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The lichen genus *Usnea* in East Fennoscandia. III. The shrubby species

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Nine shrubby *Usnea* species are reported from East Fennoscandia: *Usnea diplotypus* Vain., *U. fulvoreagens* (Räsänen) Räsänen, *U. glabrata* (Ach.) Vain., *U. glabrescens* (Nyl. ex Vain.) Vain. ex Räsänen, *U. hirta* (L.) F. H. Wigg., *U. lapponica* Vain., *U. subfloridana* Stirt., *U. substerilis* Motyka and *U. wasmuthii* Räsänen. New chemotypes are reported in *U. glabrescens*, *U. substerilis* and *U. wasmuthii*. Some chemotypes have geographical tendencies in their distribution. For instance, the thamnolic acid strain of *U. subfloridana* is the main chemotype of the species only in some southern coastal regions. Several poorly known taxa described especially by V. Räsänen are identified and lectotypified. A key to the shrubby *Usnea* species in East Fennoscandia is provided.

Key words: Finland, lichen, Russia, secondary chemistry, taxonomy, *Usnea*

INTRODUCTION

The Finnish lichenologist Edvard Vainio (e.g., Vainio 1925) laid the foundation for the taxonomy of the lichen genus *Usnea* Dill. ex Adans. (Lecanorales, Parmeliaceae) in northern Europe. Veli Räsänen (e.g., Räsänen 1919, 1931, 1933, 1951) was also much interested in the genus, describing numerous new species and varieties. His work was much influenced by the world monograph by Motyka (1936–1938, 1947), who cites numerous Finnish specimens. Finally Räsänen (1951) reported 34 species and eight varieties from Finland.

Motyka's and Räsänen's species concepts were doubted by many authors (e.g., Keissler 1960, Klingstedt 1965), but because the taxonomy

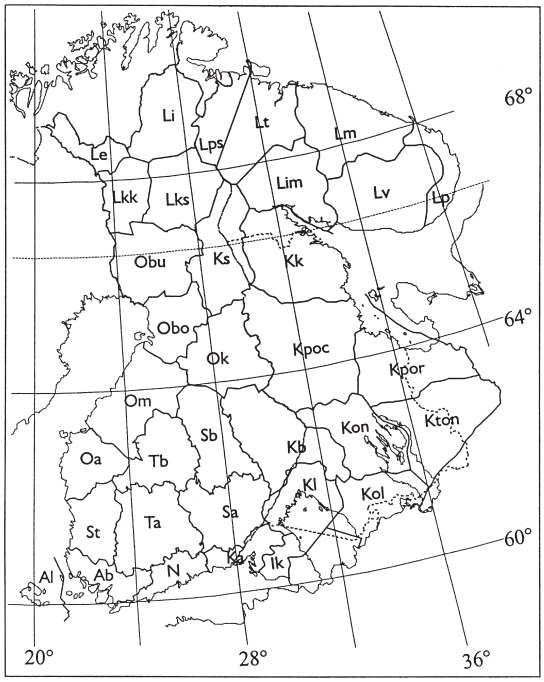

Fig. 1. The biogeographical provinces. **Finland**: 1 Åland (Alandia, Al), 2 Varsinais-Suomi (Regio aboënsis, Ab), 3 Uusimaa (Nylandia, N), 4 Etelä-Karjala (Karelia australis, Ka), 5 Satakunta (St), 6 Etelä-Häme (Tavastia australis, Ta), 7 Etelä-Savo (Savonia australis, Sa), 8 Laatokan Karjala (Karelia ladogensis, Kl), 9 Etelä-Pohjanmaa (Ostrobottnia australis, Oa), 10 Pohjois-Häme (Tavastia borealis, Tb), 11 Pohjois-Savo (Savonia borealis, Sb), 12 Pohjois-Karjala (Karelia borealis, Kb), 13 Keski-Pohjanmaa (Ostrobottnia media, Om), 14 Kainuu (Ostrobottnia kajanensis, Ok), 15 Oulun Pohjanmaa (Ostrobottnia ouluensis, Obo), 16 Perä-Pohjanmaa (Ostrobottnia ultima, Obu), 17 Koillismaa (Regio kuusamoënsis, Ks), 18 Kittilän Lappi (Lapponia kittilensis, Lkk), 19 Sompion Lappi (Lapponia sompiensis, Lks), 20 Enontekiön Lappi (Lapponia enontekiensis, Le), 21 Inarin Lappi (Lapponia inarensis, Li). **Russia**: Leningrad Region: 1 Karelia australis (Ka, Russian side), 2 Isthmus karelicus (Ik); Republic of Karelia: 3 Karelia ladogensis (Kl, Russian side; southernmost parts located in the Leningrad Region), 4 Karelia olonetsensis (Kol), 5 Karelia borealis (Kb, Russian side), 6 Karelia onegensis (Kon), 7 Karelia transonegensis (Kton), 8 Karelia pomorica occidentalis (Kpoc), 9 Karelia pomorica orientalis (Kpor), 10 Regio kuusamoënsis (Ks, Russian side; northernmost parts located in Murmansk Region), 11 Karelia keretina (Kk, northernmost parts located in the Murmansk Region); Murmansk Region: 12 Lapponia Imandrae (Lim), 13 Lapponia Varsugae (Lv), 14 Lapponia ponojensis (Lp), 15 Lapponia petsamoënsis (Lps), 16 Lapponia tulomensis (Lt), 17 Lapponia murmanica (Lm).

and nomenclature of the genus turned out to be very difficult, its thorough treatment was avoided by most lichenologists. Hakulinen (1963) reduced the number of Finnish species to 25 (plus seven varieties) and Carlin and Swahn (1977) made an attempt to establish a new taxonomy for the Swedish species. Bystrek (1994a) published a synopsis of the European *Usnea*, but because he essentially follows Motyka, we regard most of his species concepts untenable. Only Clerc (e.g., 1987a, 1997) started a serious revision of the genus *Usnea* in the Northern Hemisphere.

A project to revise the *Usnea* material collected from East Fennoscandia was started in 1993. The study area consists of Finland and the northern part of the Leningrad Region, the Republic of Karelia and the Murmansk Region in Russia (Fig. 1). The study has resulted in some earlier publications (Myllys 1994, Halonen & Puolasmaa 1995, Halonen 1997). A treatment of the pendent species, excluding *Usnea longissima*, is still under preparation. Based on the work of our project, Vitikainen *et al.* (1997) provisionally reported 13 species of *Usnea* from Finland, reducing most of the taxa recognized by Räsänen to synonymy.

As to Russian Fennoscandia, Dombrovskaya (1970) reported five species of *Usnea* from the Murmansk Region. Based on Motyka's identifications Ahlner (1937; overlooked by Dombrovskaya) reported seven more species, with four subspecies and one variety, from the present Murmansk Region (under Salla and Petsamo). Golubkova (1996) reported five species for the Murmansk Region, 15 species for the Republic of Karelia and five species for the Leningrad Region (her "widespread" species were considered to be present in all the three areas). Fadeeva *et al.* (1997) recognized only 10 species from the Republic of Karelia.

Most of the species treated here were classified by Bystrek (1994a) as belonging to *Usnea* subg. *Usnea* sect. *Barbata* subsect. *Subfloridana* Bystrek (incorrect renaming of subsect. *Comosae* Motyka) or subsect. *Silesiaca* Bystrek. *Usnea hirta* was placed in sect. *Foveata* Motyka, however, and *Usnea glabrata* in sect. *Glabrata* Motyka. We think that his classification is very artificial and it also contains numerous nomenclatural errors.

The present study is a revision of the shrubby to subpendent species found in East Fennoscandia. Special attention is paid to the identity, bibliographic citation, typification and secondary chemistry of the taxa described from the study area.

MATERIAL AND METHODS

The study is mainly based on herbarium material, including numerous type specimens, deposited in BM, H (incl. H-ACH, H-NYL), KPABG, KUO, LBL, OULU (incl. herb. Oulanka), S (incl. S-Motyka), TUR (incl. TUR-V) and UPS. However, not every single specimen in the large collections in H, for instance, was identified. The study also includes field observations. Thickness of the cortex, medulla and central axis were measured by cutting a short segment (usually 1 mm or less) of a branch, and the layers were measured along two crossed sections from both ends of the segment. Measurements were made with a stereomicroscope on the thickest part of the largest branch. For each measured specimen, thicknesses are given as an average of all measurements. The ratio of the width of the cortex, the medulla and the central axis, can be given as a percent of the radius for the cortex and the medulla, and as a percent of the diameter for the axis (%C/%M/%A). Because of the sparse material of *Usnea diplotypus,* its inner structure was studied by the method of Clerc (1984). In this method the branch is cut to the middle point, and the thickness of the layers is measured from a cross section. Chemistry was examined by means of standardized thin-layer chromatography (TLC), described by Culberson and Ammann (1979), Culberson *et al.* (1981), and White and James (1985).

