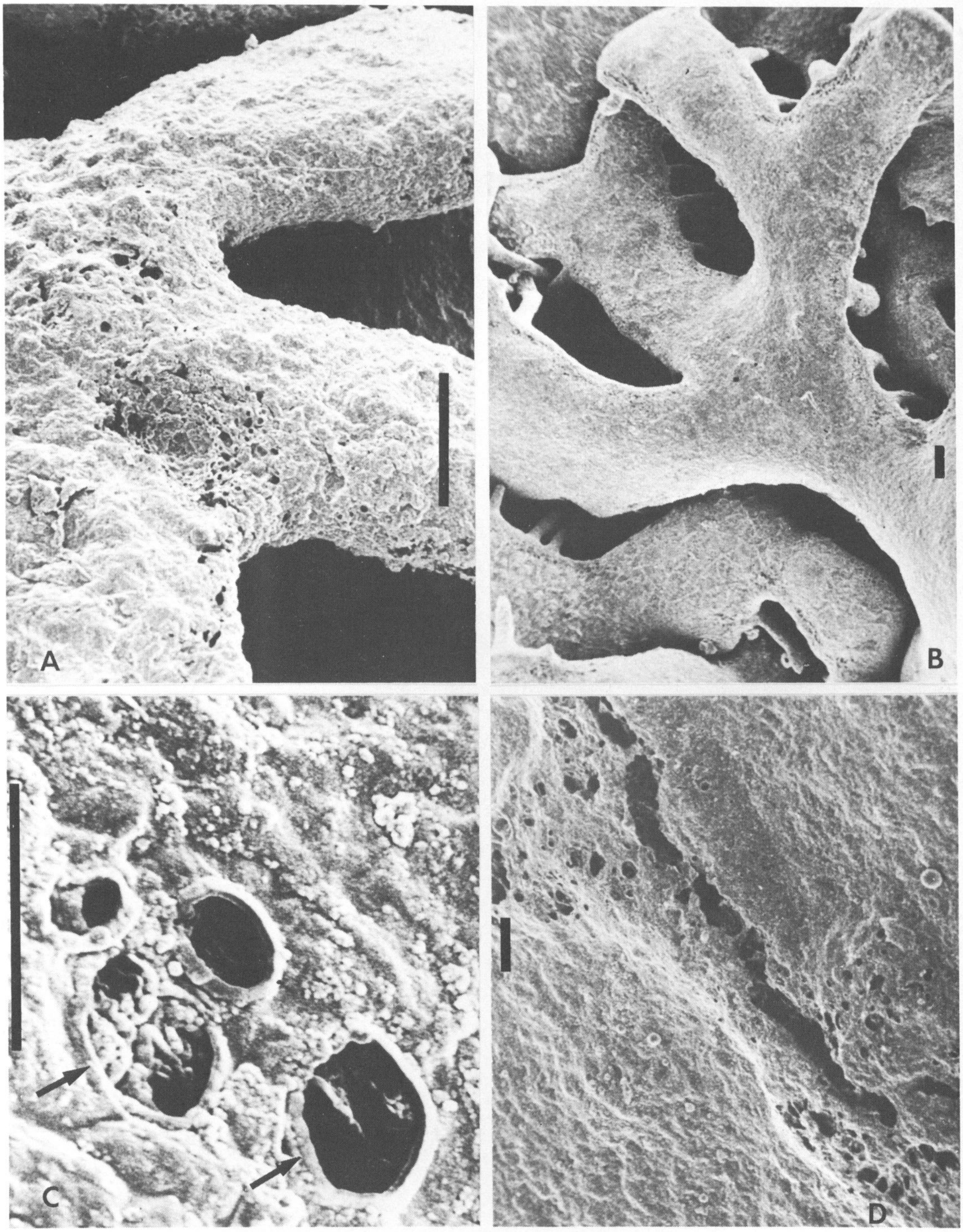


Fig. 3A-D. Surface structures in thalli of *Parmelia omphalodes* s. lat. A: Young lobe, scattered pseudocyphellae (Finland: Al, Eckerö 1981 Skult (TURA)). B: Young lobes, marginal pseudocyphellae (U.S.S.R.: K1, Hiitola 1935 Laurila (H). C: Supporting rings around apertures of pseudocyphellae (the same specimen as A). D: Old, laminal pseudocyphellae (Finland: Ab, Korpo 1981 Skult (TURA)). — Bar, in A-B = 100 μm, in C-D = 20 μm.

discontinuous, showing epicortical sheets (Fig. 4B) similar to those in the thalli of *Parmelia* species with a pored epicortex, in the sense of Hale (1973:figs. 53, 54).

Rhizines. — The lower cortex surface is very similar to the upper one, but lacks pseudocyphellae. It bears compact, simple or weakly furcate, black rhizines, which are structurally similar in all three strains (see also Jahns 1973 and Peveling 1973).

Internal structure of the thallus. — The anatomy of the heteromerous thallus is similar in the three strains and also agrees well with observations made by Hale (1973:fig. 7). Under the thin, undulating epicortex is the upper cortex, formed of mesodermatous, partly pachydermatous paraplectenchyma (terms of Frey 1936, Hale 1976). The thicknesses of the upper and lower cortex are frequently 6–30 μm. In the medulla, consisting of medullary plectenchyma, the algae occur in groups, adhering to hyphae in a layer in the upper part of the medulla.

Apothecia

Apothecia are found in all three strains, but with different frequencies: *omphalodes* 32%, *discordans* 25%, and *pinnatifida* 4.2% only. These percentages may not be representative, since earlier lichenologists probably preferred to collect fertile specimens, and that would result in overrepresentation of fertile material. The surprisingly low fertility of *pinnatifida* might be a consequence of its climatically severe environment. The fertility of the *discordans* specimens collected by me in 1981–82 from regions 1 and 2 was also remarkably low. The *omphalodes* specimens recently collected from the same regions were mostly sterile (a first step in development into an asexual "secondary species"?). According to Magnusson (1919) and W.L. Culberson (1970), the fertility is higher in *discordans* than in *omphalodes*.

The apothecia are laminal and seemingly always sessile. Their size is very variable within the same strain, and probably does not differ significantly between the strains. The maximum

Table 4. *Some morphological parameters in three infraspecific taxa of Parmelia omphalodes: subsp. discordans, subsp. pinnatifida, subsp. omphalodes.*

Subspecies (with major constituents)	Region no.	Dominant[1] Lobe diam. % of N			Lobe min. (mm ± S.E.)	Lobe max. (mm ± S.E.)	% individuals with lobe transects mainly			% individuals with apothecia
		1	2	3			concave	convex	both	
discordans (Pr + Lo + PL)	1 (N = 39)	51.3	48.7	-	0.13 ± 0.003 s.e.	2.8 ± 0.10	43.6	12.8	43.6	25 (2.9 in material 1981–1982: reg. 1,2)
	2 (N = 70)	42.9	55.7	1.4	0.15 ± 0.003	2.4 ± 0.06	14.3	17.1	68.6	
pinnatifida (Sa)	2 (N=10)	75.0	25.0	-	0.14 ± 0.006	2.7 ± 0.19	100.0	-	-	4.2
	3 (N = 20)	65.0	35.0	-	0.13 ± 0.006	2.7 ± 0.11	75.0	-	25.0	
	4 (N = 45)	77.8	22.2	-	0.15 ± 0.005	2.9 ± 0.12	75.6	-	24.4	
(Sa + PL)	3 (N = 8)	87.5	12.5	-	0.17 ± 0.009	2.1 ± 0.12	87.5	-	12.5	
	4 (N = 8)	87.5	12.5	-	0.15 ± 0.009	1.8 ± 0.12	100.0	-	-	
omphalodes (Sa + Lo + PL)	1 (N = 32)	12.1	66.7	21.2	0.18 ± 0.005	3.0 ± 0.11	78.1	-	21.9	32
	2 (N = 188)	21.8	70.8	7.4	0.21 ± 0.005	2.9 ± 0.05	80.8	1.1	18.1	
	3 (N = 10)	30.0	70.0	-	0.20 ± 0.015	2.9 ± 0.24	80.0	-	20.0	
	4 (N = 26)	38.5	50.0	11.5	0.16 ± 0.006	3.1 ± 0.14	88.5	-	11.5	