The author Halonen is responsible for the taxonomy, while the author Myllys has studied the morphology and the chemistry together with the first author. The author Ahti is responsible for the nomenclature together with Halonen, and the author Petrova has studied and collected *Usnea* specimens from the Murmansk Region.

MORPHOLOGY

According to Clerc (1987a,1987b), the most diagnostic morphological characters of *Usnea* are (1) the dominant branching patterns, (2) the shape of the secondary branches, (3) the colour and frequency of segmentation of the basal portions, (4) the type of soralia and (5) details of the inner structure. The shape and density of papillae and the density of fibrils are also useful, but are to a considerable extent environmentally controlled. In the East Fennoscandian species, the colour of the living thallus does not have a notable diagnostic value. In contrast, the inner structure seems to have a remarkable systematic significance. The species within the *U. florida* agg. (*U. fulvoreagens*, *U. glabrescens*, *U. subfloridana* and *U. wasmuthii*), and within the *U. rigida* agg. (*U. diplotypus*, *U. lapponica* and *U. substerilis*) are similar in their anatomy (Table 1; *see* also Clerc 1984), while *U. glabrata* and *U. hirta*, which do not belong to either aggregate, differ in their anatomy from the other species.

The majority of the East Fennoscandian *Usnea* species have a shrubby, divergent thallus, which may become subpendent in most species, i.e. having pendent apical parts. Some of these species may also very rarely be pendent along the entire length of the thallus. The branching pattern is isotomic-dichotomous when dividing branches are somewhat equal in thickness, or anisotomic-dichotomous when they are not. Furthermore, specimens with an unusual branching pattern for a species are not rare. Axils of the thickest branches are

Table 1. Thicknesses of the cortex (% of the radius), the medulla (% of the radius) and the central axis (% of the diameter) of the East Fennoscandian shrubby *Usnea* species. * = thicknesses measured with a method different from that used for the other species (*see* Methods).

	Cortex	Medulla	Central axis
Usnea glabrata (*n* = 12)	4–*5*–7	32–*36*–39	13–*18*–23
Usnea hirta (*n* = 18)	6–*8*–10	19–*27*–32	21–*31*–46
*Usnea diplotypus** (*n* = 9)	7–*9*–10	17–*22*–26	33–*40*–47
Usnea substerilis (*n* = 12)	6–*9*–13	10–*20*–28	31–*42*–54
Usnea lapponica (*n* = 42)	4–*9*–12	10–*19*–32	27–*45*–72
Usnea glabrescens (*n* = 30)	9–*11*–13	10–*17*–23	32–*43*–56
Usnea fulvoreagens (*n* = 28)	8–*11*–15	8–*14*–20	38–*50*–58
Usnea subfloridana (*n* = 18)	10–*12*–15	7–*14*–21	32–*47*–66
Usnea wasmuthii (*n* = 18)	10–*12*–15	5–*10*–16	44–*55*–65

usually less than 90°, but in *U. fulvoreagens*, for instance, they are often ca. 90°, which gives a distinctly divergent habit for a thallus. The branches are circular in cross section, or slightly angular, and may have ridges and/or foveoles (round or oval pits). In longitudinal section, branches are either tapering, or about the same thickness in the whole length, or irregularly shaped. Branches are more or less segmented by well demarcated annular cracks, which may be lined by white, everted medullary rings.

The base in most of the East Fennoscandian *Usnea* species is even in thickness or slightly fusiform, and the colour varies from pale to jet black. The frequency of segmentation of the base has only minor diagnostic value in the East Fennoscandian species, but thin longitudinal cracks are common at the bases of *U. wasmuthii* while they are rare or sparse in other species.

Soralia may be tuberculate, superficial or ± excavate. They vary from minute and punctiform to large and expanded. In some species soralia may even encircle the branches, and may also become confluent. Soralia develop on local breaks of the cortex or arise from scars. Scars are borne when fibrils become detached, for instance. Clerc and Herrera-Campos (1997) call the tuberculate scars of fibrils "fibercles". Soredia are farinose to granulose. In most species soralia have isidia (isidiomorphs, according to Clerc and Herrera-Campos 1997) at least when young, in which case the isidia may partly or totally be replaced by soredia. Isidia occur single or in clusters, and develop from the cortex or from medullary tissues, i.e. scars and soralia. Many species, for instance, *Usnea glabrescens*, *U. lapponica* and *U. wasmuthii*, have modifications with tuberculate and more or less confluent soralia, which may produce spinules.

The thickness of the cortex, medulla and central axis have a significant taxonomic importance. The structure of the medulla varies from lax (loosely arachnoid in *Usnea glabrata*) to dense, or only exceptionally compact in the treated shrubby species. The surface of the cortex is usually mat, but *U. glabrata* has a somewhat shiny surface, which is typical for the species in the *U. fragilescens* agg. (Clerc 1987a, 1998, Halonen *et al.* 1998). In the East Fennoscandian species, the colour varies from pale straw-coloured, to yellowish-green, greyish-green, or deep yellow. *Usnea hirta* often shows a more intense yellow colour than the other species since it mainly grows in open sites. Specimens change colour with prolonged storage in the herbarium, when some species may turn darker in colour or even deep brown (e.g., *U. glabrata* and *U. lapponica*).

Wart-like papillae vary in shape from low and verrucous to tall and cylindric. Tubercles are similar, but differ in their often larger size and in the presence of medulla. Tubercles often produce soredia and/or isidia. The distinction between papillae and tubercles is not always clear, especially in *Usnea subfloridana* and *U. wasmuthii*, in which structures similar to papillae regularly develop into soralia. Cilia-like fibrils may be irregularly distributed on the thallus, for instance, in *U. glabrescens*, where fibrils are normally absent or sparse in the apical parts while they are more abundant near the base. Short, spinulose fibrils are often called spinules. Papillae, tubercles and fibrils have been found in every East Fennoscandian *Usnea* species, but their abundance may vary considerably within a species.

All the boreal, northern circumpolar *Usneae* are secondary species, which only rarely produce apothecia. Fertile primary species, for example, *U. florida* (L.) F. H. Wigg. and *U. rigida* (Ach.) Mot. *s. lato*, are found in temperate areas of Europe and North America (Clerc 1984, Halonen *et al.* 1998). Secondary species become dispersed almost solely by vegetative diaspores and thallus fragments, and therefore they may have apomictic populations. In East Fennoscandia, apothecia are most frequently present in *U. hirta* and *U. subfloridana*, but are also found very rarely in *U. diplotypus*, *U. fulvoreagens*, *U. glabrata*, *U. glabrescens* and *U. lapponica*.

ECOLOGY AND DISTRIBUTION

All the East Fennoscandian *Usnea* species are primarily epiphytes. The majority of them are also occasionally found growing on lignum (especially *Usnea hirta*) and more rarely on rocks. Local species may display more or less phorophyte preference. This may be partly due to bark properties such as acidity, but climatic conditions seem to have much more significance. For example, members of the *U. fragilescens* agg. are commonly

present on pines in hypermaritime regions of Norway (Clerc 1987a), while the relatively xerophytic species *U. hirta* is the only common *Usnea* on pines in East Fennoscandia. Most of the East Fennoscandian *Usnea* species are more or less hygrophilous and photophilous, and therefore they are most frequent in moist, well-lit sites, but they have quite wide ecological amplitude and may also occur near farms, in parks and in other man-made habitats. *Usnea glabrescens*, however, is more restricted to old-growth forests than the other shrubby species.

Usnea is a cosmopolitan genus occurring in all continents. The East Fennoscandian *Usnea* flora mostly consists of species that are widely distributed in the Northern Hemisphere, but also contains some species that are nearly cosmopolitan being also found in the Southern Hemisphere. The genus is probably phylogenetically very old and many of the species seemingly have reached their present wide world distribution during a long period, in which they have adapted to different habitats and climates.

East Fennoscandia mainly belongs to the boreal vegetation zone, in which coniferous forests are prevailing, except in the northernmost vegetation zones. In the majority of the East Fennoscandian areas, the climate is relatively oceanic in terms of temperature but less so in humidity conditions. The relatively low hygric oceanity is indicated by the absence of hypermaritime *Usnea* species, e.g., *U. cornuta* Körb. and *U. fragilescens* Lynge (*see* Clerc 1987a, Halonen *et al.* 1998), in the area.

All *Usnea* species have a more or less southern distribution in East Fennoscandia. *Usnea hirta*, *U. lapponica* and *U. subfloridana* are the only shrubby species that have been found occasionally in the northernmost regions. The front of the frequent occurrence of the genus roughly follows the northern limit of the Middle Boreal bioclimatic zone (*see* Ahti *et al.* 1968). Most of the species have a wide range in East Fennoscandia occurring both in western and eastern regions, but *U. glabrata* represents an eastern element in the area, although less distinctly than *U. longissima* (*see* Halonen 1997). However, the distribution of the *Usnea* species in Russia is very insufficiently known, since many regions are poorly studied. The best known Russian area is the western shore of Lake Ladoga, which has mainly been studied by V. Räsänen.

CHEMISTRY

Identifications of secondary compounds give a considerable help in the determination of *Usnea* specimens, because most of the species are very variable in morphology and different species may be morphologically overlapping. Most of the chemical compounds found in *Usnea* were not known to Motyka (1936–1938), but they were mainly detected by Y. Asahina and later chemists and chemotaxonomists. Early taxonomists did use certain colour reagents, which are often not specific enough, however.

All *Usnea* species occurring in East Fennoscandia contain a yellow pigment, usnic acid, in the cortex. The medulla has a much more complex chemistry (Table 2) containing mainly closely related β-orcinol depsidones, e.g., norstictic, stictic, psoromic, protocetraric and salazinic acids, or β-orcinol depsides, e.g., thamnolic, squamatic and barbatic acids. Also present are fatty acids, including caperatic acid and the murolic acid complex. Terpenoids, e.g., zeorin, are found in every shrubby *Usnea* species in East Fennoscandia, and they are especially common in *U. fulvoreagens* in which terpenoids have been found in almost every studied specimen. Furthermore, several unknown substances were found, but generally they are not mentioned in the section "Taxonomy", since they are not taxonomically important.

Salazinic acid is the most common secondary substance in the East Fennoscandian species. Norstictic acid is also relatively often present, whereas the other compounds of the stictic acid group (incl. connorstictic, stictic, constictic and cryptostictic acids) and protocetraric acid, for example, are less common and/or are often accessory.

Many *Usnea* species produce different chemotypes in different areas, but the same species may also have several strains in one locality. Chemotypes occurring in other regions of Europe are mentioned in the section "Taxonomy". The chemistry of *Usnea* in other parts of the world has been investigated, e.g., by Asahina (1956), Clerc (1997), Clerc and Herrera-Campos (1997), Halonen *et al.*

Table 2. Main secondary medullary metabolities in the shrubby species of *Usnea* in East Fennoscandia. + = present in all specimens examined, ± = present in some specimens, – = not present, a = accessory substance, not important for taxonomy and often present in small amounts, * = the strain may represent a hybrid. BAR = barbatic acid, CNSTI = connorstictic a., Cph-1 = convirensic a., Cph-2 = confumarprotocetraric a., CPSO = 2'-*O*-demethylpsoromic a., CRSTI = cryptostictic a., CSTI = constictic a., DBAR = 4-*O*-demethylbarbatic a., DIF = diffractaic a., FAT = fatty acids (the murolic acid complex in *U. hirta* and usually caperatic acid in *U. lapponica*), FUM = fumarprotocetraric a., NSTI = norstictic a., PRO = protocetraric a., PSO = psoromic a., SAL = salazinic a., SQU = squamatic a., STI = stictic a., THA = thamnolic a.

	DIF	BAR	DBAR	SQU	THA	Cph-1	Cph-2	FUM	PRO	NSTI	CNSTI	STI	CSTI	CRSTI	SAL	PSO	CPSO	FAT
Usnea diplotypus	–	±	a	–	–	–	–	–	a	–	–	–	–	–	+	–	–	a
Usnea fulvoreagens	±	–	–	–	–	–	–	–	a	±	a	±	a	a	±	–	–	–
Usnea glabrata	–	–	–	a	–	a	a	a	±	±	a	–	–	–	±	–	–	a
Usnea glabrescens	–	–	–	–	–	–	–	–	a	±	a	±	a	a	±	–	–	–
Usnea hirta	–	–	–	–	–	–	–	–	–	±	–	–	–	–	–	–	–	±
Usnea lapponica	–	–	–	–	–	–	–	–	a	–	–	–	–	–	±	±	a	±
Usnea subfloridana	–	–	–	±	±	–	–	–	–	–	–	–	–	–	–	–	–	–
Usnea substerilis	–	±	a	–	–	–	–	–	a	±*	–	–	–	–	±	–	–	a
Usnea wasmuthii	–	±	a	–	–	–	–	–	a	–	–	–	–	–	±	–	–	–

(1998), and Stevens (1999). Chemotypes may be more or less artificial, since compounds may occasionally occur in very low amounts and therefore be overlooked in TLC studies.

TAXONOMY

Descriptions given in the key and under the species refer to the variation present in the East Fennoscandian material. Norstictic and salazinic acids give K+ yellow and PD+ yellow reactions in low concentrations, but turn slowly to orange or red at higher concentrations (the CK reagent gives reactions similar to the K reagent with norstictic and salazinic acids). The provincial distribution of each species in Finland and Russian Fennoscandia is given using the traditional biogeographic provinces (Fig. 1).

Key to the shrubby *Usnea* species in East Fennoscandia

1. Papillae absent (very rarely present); cortex thin and medulla normally thick and lax 2
1. Papillae present (may be absent in juvenile thallus); cortex and medulla various 3
2. Soralia minute; isidia numerous; fatty acids normally present (usually K–, PD–); common ..... 5. *U. hirta*
2. Soralia large; isidia absent; protocetraric acid group normally present (K– or K+ brownish, PD+ red-orange); rare ..... 3. *U. glabrata*
3. Branches mainly anisotomic-dichotomous; never with stictic acid group, squamatic or thamnolic acids present 4
3. Branches mainly isotomic-dichotomous; stictic acid group, squamatic or thamnolic acid may be present (except in *U. wasmuthii*) 6
4. Mature soralia deeply excavate; isidia absent ..... 6. *U. lapponica*
4. Mature soralia tuberculate to slightly excavate; isidia normally present at least on young soralia 5
5. Mature soralia enlarged, plane to slightly excavate; isidia short, often sparse and may be present only on young soralia ..... 8. *U. substerilis*
5. Mature soralia punctiform, with numerous tall isidia .. .. 1. *U. diplotypus*
6. Isidia very rare; stictic acid group normally present 7
6. Isidia present at least on young soralia; never with stictic acid group 8
7. Mature soralia mostly plane to slightly excavate, discrete; fibrils usually sparse at least near apical parts; mature thallus normally relatively tall, usually with sala-

zinic acid ..... 4. *U. glabrescens*

7. Mature soralia mostly deeply excavate, ± confluent; fibrils usually abundant; mature thallus normally relatively small, usually without salazinic acid .... 2. *U. fulvoreagens*
8. Mature soralia tuberculate to slightly excavate; longitudinal cracks rare at the basal part; squamatic and/or thamnolic acids present (K–, PD–, or K+ yellow, PD+ yellow-orange) ..... 7. *U. subfloridana*
8. Mature soralia usually plane to slightly excavate and often elongated; longitudinal cracks common at the basal part; barbatic and/or salazinic acids or very rarely usnic acid alone present (K–, PD–, or K+ yellow, orange or red, PD+ yellow or orange) .... 9. *U. wasmuthii*

1. ***Usnea diplotypus*** Vain.

Meddeland. Soc. Fauna Fl. Fenn. 48: 172. 1925 ('1924'). — Type: Finland, Varsinais-Suomi, Turku, Pahaniemi, in latere abrupto rupis graniticae, 1923 *Vainio* (TUR-V 530!, lectotype, here designated; TUR-V 534a!, isolectotype). Chemistry: usnic and salazinic acids and unknown fatty acid A4/B5/C5 (Clerc 1987a).