[1] Scale: 1 = 0.9 > mm, 2 = 1–1.4, 3 = 1.5 <

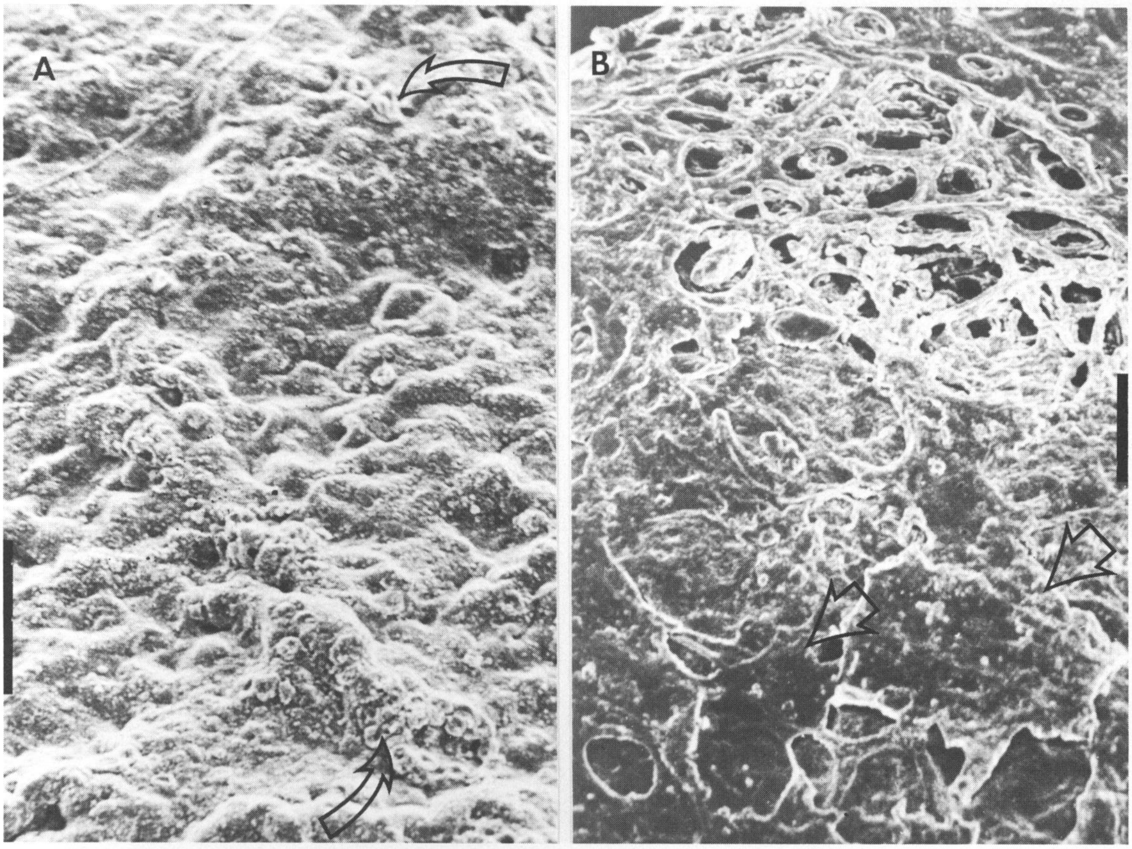


Fig. 4. A: A curved ridge in the upper cortex of *Parmelia omphalodes* s. lat. (the same specimen as in Fig. 3A). B: Epicortical sheets in the vicinity of pseudocyphellae (the same specimen as in Fig. 3B). — Bar = 20 μm.

diameter is seldom over 10 mm (according to Fries 1871, up to 20 mm). The apothecia are lecanorine and in the younger ones the margin is fairly entire and even; in older ones it is rather uneven to lobate.

The spores are elliptic and have a fairly smooth surface. No clear differences in their size or shape were found between the three strains. The following spore measurements were obtained: 9(7–11)×15(12–19) μm (Fig. 5). These agree fairly well with the spore sizes given by Fries (1871): 9–12×14–19 μm, and the data on spore shape presented by Galløe (1947) and Duncan & James (1970).

Pycnidia

Pycnidia in various states of development were visible on the lobe surfaces in specimens of each strain. They are spherical and largely buried in the thallus. The conidia are hyaline and bifusiform. No clear differences in shape or length could be detected between the strains. These observations correspond to those made by Krog (1982).

Cluster analyses

Cluster analyses were made, using the chemical and morphological attributes together or separately. According to the null hypothesis, absence of correlation between the morphology and chemistry appears as a lack of similarity between the dendrograms based on the morphological and chemical characters. The following classifications were performed:

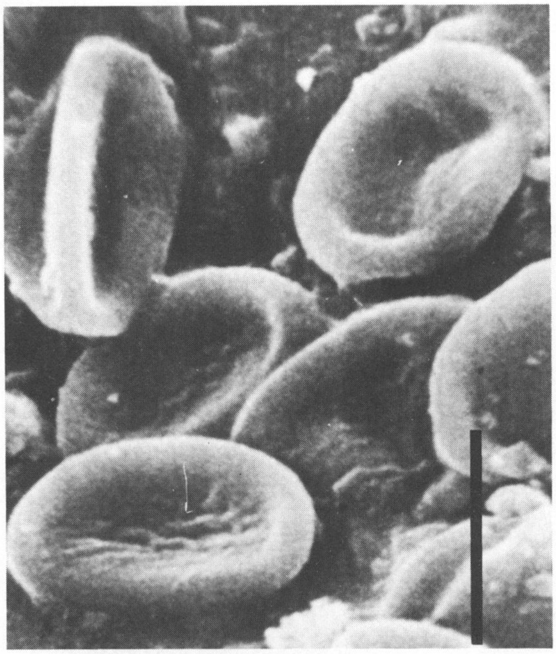


Fig. 5. Mature, crumpled spores of *Parmelia omphalodes* on the hymenial surface, seen in SEM (Finland: N, Tvärminne 1912 Häyrén (H)). — Bar = 10 μm.

1. Classification in which the chemical characters were excluded,
2. morphological characters excluded,
   a) all the chemical characters included,
   b) chief chemical characters (mainly major compounds) included,
3. a special morphological character included, and given the same weight as an individual chemical character.

These cluster analyses were made in parallel for the four geographical regions (Fig. 8).

Region 3

It is convenient to start the survey with the dendrograms for region 3, which has the smallest number of individuals (46). Fig. 6A (11 chemical attributes): There are two well-separated clusters, on the left a small cluster of protocetraric acid-rich individuals, on the right a large cluster containing several subclusters. A closer analysis shows 29± clearly differentiated chemical combinations. All the individuals contained in the large cluster are rich in salazinic acid, but their composition varies widely in other respects. All the specimens marked white lack lobaric acid. Fig. 6B (only morphological characters): The pattern of clusters differs greatly from that in Fig. 6A. The specimen combinations are largely new. Many of the clusters occur within one another. No clear morphological 'entities' appear to exist. The small cluster (Pr-rich) in Fig. 6A has been split (arrows!) and its individuals occur in new clusters together with salazinic acid-rich ones. Comparison of dendrograms based on all the morphological or chemical attributes appears to yield little of value for infraspecific classification.

The *Parmelia omphalodes* complex is known to have very few constant morphological characters. According to Kurokawa (1976), differences in the distribution of pseudocyphellae on the upper cortex are of taxonomic value. In his cluster analysis of chemical attributes Sheard (1978a) used major compounds only. I tested this method on *Parmelia omphalodes* and obtained a clearer grouping of the material. Fig. 6C is based on five chemical attributes (including Pr and its satellite compound omp-1). An essentially similar dendrogram was obtained, when the chemical attribute Pr was dropped. The dendrogram in Fig. 6C resembles Fig. 6A in having two main clusters: on the left a small cluster built up of protocetraric acid-rich individuals, on the right a large cluster. The latter is split into two main parts, the left part containing individuals with salazinic acid but lacking lobaric acid, the right part with individuals possessing both salazinic and lobaric acid. Fig. 6D: The main structure is the same as in Fig. 6C; for instance, the individuals lacking lobaric acid are all in the same subcluster as before. Their internal order is to some extent changed due to the added character "laminal pseudocyphellae". When the clusters in Fig. 6A,C,D are surveyed and the chief chemical attributes (major compounds) are taken as the primary characters for division, three main chemical strains (two with "substrains") can be separated. (Table 5).