Thallus erect, more rarely subpendent, to ca. 7(–12) cm long, richly branched. Branching mainly anisotomic-dichotomous. Branches slender, to ca. 1(–1.5) mm in diam., occasionally with foveoles or depressions. Annular cracks sometimes slightly constricted, rarely with white medullary rings. Base slightly to distinctly blackened. Cortex relatively thin, 7–*9*–10% ($n = 9$). Medulla normally lax and relatively thick, 17–*22*–26% ($n = 9$). Central axis relatively thick, 33–*40*–47% ($n = 9$). Papillae mostly cylindric and numerous. Fibrils usually abundant and often present also near apical parts. Soralia (*see* Clerc 1987b: 101) minute, usually tuberculate, developing mainly from tubercles; soredia usually farinose. Isidia generally numerous and often relatively tall.

Chemistry. Strain 1 ($n = 11$): usnic + salazinic ± protocetraric acids (trace) ± unknown fatty acid (K+ yellow, orange or red, PD+ yellow or orange); strain 2 ($n = 3$): usnic + salazinic + barbatic acids (K+ yellow or orange, PD+ orange).

Remarks. *Usnea diplotypus* is a species close to *U. substerilis* (Clerc 1987a) and *U. lapponica*, and they probably belong to the *U. rigida* agg. (Halonen *et al.* 1998) in which *U. rigida s. lato* is the primary, regularly fertile counterpart. The aggregate is characterized by the relatively thin cortex, usually lax and fairly thick medulla, pale to distinctly blackened base and branches which are not clearly tapering and are often ± foveolate. The chemistry of the aggregate is quite variable, but strains with salazinic acid are very common. Furthermore, distributions of the species in the aggregate have continental tendencies. All the East Fennoscandian *U. diplotypus* specimens are shrubby to subpendent, but the species is often pendent in Central Europe. Those populations also may have a different chemistry, including a strain with alectorialic acid (Clerc 1987a).

Many of the *Usnea diplotypus* specimens have previously been determined as *U. subfloridana* (incl. *U. comosa* and *U. similis*), but the latter species has a mainly isotomic-dichotomous branching pattern, often enlarged soralia, usually shorter papillae and it contains squamatic and/or thamnolic acids. *U. substerilis*, which is also an isidiate species, differs by its ± enlarged soralia and minute isidia that are normally present only on young soralia.

Ecology. The species has been collected from *Picea* ($n = 4$), *Betula* ($n = 3$), *Alnus* ($n = 2$), *Salix* ($n = 1$), *Sorbus* ($n = 1$) and rocks ($n = 1$) (in total 12 specimens). *Usnea diplotypus* grows in mesic forests and often in inhabited sites. As pointed out by Clerc (1987a: 493), the species is not primarily saxicolous as believed by Räsänen (1951) and Carlin and Swahn (1977).

Distribution. Finland: 2, 3, 5, 11, 12, 14–16. Russia: 1, 8, 10. World distribution: Europe, with continental tendencies, and Pacific coast of North America (Clerc 1987a, Halonen *et al.* 1998). *Usnea diplotypus* is apparently rare and southern in East Fennoscandia, but it is easily confused with modifications of some other species and thus it may have been overlooked.

Selected specimens examined. — **Finland**. Varsinais-Suomi: Naantali, Luonnonmaa, Käkölä, 1961 *Klingstedt* (H), strain 1. Uusimaa: Espoo, 1926 *Mannermaa* (OULU), strain 1. Satakunta: Kankaanpää, 1935 *Laurila* (H), strain 1. Pohjois-Savo: Kuopio, Levänen, 1941 *Räsänen* (H), strain 1. Pohjois-Karjala: Kaavi, Peuramäki, 1941 *Räsänen* (H), strain 2. Oulun Pohjanmaa: Kiiminki, Takalankylä, 1973 *Ulvinen* (OULU), strain 2. Perä-Pohjanmaa: Kemi, Niemelä, 1864 *Brenner* (H), strain 1. **Russia**. Leningrad Region. Karelia australis: Yashino (Vahviala), Hämeenvaara, 1938 *Fagerström* (H), strain 1. Republic of Karelia. Karelia pomorica occidentalis: between Syargozero (Särkijärvi) and Padany (Paadene), 1942 *Huuskonen* (H), strain 1. Regio kuusamoënsis: Paanajärvi National Park, Niskakoski, 1938 *Laurila* (H), strain 1.

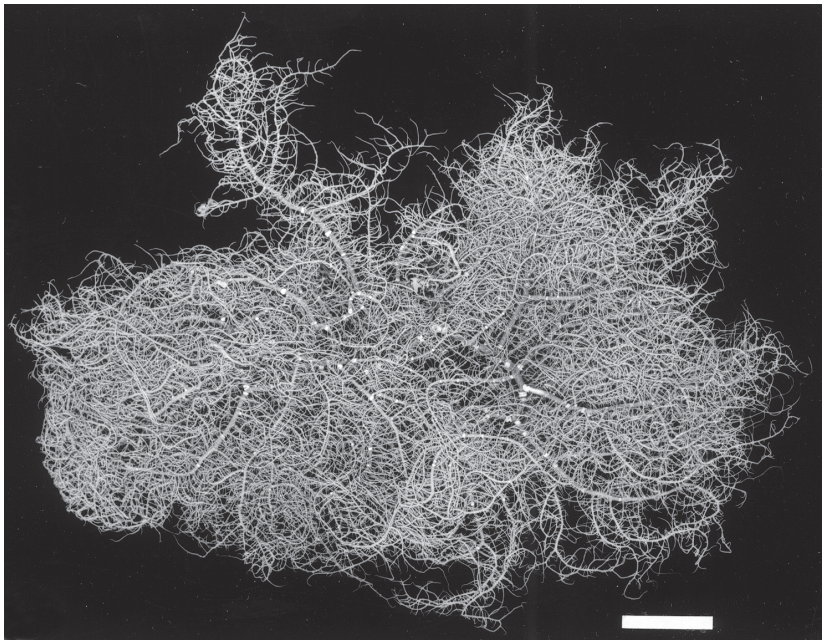

Fig. 2. Shrubby thallus of *Usnea fulvoreagens* (Räsänen) Räsänen with dense branches and fibrils. From 1929 *Räsänen* (H). Scale = 1 cm.

2. ***Usnea fulvoreagens*** (Räsänen) Räsänen

Lich. Fenn. Exs. no. 13 (Schedae: 5). 1935. — *Usnea glabrescens* (Nyl. ex Vain.) Vain ex. Räsänen var. *fulvoreagens* Räsänen, Ann. Acad. Sci. Fenn. Ser. A4, 34(4): 20. 1931. — Type: Estonia. Virumaa, Vägeva, 1924 *Kari* (TUR!, syntype). Chemistry: usnic and thamnolic acids. — The collection (two thalli) represents *Usnea subfloridana*. — Other syntypes: Estonia. Saaremaa, Kuressaare, an Lärche, and Kihelkonna, an *Picea excelsa*, 1929 *Räsänen* (not found). — Proposed conserved type: Russia. Republic of Karelia, Kurkijoki, Lapinlahti, 1923 *Räsänen* (H!). Chemistry: usnic, norstictic, stictic, cryptostictic and constictic acids (*see* also Clerc 1987a: 494).

Usnea fulvoreagens f. *incolorascens* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 12(1): 50. 1939. — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Lapinlahti, ad corticem alni, 1932 *Räsänen* (H!, lectotype, here designated). Chemistry: usnic and constictic (trace) acids. — Syntypes: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Majalampi, ad corticem alni, 1932 *Räsänen* (H!), and Maasilta, ad corticem alni, 1933 *Räsänen* (S!). Chemistry: usnic and constictic acids in both syntypes.

Thallus (Fig. 2) erect, rarely subpendent, to ca. 10(–15) cm long, sparsely to more often richly branched, branches occasionally very densely arranged. Branching mostly isotomic-dichotomous. Branches normally slender, up to ca. 1.3(–1.8) mm in diam., apices quite often recurved. Annular cracks ± abundant, often with thick medullary rings (Fig. 3). Base distinctly blackened. Cortex usually relatively thick, 8–*11*–15% ($n = 28$). Medulla lax to dense, generally relatively thin, 8–*14*–20% ($n = 28$). Central axis relatively thick to thick, 38–*50*–58% ($n = 28$). Papillae usually cylindric, abundant on main branches. Fibrils numerous to very dense, rarely sparse. Soralia deeply excavate when mature with torn cortex around them, often confluent; soredia farinose. Isidia absent.

Chemistry. Strain 1 ($n = 97$): usnic acid + various combinations of compounds of the stictic acid group ± protocetraric acid (trace) (K+ yellow, orange or red, PD+ yellow or orange, or K–, PD– when only low amounts of compounds); strain 2 ($n = 7$): usnic + salazinic + norstictic acids ± other compounds of the stictic acid group ± protocetraric acid (trace) (K+ yellow, orange or red, PD+ yellow or orange); strain 3 ($n = 5$): usnic + diffractaic ± norstictic ± connorstictic acids (K+ yellow, orange or red, PD+ yellow or orange, or K–, PD– when the stictic acid group is absent); strain 4 ($n = 1$): usnic + unknown substance A2/B2 + traces of unknown substances (K+ yellowish, PD–). Norstictic acid is present in most specimens of strain 1. There are also many specimens which solely contain very low amounts of constictic acid, in addition to usnic acid (*Usnea fulvoreagens* f. *incolorascens* according to Räsänen, since it does

not give any medullary colour reactions with the K reagent). It is notable that four of the five specimens containing diffractaic acid have been collected from the Lake Ladoga area in Russia. Clerc (1992) did not detect salazinic acid in *U. fulvoreagens* in the British Isles, but diffractaic acid seems to be more common there than in East Fennoscandia.

Remarks. The name *Usnea fulvoreagens* is incorrect for this species, because the lectotype represents *U. subfloridana*. Unfortunately, two syntypes have disappeared. The type indicated by Motyka (1936: 284) and Clerc (1987a: 494) is not a type, since it is not cited in the protologue. The authors of the type are also cited incorrectly as "(Räsänen) Motyka" by Motyka. The name is well established, however, and therefore we propose a new conserved type for *U. glabrescens* var. *fulvoreagens* (P. Halonen & T. Ahti unpubl.).

The species probably belongs to the same aggregate with *Usnea glabrescens*, *U. subfloridana* and *U. wasmuthii*, in which *U. florida* is the primary fertile species. *Usnea florida* agg. is characterized by the usually isotomic-dichotomous branching pattern, cylindric and tapering branches rarely with foveoles, relatively thick cortex, usually dense medulla, distinctly blackened base and copious papillae. The chemistry of the aggregate is very variable and most of the species have oceanic tendencies in their distribution.

Usnea fulvoreagens is closely related to *U. glabrescens*, but is distinguished by the usually smaller, more divergent thallus, normally more abundant branches and fibrils, often taller papillae and soralia that are ± confluent and deeply excavate when mature. Furthermore, annular cracks with thick white medullary rings are more common in *U. fulvoreagens*, and the species only rarely produces salazinic acid, which is very often present in *U. glabrescens*. The delimitation of *U. fulvoreagens* and *U. glabrescens* can be difficult, however, and intermediate morphs are found (see also Halonen *et al.* 1998). As pointed out by Clerc (1992), *Usnea lapponica*, which also has deeply excavate soralia, is formerly often regarded as a synonym of *U. fulvoreagens*. *Usnea lapponica* differs, for instance, by its usually anisotomic branching pattern, thicker medulla and different chemistry without the stictic acid group.

Ecology. The species has mainly been collected from *Alnus* (35%), *Betula* (18%), *Picea* (13%), *Sorbus* (12%) and *Populus* (12%), and less frequently from *Prunus*, *Pinus*, *Salix*, *Juniperus*, *Tilia* and rocks (in total 96 specimens). *Usnea fulvoreagens* is likely to be most common in moderately open and humid mixed forests, and often occurs close to farmlands or other inhabited areas. The primary phorophytes are second-growth forest species.

Fig. 3. Annular cracks with white medullary rings on branches of *Usnea fulvoreagens* (Räsänen) Räsänen. From 1944 *Fagerström* (H). Scale = 1 mm.

Distribution. Finland: 1–7, 9–13, 15, 16; Russia: 2–4, 8. World distribution: Europe (Clerc 1992) and western North America (P. Halonen & L. Geiser unpubl.), with oceanic tendencies. The world distribution, however, is still poorly known. *Usnea fulvoreagens* is rare to scattered in East Fennoscandia with a relatively southern, i.e. middle to southern boreal distribution. The species has been collected more frequently in the inland lake area than in the coastal regions and it is distinctly less common than *U. glabrescens*.

Selected specimens examined. — **Finland**. Åland: Eckerö, 1935 *Räsänen* (H), strain 1. Etelä-Karjala: Vehkalahti, Pyhältö, 1947 *Fagerström* (H), strain 1. Satakunta: Eura, Kauttua, 1946 *Klingstedt* (H), strain 1. Etelä-Häme:

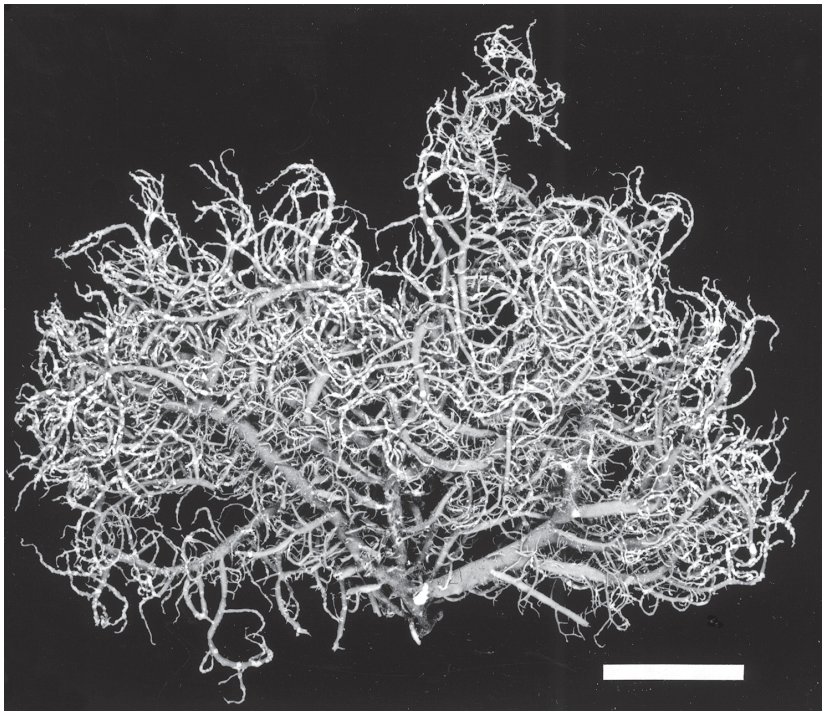

Fig. 4. Small, shrubby thallus of *Usnea glabrata* (Ach.) Vain. with inflated branches. From 1932 *Räsänen* (H). Scale = 1 cm

Lammi, Evo, 1909 *Backman* (H), strain 2. Pohjois-Häme: Saarijärvi, Mahlu, Lylymäki, 1944 *Koskinen* (H), strain 3. Keski-Pohjanmaa: Munsala, Gräsön, 1957 *Bäck* (H), strain 4. Oulun Pohjanmaa: Muhos, Poikakoti, 1923 *Räsänen* (H), strain 1. Perä-Pohjanmaa: Simo, Pahnila, 1946 *Räsänen* (H), strain 1. **Russia**. Leningrad Region, Isthmus karelicus: Zelenogorsk (Terijoki), Komarovo (Kellomäki), 1938 *Fagerström* (H), strain 3. Republic of Karelia. Karelia ladogensis: Sortavala, Mäkisalo, 1923 *Linkola* (TUR-V), strain 4. Karelia olonetsensis: Vedlozero (Vieljärvi), Kukkozero (Kukkajärvi), 1942 *Railonsala* (OULU, TUR), strain 1.

3. ***Usnea glabrata*** (Ach.) Vain.

Ann. Acad. Sci. Fenn., Ser. A4, 6(7): 7. 1915. — *Usnea plicata* (L.) F. H. Wigg. var. *glabrata* Ach., Lichenogr. Universalis 624. 1810. — Type: Switzerland. *Schleicher 318* (H-ACH 1854A!, holotype). Chemistry: usnic and fumarprotocetraric acids (TLC by P. W. James, protocetraric acid may have been overlooked).

Usnea barbata (L.) F. H. Wigg. var. *sorediifera* Arnold, Verh. K. K. Zool.-Bot. Ges. Wien 25: 471. 1875. — *Usnea sorediifera* (Arnold) Lynge, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 1921 (7): 229. 1921. — Type: Austria. Tyrol, on road Seefelt to Scharnitz ('Scharniz'), 3600 ft., 1874 *Arnold*, Lich. Exs. no. 572a (H-NYL 36544!, isolectotype). Chemistry: usnic, norstictic (trace), stictic, cryptostictic (trace) and constictic (trace) acids (isolectotype in H-NYL).