Region 4

The samples from the northernmost region were analysed in a similar way. In this case also, the

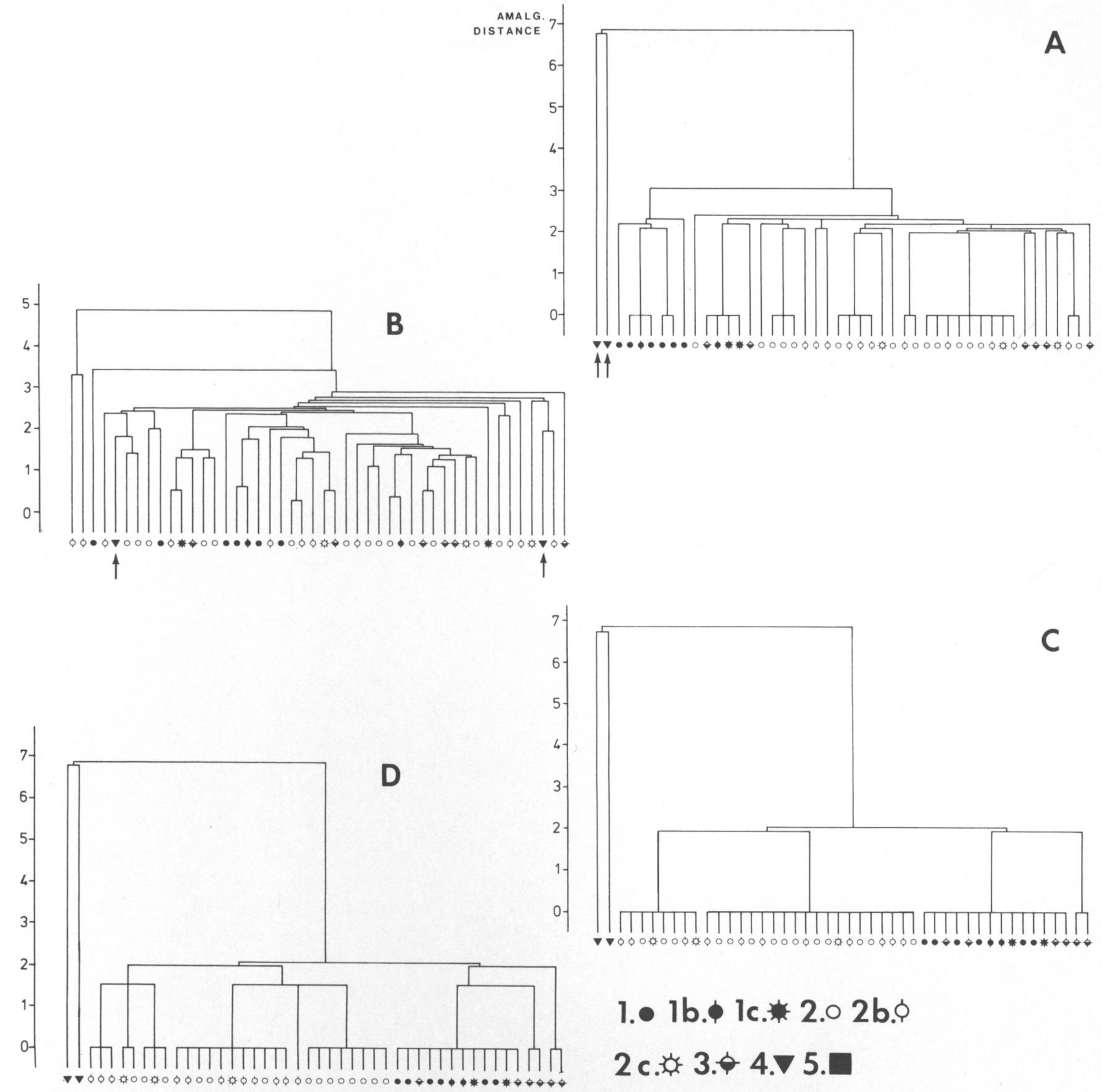


Fig. 6A–D. Dendrograms of classification of data sets of *Parmelia omphalodes* s. lat. from Region 3 (46 exx.). A: 11 chemical characters, B: 10 morphological characters, C: 5 chemical characters (Sa, Pr, Lo, PL, omp-1), D: 5 chemical (as in C) and one morphological character (laminal pseudocyphellae). — Symbols: 1, 1b, 1c = Sa-, Lo-, PL-rich specimens; 2, 2b, 2c = Sa-rich, Lo-lacking specimens; 3 = intermed. of 1 & 2; 4 = Pr-rich specimens; 5 = intermed. of 1 & 4. For further explanations, see the text.

dendrogram based on all the chemical attributes (11) exhibited a small cluster (one Pr-rich specimen — "control specimen" from Norway: Svolvaer) at a distinct distance from a large composite cluster containing several subclusters. Here, too, the dendrogram based on all the morphological characters (10) differed greatly from the chemical one. The limits between several of these subclusters were indistinct and the distances between them small. The Pr-rich cluster in the chemical dendrogram was now included in a Sa-rich cluster. Very few

Table 5. *Chemical strains of Parmelia omphalodes in Region 3 (N = 46) in Eastern Fennoscandia.*

Cluster	Chemical strain	Lichen acids	Pseudocyphellae [1]		N	%
Left cluster	1	Pr, Lo, PL, At Ga, omp-1(±)	L+	M+	2	4.3
Central cluster	2a	Sa, PL, At Csa(±), Pr(±), Ga(±), omp-2(±) Fa-2, Fa-3(±)	L +(62.5 %) −(37.5 %)	M+	8	17.4
	2b	Sa, At Pr(±), Csa, Ga(±), Fu(±), omp-2(±), Fa-2, Fa-3	L +(65 %) −(35 %)	M+	20	43.5
Right cluster	3a	Sa, Lo, PL, At Pr(±), Csa(±), Ga(±), Fu(±), Fa-2(±), Fa-3(±)	L +(85.7 %) −(14.3 %)	M+	14	30.4
	3b	Sa, Lo, At Pr(±), Csa(±), Ga(±), Fa-2, Fa-3	L+	M+	2	4.3

[1] L = laminal, M = marginal pseudocyphellae

similarities existed between these two dendrograms. When the same five chemical attributes used for region 3 are complemented with the character "laminal pseudocyphellae", a clearer picture of the chemical strains in region 4 is obtained. The dendrogram is essentially the same as that for region 3, with the exception of some sequential changes in the clusters — an effect of the introduction of the morphological character. Accordingly, only this dendrogram is published here (Fig. 7A).

The dendrogram has the following main structure (Fig. 7A): On the left is the small Pr-rich "cluster" A, on the right a large composite cluster containing Sa-rich individuals only. Part B of this large cluster is characterized by individuals (N = 33) with Lo; part C on the right has individuals (N = 53) lacking Lo. Part B is split into subclusters with (N = 26) and without (N = 7) protolichesterinic acid, and part C also contains subclusters with (N = 8) and without (N = 45) this acid. A detailed study of Fig. 7A complemented with data from the dendrogram based on all the chemical attributes reveals 11 smaller poorly defined clusters within the large cluster (B + C). Combining some of these entities, I found approximately the same chemical strains as for region 3 (Table 6).

Region 1

Dendrograms based on the same five chemical attributes as before, with and without the morphological character "laminal pseudocyphellae" give the clearest picture of the chemical grouping of the material in this region also. The same result was obtained when Pr was excluded; its satellite substance omp-1 compensated for its absence. In Fig. 7B four clusters can be seen, two very small clusters outermost on the left and right (A and D), and between these two larger clusters (B and C). Cluster A contains two Sa-rich individuals (lacking Lo and PL); cluster B (N = 31) is characterized by Sa, Lo and PL. Cluster D differs from A in having accessory Pr (traces) and lacking laminal pseudocyphellae. The chemical pattern of Fig. 7B seems to be rather simple. But in fact cluster C, containing Pr-rich specimens, has an especially complicated internal structure. The dendrogram based on all the chemical attributes (Fig. 7C) shows essentially the same pattern, but several changes have taken place within the large clusters. Closer study of Fig. 7C revealed the rather indistinct subgroups presented in Table 7. These subgroups illustrate the great chemical variation

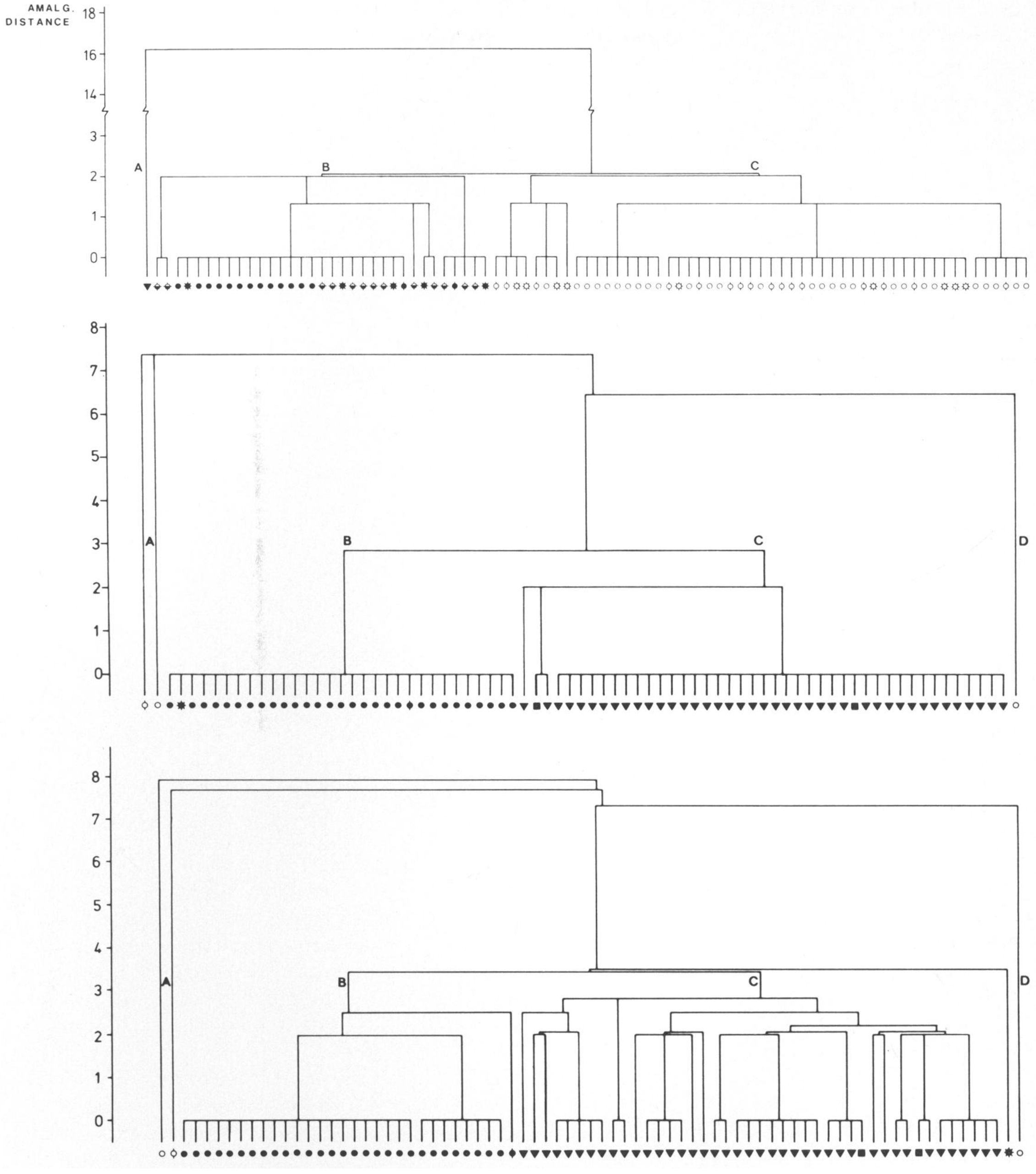


Fig. 7A–C. Dendrograms of classification of data sets of *Parmelia omphalodes* s. lat. A: Region 4 (87 exx.): 5 chemical and one morphological character (the same as in Fig. 6D). B: Region 1 (77 exx): 5 chemical and one morphological character (as in Figs. 6D, 7A). C: Region 1: 11 chemical characters.

Table 6. *Chemical strains of Parmelia omphalodes in Region 4 (n = 87) in Eastern Fennoscandia.*

Cluster	Chemical strain	Lichen acids	Pseudocyphellae		N	%
A	1	Pr, Lo, PL, At omp-1, omp-2, Fa-2, Fa-3	L+	M+	(1)[1]	
B	3a	Sa, Lo, PL, At Pr(±), Csa(±), Ga(±), Fu(±), omp-2(±), Fa-2(±), Fa-3(±)	L +(88 %) (+)(8 %) −(4 %)	M+	26	30.2
	3b	Sa, Lo, At Pr(±), Csa(±), Ga(±), omp-2(±), Fa-2, Fa-3	L +(86 %) (+)(14 %)	M+	7	8.1
C	2a	Sa, PL, At Pr(±), Csa(±), Ga(±), Fu(±), Fa-2, Fa-3(±)	L +(13 %) (+)(50 %) − (37 %)	M+	8	9.3
	2b	Sa, At Pr(±), Csa(±), Ga(±), Fu(±), omp-2(±), Fa-2, Fa-3	L +(67 %) (+)(13 %) −(20 %)	M+	45	52.4

[1] A specimen from outside Region 4 (from Norway: Svolvær).

Table 7. *Survey of chemical subgroups of Parmelia omphalodes in Region 1 (N = 77)* in Eastern Fennoscandia.

Pr-rich	No.	1: Pr, Lo, PL, At, Ga, omp-1, omp-2(±), Fu, Fa-2(±), Fa-3(±)
subgroups:		2: Pr, Lo, PL, At, omp-1, Fu, Fa-2, Fa-3
nos. 1–8		3: Pr, Lo, PL, At, omp-1(±), omp-2(±), Fa-2(±), Fa-3
(52 % of total N		4: Pr, Lo, PL, At, Ga, omp-1, Fa-2
in Region 1)		5: Pr, Lo, PL, At, Ga, omp-1, omp-2, Fa-2
		6: Pr, Lo, PL, At, Ga, omp-1, omp-2
		7: Pr, Lo, PL, At, omp-1, omp-2(±), Fa-2(±)
		8: Pr, Lo, PL, At, omp-1
Sa-rich		9: Sa, Lo, PL, At, Pr(+), Ga, Csa, omp-2, Fu, Fa-3
subgroups:		10: Sa, Lo, PL, At, Pr(+), Ga, Csa(±), omp-2(±), Fa-3(±)
nos. 9–13		11: Sa, Lo, PL, At, Pa(+). Ga, Csa(±)
(54.3 %)		12: Sa, At, Ga, Pa(+), omp-2(±), Fa-2, Fa-3
		13: Sa, At, Ga, Pr(+) omp-2, (±) Fa-2, Fa-3
Sa + Pr-rich		14: Sa, Pr, Lo, PL, At, omp-1
		(14b): Sa, Pr, Lo, PL, At, Ga,
(2.7 %)		omp-2, Fa-2(not included in the dendrogram)

existing in this material and the results seem to be of limited value for practical taxonomic work.

By using a coarser basis for division I obtained the following chemical strains, which vary somewhat in their accessory compounds (Table 8). A conspicuous feature of region 1 (Alandia) is the rich occurrence of protocetraric acid-rich individuals, but salazinic acid-rich individuals are rather frequent too (especially on the outer skerries).

Region 2

This region consists of the southern and southwestern parts of the Finnish mainland and the adjacent archipelago, and climatically is partly very similar to region 1. Owing to the bulky primary material (N = 272) the dendrograms are too extensive to reproduce. But the most important results are presented here. Twenty subgroups with variable accessory compounds were revealed by the dendrograms:

Table 8. *Chemical strains of Parmelia omphalodes in Region 1 (N = 77) in Eastern Fennoscandia.*

Cluster	Chemical strain	Lichen acids	Pseudocyphellae		N	%
A + D	2	Sa, At Pr(±), Ga(±), omp-2(±), Fa-2, Fa-3	L { + (2 ind.) − (1 ind.)	M+	3	3.9
B	3a	Sa, Lo, PL, At Pr(±), Csa(±), Ga, omp-2(±), Fu(±), Fa-3(±)	L+	M+	31	40.3
C	1a	Pr, Lo, PL, At omp-1, Ga(±), omp-2(±) Fu, Fa-2(±), Fa-3(±)	L+	M+	35	45.4
	1b	Pr, Lo, PL, At omp-1	L+	M+	5	6.5
C	4	Sa, Pr, Lo, PL, At omp-1(±), Ga(±), omp-2(±), Fa-2(±)	L+	M+	3	3.9

Table 9. *Survey of chemical subgroups of Parmelia omphalodes in Region 2 (N=272) in Eastern Fennoscandia.*

Pr-rich subgroups nos. 1–11 (23 % of total N)	No.	1: Pr, Lo, PL, At, Ga, omp-1, omp-2(±), Fu, Fa-2(±), Fa-3(±)
		2: Pr, Lo, PL, At, omp-1, Fu, Fa-2, Fa-3
		3: Pr, Lo, PL, At, omp-1(±), omp-2(±), Fa-2(±), Fa-3
		4: Pr, Lo, PL, At, Ga, omp-1, Fa-2(±), Fa-3(±)
		5: Pr, Lo, PL, At, Ga, omp-1, omp-2, Fa-2, Fa-3
		6: Pr, Lo, PL, At, Ga, omp-1, omp-2
		7: Pr, Lo, PL, At, omp-1, omp-2(±), Fa-2(±)
		8: Pr, Lo, PL, At, omp-1
		9: Pr, Lo, PL, At, omp-1, Fa-3
		10: Pr, Lo, PL, At, Ga
		11: Pr, Lo, PL, At, omp-1, omp-2, Fu, Fa-2, Fa-3(±)
Sa-rich subgroups nos. 12–19 (76 % of total N)		12: Sa, Lo, PL, At, Pr(+), Csa, Ga, omp-2(±), Fu(±), Fa-2(±), Fa-3(±)
		13: Sa, Lo, PL, At, Pr(+), Ga, Csa(±), omp-2(±), Fa-2(±), Fa-3(±)
		14: Sa, Lo, PL, At, Pr(+), Ga, Csa(±), omp-2(±)
		15: Sa, Lo, PL, At, Pr(+), Ga, omp-2(±), Fu(±), Fa-2(±), Fa-3(±)
		16: Sa, Lo, PL, At, Pr(±), Ga(±), Csa(±), omp-2(±), Fu(±), Fa-2(±), Fa-3(±)
		17: Sa, Lo, At, Pr(+), Csa, Ga, omp-2(±), Fa-2(±), Fa-3(±)
		18: Sa, PL, At, Pr(±), Csa(±), Fu(±), Fa-2(±), Fa-3(±)
		19: Sa, At, Pr(±), Csa, Ga(±), omp-2(±), Fu(±), Fa-2, Fa-3
Sa + Pr-rich (1 %)		20: Sa, Pr, Lo, PL, At, Ga(±), omp-1

11 Pr-rich (23 %), eight Sa-rich (76 %, 5.1 % lacking Lo) and one Sa + Pr-rich (1 %). For details, see Table 9. By combining some of these subgroups (accepting a rough clustering based on a few attributes) I obtained chemical strains more comparable to those of the other regions (Table 10).