Usnea barbata [subsp.] *florida* Fr. var. *pilina* Vain., Acta Soc. Fauna Fl. Fenn. 13: 4. 1896. — *Usnea pilina* (Vain.) Räsänen, Lich. Fenn. Exs. no. 11 (Schedae: 4). 1935, *nom. illeg.* (*pro syn.*). — Type: Russia. Sibiria, Tyumen Region, Sotigovskaya (Sotigowskaja) by Konda River, 1880 *Vainio* (TUR-V 837!, lectotype, here designated; TUR-V!, three isolectotypes). Chemistry: usnic, norstictic and barbatic (trace) acids. The type material also contains three other strains: (1) usnic acid (trace); (2) norstictic acid (trace) and an unknown fatty acid A6 (usnic acid not found by TLC); (3) usnic, protocetraric, fumarprotocetraric, confumarprotocetraric (Cph-1) and convirensic (Cph-2) acids — *see* Myllys (1994: 126) and Halonen *et al.* (1998: 50), though Myllys (1994) exluded *U. florida* var. *pilina* from *U. glabrata*.

Usnea kujalae Räsänen, Ann. Missouri Bot. Garden 20: 9. 1933. — *Usnea glabrata* var. *kujalae* (Räsänen) Räsänen, Revista Univ. (Santiago) 21: 139. 1936. — Type: Canada. British Columbia, Hazelton, ad ramos pini, 1931 *Kujala* (H!, lectotype designated by Myllys 1994: 126; H!, isolectotypes). Chemistry: usnic acid — *see* Myllys (1994: 126–127).

For further synonyms and distribution of the species, *see* Keissler (1960), and Bystrek and Górzyńska (1985).

Thallus (Fig. 4) erect, small, to ca. 5(–10) cm long, sparsely to more often densely branched. Branching mostly anisotomic-dichotomous. Branches generally slender, to ca. 1.5(–1.8) mm in diam., inflated, ± foveolate, usually constricted

or fusiform at bases, apices often recurved. Annular cracks normally sparse, ± constricted, sometimes with thin, everted medullary rings. Base usually constricted to fusiform, pale to slightly blackened. Cortex somewhat shiny, thin, 4–*5*–7% (n = 12). Medulla loosely arachnoid, thick, 32–*36*–39% (n = 12). Central axis thin, 13–*18*–23% (n = 12). *Papillae* absent or occasionally low and sparse, very rarely tall and numerous. Fibrils usually abundant. Soralia mostly near the apices, tuberculate to distinctly excavate (especially when eroded in old herbarium material), relatively large, often becoming confluent, developing from plane cortex or from tubercles; soredia ± granulose. Isidia absent, but isidia-like spinules are occasionally present on soralia.

Chemistry. Strain 1 (n = 46): usnic + protocetraric + fumarprotocetraric acids ± convirensic acid ± confumarprotocetraric acid ± squamatic acid (1 specimen) (K– or K+ brownish, PD+ red-orange); strain 2 (n = 2): usnic + salazinic + norstictic ± stictic (trace) ± connorstictic (trace) + protocetraric (trace) acids + unknown fatty acid A6/B3 (K+ orange or red, PD+ yellow).

Remarks. *Usnea glabrata* is the only representative of the *U. fragilescens* agg. in East Fennoscandia. The aggregate is charactarized by the shiny, normally thin cortex, lax medulla and thin central axis and by the branches that are often fairly swollen and fusiform to constricted at the bases (Clerc 1987a, Halonen *et al.* 1998). The chemistry is very variable, however. Most of the species in the aggregate are distinctly oceanic or have oceanic tendencies in their distributions. *Usnea glabrata* normally has at most low and sparse papillae, but strain 2 specimens have tall and abundant papillae. Furthermore, one thallus is exceptionally tall (ca. 10 cm), part of the thalli has annular cracks with everted medullary tissues, and the chemistry is unusual. They resemble in chemistry some thalli of the type material of *U. barbata* var. *pilina* and *U. sorediifera*. It is possible that the strain 2 specimens are hybrids of *U. glabrata* and another species.

Ecology. The species has been collected from *Alnus* (n = 24), *Picea* (n = 10), *Betula* (n = 4), *Salix* (n = 4), *Populus* (n = 2) and *Sorbus* (n = 1) (in total 45 specimens). The species is likely to be most common in moderately open and humid mixed forests, and it often occurs along shores of water-courses and in inhabited areas.

Distribution. Finland: 5–8, 11, 12, 15–17, 19; Russia: 2–5. World distribution: circumpolar in boreal and temperate regions with continental tendencies (Myllys 1994). *Usnea glabrata* mainly occurs in southeastern regions of East Fennoscandia being very rare elsewhere (map by Myllys 1994: 128). There is only one *U. glabrata* collection from East Fennoscandia from last decades (Oulun Pohjanmaa, Kuivaniemi, Taipale, 1989 *Halonen*, OULU) and the species is regarded as vulnerable in Finland and in the Republic of Karelia (Kotiranta *et al.* 1998). *Usnea glabrata* has a conspicuous morphology, but it may easily become overlooked in the field because of its small size, however, and there are relatively sparse new *Usnea* collections from Pohjois-Savo and Pohjois-Karjala which form the main distribution area of the species in Finland.

Specimens examined. — East Fennoscandian herbarium specimens were listed by Myllys (1994). The following ones are additions. **Finland**. Pohjois-Savo: Tuusniemi, Laukansalo, 1924 *Räsänen* (H), strain 2; Kuopio, Rauhalahti, 1950 *Nauha* (OULU), strain 1. Pohjois-Karjala: Värtsilä, 1949 *Huuskonen* (H), strain 1. Perä-Pohjanmaa: Tervola, Koivu, 1936 *Ahlner* (S), strain 1. Koillismaa: Kuusamo, Joukamojärvi, Taivalperä, 1936 *Ahlner* (S), strain 1. **Russia**. Republic of Karelia. Karelia ladogensis: Kurkijoki, Otsanlahti, 1932 *Räsänen* (H), strain 2; Kurkijoki, Riekkala, 1933 *Räsänen* (S), strain 1.

4. ***Usnea glabrescens*** (Nyl. ex Vain.) Vain. ex Räsänen

Luonnon Ystävä 23: 9. 1919. — *Usnea barbata* (L.) F. H. Wigg. var. *glabrescens* Nyl. ex Vain., Meddeland. Soc. Fauna Fl. Fenn. 2: 46. 1878. — Type: Russia. Leningrad Region, Karelia australis, Vyborg (Viipuri), Vysotsk (Uuras), ad corticem betulae, 1875 *Vainio* (TUR-V 708!, holotype). Chemistry: usnic, salazinic (trace) and norstictic acids.

Usnea extensa Vain., Ann. Acad. Sci. Fenn., Ser. A4, 27 A(6): 68. 1928. — Type: Russia. Sibiria, Tyumen Region, Leuschi (Levusch) by the Konda River, 1880 *Vainio* (TUR-V 558!, lectotype, here designated; TUR-V, four isolectotypes). Chemistry: usnic, salazinic and norstictic acids (TLC by P. Clerc).