Some of the regional chemical differences have already been presented in Tables 2 and 3. The results of the chemical and cluster analyses can be summarized as follows:

The strain with protocetraric acid as a major compound is especially characteristic of region 1 (over 50 % of the samples analysed), and to a

Table 10. *Chemical strains of Parmelia omphalodes in Region 2 (N=272) in Eastern Fennoscandia.*

Chemical strain	Lichen acids	Pseudocyphellae		N	%
1a	Pr, Lo, PL, At omp-1, Ga(±), omp-2(±), Fu(±) Fa-2(±), Fa-3(±)	L+	M+	50	18.3
1b	Pr, Lo, PL, At, omp-1	L+	M+	12	4.4
2a	Sa, PL, At Pr(±), Csa(±), Fu(±), Fa-2(±), Fa-3(±)	L +(2 ind.) L −(1 ind.)	M+	3	1.1
2b	Sa, At Pr(±), Csa, Ga(±), omp-2(±), Fu(±), Fa-2, Fa-3	L +(91 %) L (+)(9 %)	M+	11	4.1
3a	Sa, Lo, PL, At Pr(±), Csa(±), Ga(±), Fu(±), omp-2(±), Fa-2(±), Fa-3(±)	L +(99 %) L −(1 %)	M+	182	66.9
3b	Sa, Lo, At Pr(+), Csa, Ga, omp-2(±), Fa-2(±), Fa-3(±)	L+	M+	11	4.1
4	Sa, Pr, Lo, PL, At omp-1, Ga(±)	L+	M+	3	1.1

smaller extent of region 2 (c. 23 %). In region 3 this strain is exceptional and in region 4 absent. The strain containing salazinic acid as a major compound, but lacking lobaric acid, occurs in very low frequencies in regions 1 and 2, but is rather dominant in regions 3 and 4. The strain characterized by the simultaneous occurrence of salazinic and lobaric acid is distributed in all four regions with intermediate (regions 1, 3 and 4) or high (region 2) frequency (Fig. 8).

The chemotypes or chemical strains of *Parmelia omphalodes* s. lat. observed in the material from Eastern Fennoscandia can be united into three "main" strains:

1. Protocetraric + lobaric acid
2. Salazinic acid
3. Salazinic + lobaric acid

and a combination strain 1 + 3 (Pr and Sa in comparable quantities). All these represent the same chemosyndrome (Culberson & Culberson 1976, Elix 1982).

Taxonomy of the Eastern Fennoscandian material

One purpose of a functioning taxonomy at species level must be, in my opinion, to establish entities which can be identified with some degree of accuracy in the field, preferably by morphological characters. The growth of knowledge in lichen chemistry has led to diverging opinions about the species concept in lichenology, which have been discussed by, for example, Hawksworth (1976).

An important consideration in discussions of the relations between the present taxa is their chemical background. As stated before, they all represent the same chemosyndrome, a group of related β-orcinol depsidones. The salazinic acid-rich and protocetraric acid-rich strains can be regarded as chemical variants of the replacement type (Elix 1982). The former strain was subdivided into a 'Sa + Lo' and a 'Sa' race. Sa is usually accompanied by consalazinic acid (minor compound) and Pr by the unknown compound omp-1. The majority of the other accessory compounds occur in all strains, regularly or sporadically.

The protocetraric acid-rich strain, *discordans*, differs from the salazinic acid-rich ones by growing in more oceanic environments and having its distribution restricted to western Europe, the coastal parts of Norway and the coast of the Baltic Sea. The salazinic acid-rich races, *omphalodes* and *pinnatifida*, can be regarded as climatically more continental, and have extensive ranges, occurring in Europe, Asia and North America. In Finland the area of *discordans* is restricted to the southwest, where it meets *omphalodes*, but very seldom *pinnatifida*. In the archipelago, thalli of protocetraric acid-rich and salazinic acid-rich strains sometimes grow side by side, as a rule without losing their chemical integrity. There are some exceptions (six samples known by me) to this rule: thalli containing Sa and Pr in comparable amounts (samples from the provinces Al, Ab and N). These "aberrations" (Brodo 1978) or representatives of a "combination strain" (Elix 1982) are morphologically more similar to *discordans* than to *omphalodes* s.str. They could be placed in aberration category no. 1 (Brodo 1978). In view of these examples of sporadic exchanges of genetic material between thalli of *discordans* and *omphalodes* s. str., and in view of the lack of sharp morphological boundaries between these strains, the strain *discordans* cannot in my opinion be accorded recognition at the species level. Differences in geographical ranges, and probable subtle differences in ecological requirements, justify recognition at the subspecies level.

The remaining replacement type, the strain rich in salazinic acid, with or without lobaric acid, is represented by *omphalodes* s. str. and *pinnatifida*. From a chemical standpoint, the similarities in this complex are great. Consalazinic acid and the unknown compound omp-3 seem to be constant minor compounds here. Almost all the other compounds are common to these two variants, occurring regularly or sporadically. Lobaric acid, a compound considered by some lichenologists to be associated with some environmental factor (Krog 1978, Elix 1982), is very typical of specimens whose morphological characters are diagnostic of *omphalodes* s. str. (in Eastern Fennoscandia). 'Typical' *pinnatifida* specimens (morphotypes), mostly collected in the oroarctic and northern boreal zones of Eastern Fenno-

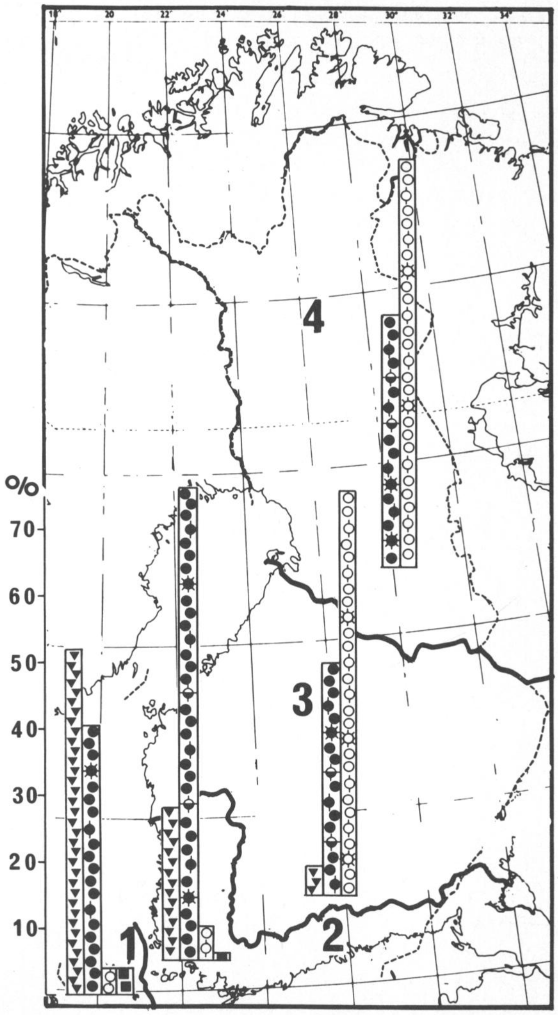


Fig. 8. The relative occurrence of different *Parmelia omphalodes* strains in Regions 1–4 in Eastern Fennoscandia.

scandia (for zones, see Ahti et al. 1964, 1968) are chemically characterized by the lack of lobaric acid. The morphological differences between *omphalodes* s. str. and *pinnatifida* are rather diffuse. The *pinnatifida* variant, most 'typical' when growing in colder regions, is usually rich in small, narrow, fairly dense and often ± vertical lobes. These narrow lobes frequently bear marginal pseudocyphellae only, whereas old lobes of larger diameter also have some laminal pseudocyphellae. Common habitats of *pinnatifida* in the oroarctic and northern boreal zones are steep cliffs or exposed mountain slopes. These habitats are very extreme with regard to wind, temperature and light. In the southern parts of Finland, this race mostly grows on cliffs and rock outcrops in shadier pine or spruce woods.

The main distribution of *pinnatifida* is concentrated in the northernmost parts of Europe, Asia and North America, but it also seems to grow in high mountains in Central Europe, Central Asia and Japan. The total range of *omphalodes* s. str. may be more extensive than that of *pinnatifida*, but its distribution seems to be centred in areas with a boreal climate.

The small, sometimes almost non-existent, chemical differences between *pinnatifida* and *omphalodes* s. str. speak in favour of treating them as the same taxon. But the partly diverging geographical areas and differences in habitat justify recognizing them as separate subspecies. Several intermediate stages exist between them. In some cases these have the morphology of *omphalodes* s. str., but the chemistry of *pinnatifida*. In other cases they are more truly intermediate in both the morphological and chemical sense.

Parmelia omphalodes (L.) Ach.

Thallus of variable size, rather irregular in outline, often confluent with other thalli, mostly loosely attached to the substrate. Lobes branched, diameter up to c. 3.5 mm, and expanding markedly at the apices, which are ± notched (lobes with greatly expanding apices mainly in the periphery of the thallus). Lobes sometimes imbricate. Old thalli rather frequently proliferate in the centre, developing a conglomerate of young, narrow lobes. Upper cortex ash grey (in shade sometimes greenish grey) to dark brown or blackish brown. In upper cortex a ± well- developed reticulum of white or pale grey pseudocyphellae (Fig. 2A). Isidia and soredia absent. Underside black, but lobe apices sometimes brown. Simple and furcate, black rhizines are rather abundant, and always present. The degree of pigmentation evidently primarily determined by exposure to light. Shaded parts of a thallus in an open habitat regularly paler than the superficial parts. Apothecia rather rare, with dark red brown disc and paler, thalline margin.

Parmelia omphalodes subsp. *omphalodes*

Lichen omphalodes L., Spec. Plant. 1143. 1753. — *Parmelia omphalodes* (L.) Ach., Meth. Lich. 204. 1803. — *Parmelia saxatilis* var. *omphalodes* (L.) Fr., Lich. Eur. Ref. 62. 1831. — *Imbricaria saxatilis* var. *omphalodes* (L.) Körber, Lichenogr. German. 10. 1846. — *Imbricaria omphalodes* (L.) Jatta, Sylloge Lich. Ital. 131. 1900. — Type: Sweden (n. v., but expected to belong here).

Lobaria adusta Gärtner, Meyer & Scherbius, Fl. Wetterau 3: 196. 1801. — *Imbricaria adusta* (Gärtner et al.) DC. in Lam. et DC., Fl. Franc. (ed. 3)2: 589. 1805. — Type: Germany (n. v.).

Parmelia saxatilis var. *omphalodes* f. *caesia* Nyl. ex Th. Fr., Lichenogr. Scand. 1: 115. 1871, nom. inval. (not accepted by the author). — *Imbricaria omphalodes* var. *caesia* Nyl. ex Arnold, Verhandl. zool.-bot. Ges. Wien 24: 255. 1874. — *Parmelia omphalodes* f. *caesia* (Nyl. ex Arnold) Lynge, Stud. Lich. Flora Norway 176. 1921. — Lectotype: U.S.S.R. Murmansk Region: Oleniy (Olenji), 1861 P.A. Karsten (H).

Parmelia saxatilis [subsp.]* *omphalodes* f. *caesiopruinosa* Nyl. in Norrlin, Notiser Sällsk. F. Fl. Fenn. Förh. 13: 324. 1871 (nom. nud.). — *Parmelia omphalodes* f. *caesiopruinosa* Nyl. ex Crombie, Monogr. Lich. Brit. 1: 244. 1894. — Orig. coll.: Finland, Lapponia enontekiensis, Pahtavaara, 1867 Norrlin (H).

Parmelia omphalodes var. *leucodes* Nyl., Flora 34: 537. 1881. — Type: France? (n. v.).

Parmelia omphalodes var. *panniformis* f. *subalbicans* Nyl. ex Räsänen, Ann. Bot. Soc. Vanamo 12(1): 22. 1939 (nom. superfl. illeg.). — Type: Homotypic with *P. saxatilis* var. *panniformis* f. *cinereoalbida* Harmand.

Parmelia omphalodes f. *subimbricata* Norrlin in Norrlin & Nyl., Herb. Lich. Fenn. 206. 1882 (nom. nud.). — Orig. coll.: Finland, Helsingfors, Stansvik, 1880 Norrlin & S.O. Lindberg (H).

Parmelia omphalodes var. *alpestris* Lamy, Bull. Soc. Bot. France 30: 352. 1883. — *Parmelia saxatilis* var. *omphalodes* f. *alpestris* (Lamy) Harmand, Lich. de France IV: 564. 1910 ('1909'). — Type: France. Hautes Pyrénées: col du Riou, Marc (n. v.).

Parmelia saxatilis var. *fusco-olivacea* Koltz, Recueil Mémoir. Trav. Soc. Bot. Luxembourg 13: 153. 1897 (n. v.).

Parmelia saxatilis var. *panniformis* f. *brunnea* Harmand, Lich. de France IV: 565. 1910 ('1909'). — *Parmelia omphalodes* var. *panniformis* f. *brunnea* (Harm.) Zahlbr., Cat. lich. univ. 6: 182. 1929. — Type: France (n. v.).

Parmelia saxatilis var. *panniformis* f. *cinereoalbida* Harmand, Lich. de France IV: 565. 1910 ('1909') — *Parmelia omphalodes* f. *cinereoalbida* (Harm.) Zahlbr., Cat. lich. univ. 6: 183. 1929. — *Parmelia omphalodes* f. *cinereoalbida* (Harm.) H. Magn., Flora över Skand. busk-och bladlavar, 89. 1929. — Type: France (n. v.).

Parmelia saxatilis var. *panniformis* f. *nigrescens* Harmand, Lich. de France IV: 565. 1910 ('1909'). — *Parmelia omphalodes* var. *panniformis* f. *nigrescens* (Harm.) Zahlbr., Cat. lich. univ. 6: 183. 1929. — *Parmelia omphalodes* f. *nigrescens* H. Magn., Flora över Skand. busk- och bladlavar, 89. 1929. — Type: France (n. v.).

Parmelia omphalodes f. *corticola* Koskinen, Über die Kryptogamen der Bäume ... (Diss.), 79. 1955. — Lectotype: Finland, Tavastia australis, Jämsä, Vaheri, ad basim ligneum betulae in ripa, 19.VIII.1952 A. Koskinen (H).