Usnea glabrescens var. *glabrella* Motyka, Wydaw. Muz. Śląsk. Katowice, Dział 3, 2: 24. 1930. — *Usnea glabrescens* subsp. *glabrella* Motyka, Usnea 1: 301. 1936. — *Usnea glabrella* (Motyka) Räsänen, Ann. Mus. Nat. Hung. 33: 117. 1940. — Type: Ukraine (Poland). Carpathian Mts., Chernohory (Czarnohora), Mt. Pozyzewska, ad *Picea*, 1929

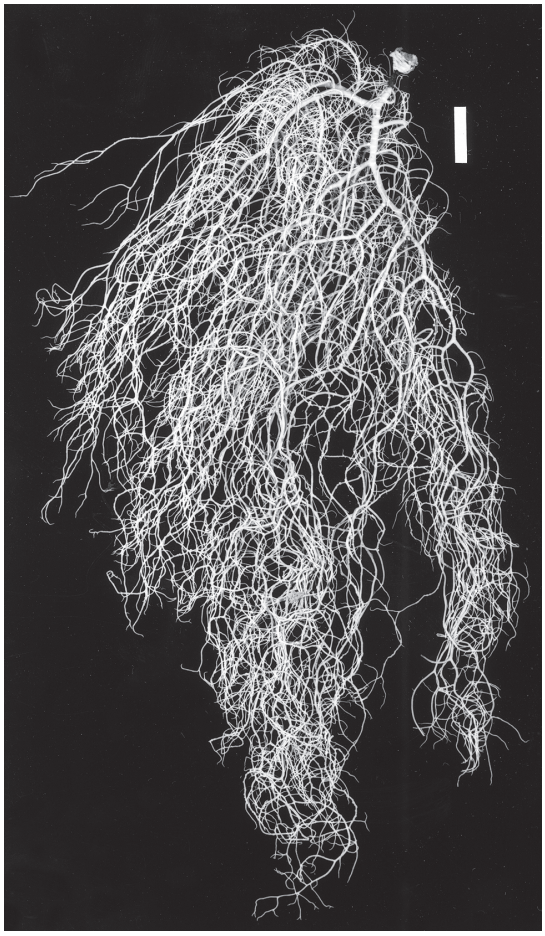

Fig. 5. Subpendent thallus of *Usnea glabrescens* (Nyl. ex Vain.) Vain. ex Räsänen with sparse fibrils. From 1964 *Ulvinen* (OULU). Scale = 1 cm

Motyka (LBL!, holotype). Chemistry: usnic, norstictic, cryptostictic and stictic acids (TLC by P. Clerc).

Usnea compacta Motyka ex de Lesdain, Ann. Crypt. Exot. 5: 123. 1932, *nom. nud.* — *Usnea compacta* Motyka, Usnea 1: 294. 1936. — Type: Poland. Tatra Mts., Kościeliska valley, *Sorbus*, 1923 *Motyka* (LBL!). — This is technically a new species with a type different from *Usnea glabrescens* var. *compacta* Räsänen. [There are annotations on the type sheet, however, which indicate that the specimen has been collected from Sweden, Örebro, 1908 (?) by *Svedberg*!].

Usnea glabrescens var. *compacta* Räsänen, Memoranda Soc. Fauna Fl. Fenn. 8: 188. 1933, as "(Motyka) Räsänen". — Type: Finland. Keski-Pohjanmaa, Lappajärvi, Salmela, in saepe veteri, 1914 *Nyström* (H!, holotype?). Chemistry: usnic, salazinic, norstictic, connorstictic (trace) and stictic (trace) acids.

Usnea betulina Motyka, Usnea 1: 297. 1936. — Type: Finland. Etelä-Häme, Hollola, Hersala, in *Betula*, 1873 *Vainio* (H-NYL 36522!, holotype; LBL!, isotype). Chemistry: usnic, salazinic (trace) and norstictic acids.

Usnea distincta Motyka, Usnea 1: 298. 1936, *nom. illeg.* (*non Usnea distincta* Motyka ex Räsänen 1935). — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Pieni Heposaari ["Pieni Heposou (?)"], 1925 *Räsänen* (LBL!, holotype; S-Motyka 206!, isotype). Chemistry: usnic, salazinic and norstictic acids (lectotype).

Usnea extensa Vain. subsp. *gemina* Motyka, Usnea 1: 304. 1936. — Type: Norway. Sør-Trøndelag, Buvika, *Picea*, 1934 *Degelius* (LBL, holotype, *n.v.*; UPS!, isotype). Chemistry: usnic acid (isotype). — The isotype collection also contains a thallus of *Usnea subfloridana* with usnic and thamnolic acids.

Usnea wasmuthii Räsänen var. *subglabrescens* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 12(1): 51. 1939. — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Otsanlahti, ad corticem alni, 1932 *Räsänen* (H!, lectotype, here designated). Chemistry: usnic, salazinic (trace) and norstictic acids. — Syntype: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Rahola, Kuoksvuori, ad corticem *Alni incanae*, 1935 *Räsänen*. Chemistry: usnic, salazinic, norstictic and connorstictic acids.

Usnea similis (Motyka) Räsäsnen var. *globigera* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 20(3): 7. 1944. — Type: Finland. Varsinais-Suomi, Nauvo, Pensar, ad rupem praeruptam, 1940 *Auer* (H!, holotype). Chemistry: usnic, norstictic, cryptostictic and stictic acids.

Usnea wasmuthii var. *sphaeroidea* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 20(3): 7. 1944. — Type: Finland. Pohjois-Savo, Kuopio, Levänen, ad corticem *Betulae*, 1941 *Räsänen* (H!, holotype). Chemistry: usnic, salazinic, norstictic, connorstictic and stictic acids.

Thallus (Fig. 5) at first erect, later becoming subpendent or rarely pendent, often relatively tall, to ca. 15(–25) cm long, rather sparsely or more rarely densely branched. Branching mostly isotomic-dichotomous. Branches slender to thick, to ca. 1.8(–2.5) mm in diam. Annular cracks common, often with a thin, white medullary ring. Base distinctly blackened. Cortex usually relatively thick, 9–*11*–13% (n = 30). Medulla relatively thin to relatively thick, 10–*17*–23% (n = 30). Central axis generally relatively thick, 32–*43*–56% (n = 30). Papillae usually low, abundant on main branches, but lacking or sparse on secondary branches. Fibrils rarely copious, generally sparsely present at basal parts and absent to sparse near apices. Soralia (*see* Clerc 1987b: 101) usually widely spaced, rounded and flat, sometimes tuberculate, later occasionally becoming ± excavate (especially near apices) and locally confluent and/or irregular in shape; soredia farinose. Isidia rarely

present only on young soralia, but tuberculate soralia may have spinules.

Chemistry. Strain 1 (n = 167): usnic + salazinic + norstictic acids ± other compounds of the stictic acid group ± protocetraric acid (trace) (K+ yellow, orange or red, PD+ yellow or orange); strain 2 (n = 35): usnic + norstictic acids ± other compounds of the stictic acid group (K+ yellow, orange or red, PD+ yellow or orange); strain 3 (n = 7): usnic acid (K–, PD–). The strain with only usnic acid, which is also represented by *Usnea extensa* subsp. *gemina*, has not previously been reported to occur in *U. glabrescens*. Clerc (1992) found menegazziaic and psoromic acids in *U. glabrescens* in the British Isles, but those compounds have not been found in the East Fennoscandian material.

Remarks. The "type" for *Usnea barbata* var. *glabrescens* indicated by Motyka (1936: 300) is not a type, because it is not cited in the protologue. The species is closely related to *U. fulvoreagens* (*see* the comments under the species).

Ecology. The species has been collected mainly from *Betula* (34%), *Picea* (29%) and *Alnus* (15%), and less frequently from *Pinus*, *Sorbus*, *Populus*, *Salix*, *Prunus*, *Larix*, *Juniperus*, lignum and rocks (in total 190 specimens). The species occurs in various forests, but it avoids dry sites, and it is relatively less frequent in inhabited areas than *U. fulvoreagens* and *U. wasmuthii*, for instance.

Distribution. Finland: 1–17, 19; Russia: 1–3, 5–8, 10, 11. World distribution: incompletely circumpolar from northern boreal to temperate regions. Widely distributed in Europe, but south of Fennoscandia it is mostly found in alpine and ± continental areas (Motyka 1936, Wirth 1995). *Usnea glabrescens* has a wide distribution in East Fennoscandia being rare in northern regions. It is locally quite common especially in the central parts of Finland, but it is less frequent than *U. hirta*, *U. subfloridana* and *U. lapponica*, and the pendent species *U. filipendula* Stirt.

Selected specimens examined. — **Finland**. Uusimaa: Espoo, Nuuksio (Nouks), Långträsk, 1934 *Linkola* (H), strain 3. Etelä-Savo: Luumäki, 1965 *Takala 1524* (H), strain 2. Pohjois-Savo: Kaavi, Peuramäki, 1941 *Räsänen* (H), fertile, strain 1. Pohjois-Karjala: Tohmajärvi, 1914 *Oesch* (H), strain 1. Keski-Pohjanmaa: Kälviä, Ruotsalo, Pirskeri, 1933 *Auer* (TUR), strain 1. Koillismaa: Kuusamo, Toranginaho, 1960 *Ahti 11879a* (H), strain 1. Sompion Lappi: Sodankylä, Korvanen, 1958 *Ulvinen* (OULU), strain 3. **Russia**. Leningrad Region. Isthmus karelicus: Zelenogorsk (Terijoki), Puhtula, 1938 *Fagerström* (H), strain 1. Republic of Karelia. Karelia borealis: Korpiselkä, Ägläjärvi, 1929 *Räsänen* (H), strain 2. Karelia pomorica occidentalis: Kuusijärvi, Pokonvaara, 1942 *Huuskonen* (H), strain 1. Murmansk Region. Regio kuusamoënsis: Kutsa area, Tuorusjoki, 1925 *Linkola* (H), strain 2. Lapponia Imandrae: Cape Turii, 1967 *Dombrovskaya* (KPABG), strain 2.