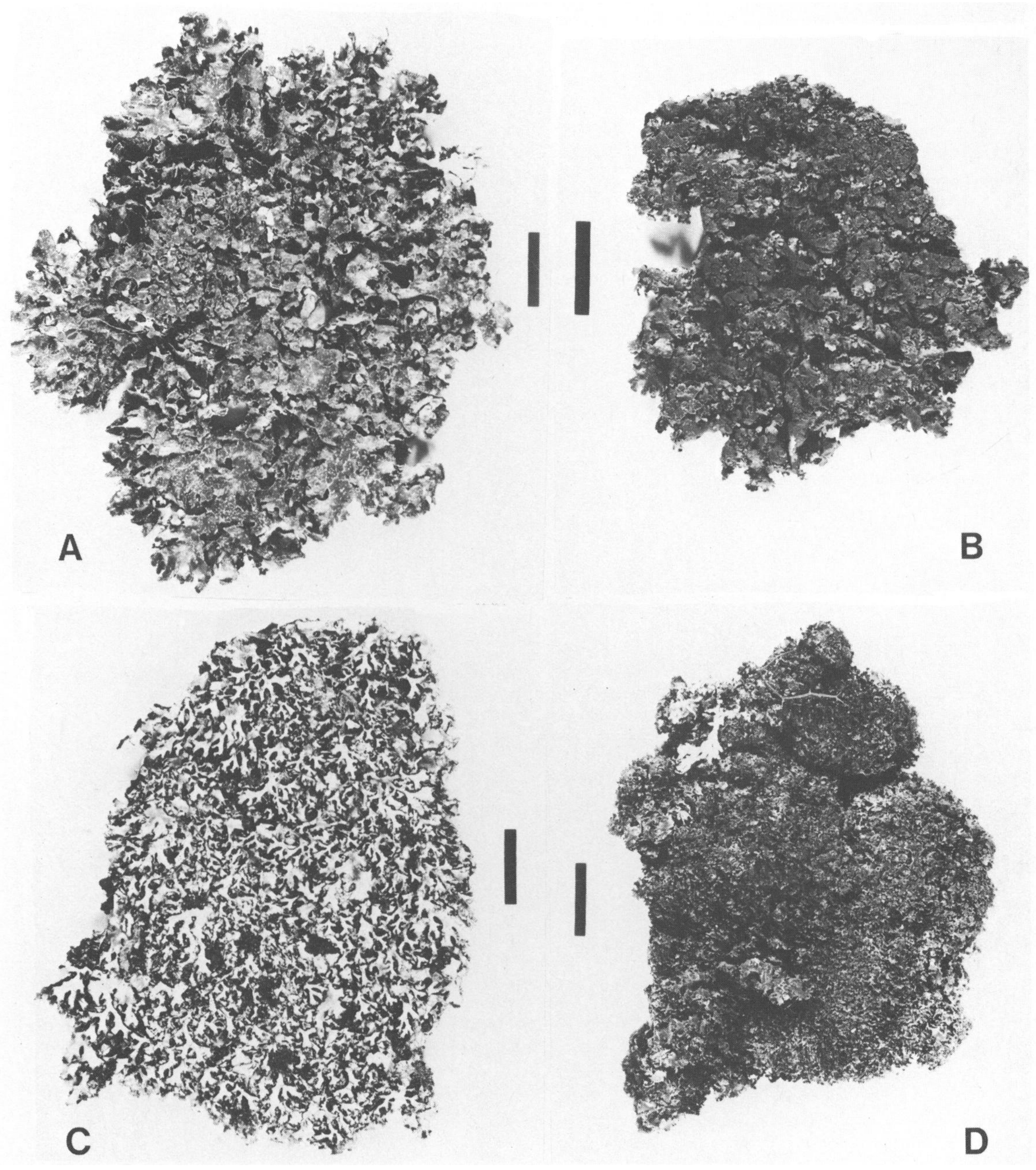


Fig. 9A–D. General habit of the subspecies of *Parmelia omphalodes.* A: subsp. *omphalodes*, Finland: N, Tvärminne 1933 Häyrén, B: subsp. *discordans*, Al, Hammarland 1981 Skult, C: subsp. *pinnatifida*, N, Tuusula 1934 Linkola, D: subsp. *pinnatifida*, U.S.S.R.: Lt (Lps), Pummanki 1930 Kontuniemi. — Bar = 1 cm.

Thallus usually growing in mats of moderate thickness and width, with mostly concave lobes and well-developed laminal and marginal pseudocyphellae. The upper cortex is glossy, especially at the lobe ends. The colour of the thallus, e.g. in coastal regions and in the SW Finnish archipelago, is often very dark brown, with a purple almost metallic hue.

Chemistry. — Medulla K+ red, PD+ orange, C–, KC–. Constant (or subconstant): atranorin (in cortex), salazinic acid, lobaric acid, protolichesterinic acid (occasionally lacking), consalazinic acid, omp-3. Accessory compounds: protocetraric acid, galbinic acid, fumarprotocetraric acid, omp-2, unknown fatty acids.

Distribution and habitat. — In Eastern Fennoscandia subsp. *omphalodes* occurs mainly in the southern parts, its frequency in the north being rather low. Common on siliceous rocks in both inland areas and the coast, and on skerries almost down to sea-level (Figs. 1 and 9A).

Representative specimens examined. — Lists with complete data in H, TUR and TURA. Finland: Alandia. Eckerö 1900 Sternberg (H); Jomala 1938 Linkola (H); Regio aboensis. Dragsfjärd 1971 Vitikainen 7455 (H); Korpo 1981 Skult; Nylandia. Tvärminne 1933 Häyrén (H); Kirkkonummi 1964 Takala (H); Karelia australis. Vehkalahti 1970 Fagerström (H); Satakunta. Siikainen 1936 Laurila (H); Tavastia australis. Asikkala 1979 Ahti 37758 (H). — U.S.S.R.: Lapponia petsamoensis. Pummanki 1928 Häyrén (H). — Norway: Finnmark. Berlevåg 1973 Alava 12383 (TUR). — France: Fontainebleau 1854 W. Nylander (H-NYL 34946). — Austria: Tirol, 1872 Arnold(?) (H-NYL 34921).

Exsiccata examined. — Räsänen: Lich. Fenn. 460 (H, TUR 26768, OULU); Lynge: Krypt. exs. 2361 (H); Havås: Lich. exs. Norw. 405 (H); Claudel & Harmand: Lich. Gall. 377 (H); Savicz: Lich. Ross. 92 (H); Vězda: Lich. Sel. 1740 (H).

Parmelia omphalodes subsp. *pinnatifida* (Kurok.) Skult, comb. nova

Parmelia pinnatifida Kurokawa, J. Japanese Bot. 51: 378. 1976. — Type: Homotypic with *P. omphalodes* var. *panniformis* Ach.

Parmelia omphalodes var. *panniformis* Ach., Meth. Lich. 204. 1803. — Lectotype (sel. by Kurokawa): Switzerland, Schleicher (?) 257 (H-ACH 1297).

Parmelia omphalodes var. *panniformis* f. *grisea* Räsänen, Ann. Bot. Soc. Vanamo 18: 15. 1943. — Syntype: U.S.S.R., Murmansk Region: Pechenga (Petsamo) Porovaara ad saxa ventosa 14.VI.1931 V. Räsänen (H).

Thallus frequently congested (with several old layers of thalli) and of moderate width, with predominantly narrow, richly branched, mostly concave lobes. Narrow lobes sometimes ascending to almost erect (especially in thalli growing in the north). Pseudocyphellae in the narrow lobes marginal and often sparse, in old, broad lobes often also partly laminal. The upper cortex glossy to varying degree. Colour of thallus when growing in shady habitats (especially in South Finland) pale grey to greenish grey, in exposed habitats (especially in the north) chestnut brown to nearly black. Rhizines of variable length, when longer frequently protruding at lobe ends.

Chemistry. — The same as for subsp. *omphalodes*, with the exception that lobaric acid is lacking and protolichesterinic acid is often absent, too. Several fatty acids of unknown structure were found in samples from northern habitats.

Distribution and habitat. — Subsp. *pinnatifida* is mainly distributed in the northern parts of Eastern Fennoscandia, with scattered localities in the middle and southern parts of the study area. A typical habitat in the north is open rock faces at high altitudes, in the south ± shaded rock faces in hardwood forests. Fig. 9C – D.

Representative specimens examined. — Lists with complete data in H, TUR and TURA. Finland: Regio aboensis. Karuna 1874 Elfving (H); Nauvo 1965 Kärenlampi (TUR 1802); Nylandia. Orimattila 1919 Linkola (H); Satakunta. Ikaalinen NE 1970 Suominen (H); Kankaanpää 1935 Laurila (H); Tavastia australis. Lammi 1909 Backman (H); Ostrobottnia australis. Lappfjärd 1953 Railonsala (TUR 26764); Ostrobottnia borealis. Rovaniemi parish 1955 Ahti (H); Lapponia enontekiensis. Enontekiö 1867 Norrlin (H); Porojärvet 1955 Henssen (H); Lapponia inarensis. Utsjoki 1964 Laine (TUR 26801): — U.S.S.R.: Lapponia petsamoensis (Lt). Petsamo Kalkuoaivi 1938 Räsänen (H); Lapponia tulomensis. opp. Kola 1887 Kihlman 199 (H); Karelia ladogensis. Hiitola 1935 Laurila (H); Karelia onegensis. Tjudia 1863 Kullhem (H); Siberia. Baykal Listvenichnoe 1902 Lönnbohm (H). — Norway: Hordaland. Alten Skoddavarre 1917 Lynge (H). — Sweden: Torne Lappmark. Jukkasjärvi 1906 Vrang (H); Abisko 1916 Häyrén (H).— Canada: Northwest Territories. Mackenzie Distr. Ya Ya Lake 1966 Scotter 8374 (H); Newfoundland. Placentia West Distr. Long Pond 1956 Ahti 6296 (H). — Japan: Kozuke. Mt. Akagi 1917 Yasuda 376 (H).

Exsiccata examined. — Räsänen: Lich. Fenn. 5 (TUR, OULU); Lich. Fenn. Exs. 706 (H); Havaas: Lich. Exs. Norv. 223 (H).

Parmelia omphalodes subsp. *discordans* (Nyl.) Skult, comb. nova

Parmelia discordans Nyl. in Brenner, Medd. Soc. F. Fl. Fenn. 13: 40, 1886. — *Parmelia omphalodes* var. *discordans* (Nyl.) H. Magn., Flora över Skand. busk- och bladlavar, 89. 1929. — Lectotype (sel. by W. Culberson 1969): U.S.S.R., Hogland, 1868 Brenner (H-NYL 34916).

Parmelia omphalodes var. *fallax* Oliv., Expos. Lich. Ouest France, 2: 413. 1903. — Type: France, Sarthe: St-Léonard-des-Bois, Monguillon (n. v.).

Parmelia omphalodes f. *insensitiva* H. Magn., Svensk Bot. Tidskr. 13: 89. 1919. — *Parmelia insensitiva* (H. Magn.) Hilitzer, Ann. Mycol. 22: 223. 1924. — Syntype: Sweden, Västergötland, Göteborg, Änggården, 1.IX.1918 H. Magnusson: Malme Lich. Suec. Exs. 781 (H).

Thallus usually growing in mats of moderate thickness and width, with narrow or moderately narrow lobes predominating. Lobes frequently convex. The reticulum of pseudocyphellae less marked than in subsp. *omphalodes*; they are sparse in young lobes. Upper cortex usually less glossy than in the other taxa. Colour of exposed thalli rather dark brown, that of shaded thalli pale brown to grey white.

Chemistry. — Cortex K+ yellow (atranorin), medulla K-, C-, KC-. Constant (or subconstant): atranorin, protocetraric acid, lobaric acid, protolichesterinic acid (as a rule +), omp-1 (associated with protocetraric acid). Accessory compounds: galbinic acid, fumarprotocetraric acid, omp-2, unknown fatty acids.

Distribution and habitat. — In Eastern Fennoscandia mainly occurring in the SW archipelago and adjacent coastal sites in the southern parts of the study area. Subsp. *discordans* mostly grows at slightly "higher" levels, often about 15–100 m over sea-level, whereas subsp. *omphalodes* accepts habitats down to about 1 m over sea-level. In Sweden 'f. *insensitiva*' is reported by Magnusson (1919; 89) to be as frequent on the Swedish west coast as the 'main form' (*omphalodes*). He also found a similar negative reaction with KOH in specimens from Skåne, Södermanland and Värmland. — Fig. 9B.

Representative specimens examined. — Lists with complete data in H, TUR and TURA. Finland: Alandia. Mariehamn 1949 Häyrén (H); Stor-Sottunga 1977 Kvist (H); Geta Dånö 1981 Skult (TURA), Soltuna 1981 Skult (TURA); Saltvik 1981 Skult (TURA); Regio aboensis. Korpo 1935 Eklund (H); Nagu 1981 Kvist (H); Nystad 1949 Häyrén (H); Nylandia. Helsingfors 1938 Marklund (H). — U.S.S.R. Hogland 1868 Brenner (lectotype H-NYL 34916); Estonia. Növalt 1933 Lippmaa (H). — Norway: Nordland. Svolvaer 1959 Bäck (H). — Sweden: Dalarna. Grangärde parish 1959 Santesson 12728a (H); Västmanland. Arboga 1946 Kjellmert (H).

Exsiccata examined. — des Abbayes: Lich. Gall. 39 (H); Havaas: Lich. Norv. occ. 57 (H); Krypt. Exs. Vindobon. 2571 (H); Lich. Fenn. 195 (H, TUR); Magnusson: Lich. Sel. 106 (Bohuslän 6.VIII.1930 Magnusson; H); Malme: Lich. Suec. 781 (Västergötl., Göteborg Änggården 1.IX.1918 Magnusson; H) Vězda: Lich. Sel. 916 (H).

Notes on Parmelia omphalodes in other parts of the world

North America

Preliminary studies have been undertaken on material that is mainly from Canada and Alaska, but also from other parts of the U.S.A. The strain rich in protocetraric acid (*discordans*) seems to be absent (?) from North America. The salazinic acid-rich strain without lobaric acid and mostly also protolichesterinic acid (*pinnatifida*) is apparently frequent, especially in Canada and Alaska. Several of the samples studied are from mountains in the U.S.A. The salazinic acid-rich strain with lobaric and protolichesterinic acids is also present in North America. The material investigated is restricted, however, and perhaps not very representative.

Comparing the 'Canadian *pinnatifida*' morphotypes with Fennoscandian ones, I found that with respect to the dominant lobe width and the abundance of laminal pseudocyphellae, they usually occupy an intermediate position between the 'Fennoscandian *pinnatifida*' and *omphalodes* s. str. Laminal pseudocyphellae sometimes also occur in young, small lobes. A lingulate form of younger lobe is found. The surface of the upper cortex is fairly even in younger parts of the thallus, but in older parts it can be very wrinkled. The colour of the upper cortex varies from pale grey to chestnut brown, corresponding to the colour of specimens from northern Fennoscandia. The 'formula' for this 'Canadian *pinnatifida*' strain is the same as that found for *pinnatifida* in Eastern Fennoscandia and adjacent regions:

Major compounds: Sa, At
Accessory and minor compounds: Csa(±), Pr(±), Ga(±), omp-2 (±), Fu(±), PL(±), Fa-2(±), Fa-3(±)

Rather few samples of *omphalodes* s. str. from North America have been analysed; their chemical 'formula' is in good agreement with that for the 'Fennoscandian *omphalodes*':

Sa, Lo, PL, At
Csa(±), Pr(±), Ga(±), omp-2(±), Fa-2(±), Fa-3(±)

Morphological variability exists, as in Eastern Fennoscandia. Specimens of 'typical' *omphalodes* appearance but lacking Lo and PL are not unusual.

In the arctic parts of Canada, Spitzbergen, and in other places between c. 70° and 80° N, another salazinic acid-rich strain occurs that also contains comparable amounts of norstictic acid. In the material analysed I found twenty specimens belonging to this strain. The morphotype is rather similar to that of 'Canadian *pinnatifida*': lobes ± rounded, a little broader than in Fennoscandian *pinnatifida*, with a limb of marginal pseudocyphellae. The surface of the upper cortex is even and frequently coated with a grey white pruina. The preliminary 'formula' is:

Sa, N, At
Csa(±), Pr(±), CN(±), omp-2(±), omp-3(±), Fu (±), Ufa(±),stictic acid (±)

Representative specimens examined. — Canada: Ellesmerelandia, Innerer Gänsefjord 1901 Simmons 3417 (H). U.S.A.: Alaska, Point Barrow 1958 Thomson, Shushan & Sharp (H). Norway, Spitzbergen: Murchison Bay Korsöya 1931 Scholander (H), Edgeöya NW-coast, alt. 140 m 1969 Oosterveld 02053 (H).

Europe and Asia

About 75 samples collected outside Eastern Fennoscandia, in Europe and Asia, were analysed. The material is restricted, but some results and impressions can be given.

Western Europe (material from England, Belgium, France, Portugal incl. Madeira): The chemical strain 'Sa + Lo+ PL' (*omphalodes* s. str.) seems to be most frequent. In a chemical sense it corresponds well with the strain in Fennoscandia. Several of the samples were collected on mountains up to 1 650 m. The protocetraric acid-rich strain *discordans*, mainly collected in coastal regions is morphologically similar to the Fennoscandian one. No samples so far analysed have represented the chemical strain 'Sa' (*pinnatifida*).

Central Europe (material from Austria, Germany, Hungary and Switzerland): The material studied belongs as a rule to the strain 'Sa + Lo + PL' (*omphalodes* s. str.). An exception is the type of *P. pinnatifida* Kurok. (*P. omphalodes* var. *panniformis* Ach.), selected and analysed by Kurokawa from H-ACH (the specimen probably collected in Switzerland). The samples studied by me were partly collected in alpine habitats (alt. 1 500–2 000 m), partly in the lowlands. Morphotypes of 'normal' *omphalodes* appearance are found and also ones with smaller lobes (the latter usually determined as var. *panniformis*). It is noteworthy that lobaric acid also occurs regularly in thalli growing in extreme alpine habitats. This does not support the opinion of some lichenologists that lobaric acid occurs only occasionally and is environmentally controlled.

North, Central, and East Asia: The material studied is very restricted, but the two salazinic acid-rich strains, with and without lobaric acid, are represented. The chemical strain of the *pinnatifida* type seems to be frequent, e.g. in Altai and the adjacent highlands. In some cases these specimens are of the '*omphalodes* morphotype'. The samples from Japan mostly agree, morphologically and chemically, with Fennoscandian specimens of *pinnatifida*.

The present distribution of the *Parmelia omphalodes* populations revealed by this preliminary survey could be explained by the following postglacial history. During the latest glaciation, populations of *pinnatifida* probably survived on 'nunataks' and in refugia in Scandinavia, whereas the other strains could hardly survive there. Populations of *omphalodes* s. str. and *discordans* were presumably able to survive in some southern parts of Europe. During the postglacial time the range of *omphalodes* was greatly enlarged, this strain being adapted to high elevations and rather extreme sites, e.g. in Central Europe. Subsp. *discordans* probably spread along the Atlantic coast, mostly in a northern direction. The Fennoscandian population of *omphalodes* s. str. may be assumed to be younger than the *pinnatifida* population in that region and to be the result of postglacial spreading from the south. During the postglacial period genetic exchange apparently sometimes took place between representatives of *pinnatifida* and *omphalodes* s. str., judging from the existence of ± intermediate forms.

During the latest glaciation in North America the absence of geographic barriers presumably allowed the populations of *pinnatifida* and *omphalodes* s. str. to retire southwards and survive. Opportunities for genetic exchange between these populations must have existed for a long time. This would explain why specimens of the chemical strain *pinnatifida* in Canada are frequently of a morphotype very like that of *omphalodes* s. str. It is interesting to note that in North America the salazinic acid-rich strain without lobaric acid, but very often with morphological characters typical of *omphalodes* is dominant in climatically extreme sites. In corresponding habitats in Central Europe, the salazinic acid-rich strain with lobaric acid and fairly often with morphological characters of *pinnatifida* seems to be dominant.

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