5. ***Usnea hirta*** (L.) F. H. Wigg.

Prim. Fl. Holsat. 91. 1780. — *Lichen hirtus* L., Sp. Pl. 1155. 1753. — Type: Sweden. Fries, Lich. Suec. Exs. no. 150 (UPS!, holotype, conserved type proposed by Jørgensen *et al.* 1994: 377, accepted by Gams 1996: 309; the neotypification by Motyka 1936: 86 and Bystrek 1994b: 20 was thus devalidated). Chemistry: usnic acid and murolic acid group.

Usnea variolosa Motyka, Usnea 1: 104. 1936. — Type: USA. New Mexico, Hermit Peak near Las Vegas, corticola, 1930 *Brouard* (LBL, holotype) — *see* Clerc (1997: 211).

Further synonyms of the species are given by Halonen and Puolasmaa (1995).

Thallus erect, rarely subpendent or pendent, usually small, to ca. 6(–15) cm long, often richly branched. Branching mostly anisotomic-dichotomous. Branches slender, to ca. 1(–1.5) mm in diam., often angular with foveoles and depressions. Annular cracks sparse to relatively abundant, often ± constricted. Base pale to brownish. Cortex thin to relatively thin, 6–*8*–10% (n = 18). Medulla generally lax and thick, 19–*27*–32% (n = 18). Central axis usually relatively thin, 21–*31*–46% (n = 18). Papillae normally absent (seen in only one specimen, which may be a hybrid), but minute tubercles are common. Fibrils usually numerous near the base and sparse at apices. Soralia or soralia-like structures minute, may occasionally develop on scars when isidia become detached; soredia farinose. Isidia usually abundant and tall, spinule-like, occurring both singly and in clusters, and they grow also near apices and often along low ridges. *See* figures of *Usnea hirta* in Halonen and Puolasmaa (1995) and Halonen *et al.* (1998).

Chemistry. Strain 1 (n = 54): usnic acid + murolic acid group (K–, PD–); strain 2 (n = 9): usnic + norstictic (normally very low amounts) acids + murolic acid group (K+ yellow, orange or red, PD+ yellow or orange); strain 3 (n = 8): usnic

acid (K–, PD–). Murolic acids may be present in every specimen but sometimes in very low amounts and thus they may have not been found in TLC studies. As pointed out by Klingstedt (1965), the strain containing norstictic acid (i.e. K+ and PD+ specimens) is more common in eastern parts of Finland. In our TLC studies we indeed found only one specimen from western parts of Finland (Oulun Pohjanmaa).

Remarks. According to Clerc (1992), *Usnea foveata* Vain. is a synonym of *U. hirta*, while Bystrek (1994a) regards it as a distinct species. Our opinion is that it probably is a representative of the polymorphic *Usnea scabrata* Nyl. *s. lato.* The type material of *U. foveata* is difficult indeed, since it has characters which may occur both in *U. hirta* and *U. scabrata s. lato*, i.e. a thin cortex, a lax medulla, sausage-like segments of branches, abundant foveoles and the chemistry with usnic acid alone. *Usnea foveata* bears only relatively sparse short isidia and scars of them, however, while long and abundant isidia on a mature thallus is one of the most diagnostic morphological characters of *U. hirta*. *Usnea foveata* also is pendent and weakly papillate, and it has been cut into many fragments, which are up to 18 cm long, and fragments have been distributed in several herbaria (at least in H, LBL, S-Motyka and TUR-V). Recently Bystrek (1994b) reviewed the status of *U. hirta* in Europe, also citing many Finnish and Russian specimens. The treatment contains many nomenclatural inaccuracies, however, and we do not accept the nine infraspecific taxa that were recognized by him.

Ecology. The species has mainly been collected from *Pinus* (51%), lignum (12%), *Betula* (12%) and *Picea* (12%), and less frequently from *Alnus*, *Sorbus*, *Populus*, *Salix*, *Juniperus*, *Prunus*, *Larix*, *Quercus*, *Fraxinus*, *Acer*, *Ulmus*, *Tilia*, *Rhamnus* and rocks (in total 503 specimens). *Usnea hirta* is the most xerophytic East Fennoscandian *Usnea* species occurring most frequently in fairly open sites, e.g., in pine forests and bogs. It is relatively pollution-tolerant among *Usnea* occurring even in urban areas (Kauppi & Halonen 1992).

Distribution. Finland: 1–21; Russia: 1–4, 6–8, 10–12. World distribution: the species has been found in almost every continent (Clerc 1997) and it has continental tendencies. This is the only shrubby *Usnea* species which has been found in every province in Finland in addition to *Usnea subfloridana*, but its occurrence in the Murmansk Region is poorly known. It is locally the most common *Usnea* species, e.g., along the coast of the Gulf of Bothnia.

Selected specimen examined. — Halonen and Puolasmaa (1995) listed specimens from East Fennoscandia including southern and northernmost provinces of Finland. The following collection represents the northernmost known locality of *Usnea hirta* in the Russian Fennoscandia: Murmansk Region. Lapponia Imandrae: Khibimy Mts., 1972 *Dombrovskaya* (KPABG), strain 1.

6. ***Usnea lapponica*** Vain.

Meddeland. Soc. Fauna Fl. Fenn. 48: 173. 1925 (‘1924’). — *Usnea sorediifera* Motyka subsp. *lapponica* (Vain.) Motyka, Wydaw. Muz. Śląsk. Katowice, Dział 3, 2: 23. 1930. — Type: Russia. Murmansk Region, Lapponia Imandrae, Lovozero (Lowosersk), in ramulis *Abietis* (*Picea*), 1887 *Kihlman* (H!, lectotype designated by Clerc 1987a: 494; S!, isolectotype). Chemistry: usnic and salazinic acids.

Usnea arnoldii Motyka, Usnea 1: 288. 1936. — Type: Romania. Carpaty, Czywczyn, SE of Mt. Suligul, 1370 m, ad *Fagos*, 1935 *Madalski* (LBL!, holotype). Chemistry: usnic and salazinic acids. [Voucher of the illustration in Motyka (1962: 287): Ukraine, Carpathian Mts. (Wschodnie), Chernohora (Czarnohora), Pozyzewska, 1934 *Motyka* (LBL!). Chemistry: usnic and constictic (trace) acids. This specimen represents a pendent morph of *Usnea fulvoreagens*.]

Usnea hirta (L.) F. H. Wigg. var. *dentata* Räsänen, Arch. Soc. Zool. Bot. Fenn. Vanamo 3: 178. 1949. — Type: Finland. Varsinais-Suomi, Halikko, Joensuu (Åminne), 1918 *Häyrén* (H!, holotype). Chemistry: usnic and salazinic acids. — The specimen probably represents a strongly modified *Usnea lapponica* — *see* Halonen and Puolasmaa (1995: 134).

Thallus erect, rarely subpendent or pendent, to ca. 10(–23) cm long, usually richly branched. Branching mostly isotomic-dichotomous. Branches normally slender, rarely relatively thick, to ca. 1.3(–1.8) mm in diam., often with foveoles or depressions (Fig. 6), apices commonly recurved. Annular cracks often slightly constricted, rarely with everted medullary tissue. Base pale or shortly brown black to distinctly blackened. Cortex thin to relatively thin, 4–*9*–12% (n = 42). Medulla usually lax and relatively thick, 10–*19*–32% (n = 42). Central axis normally relatively thick, 27–*45*–72% (n = 42). Papillae generally cylindric and numerous. Fibrils fairly sparse to more often abun-

dant, usually present also near apical parts. Soralia (*see* Clerc 1987b: 101, Halonen *et al.* 1998: 39), when mature, normally deeply excavate with torned cortex around them, first ± widely spaced, later often encircling the whole branch and even becoming confluent; soredia usually farinose. Isidia absent, but sometimes tuberculate soralia may contain spinules.

Chemistry. Strain 1 (n = 166): usnic + salazinic ± protocetraric (trace) acids ± fatty acids (2 specimens) (K+ yellow, orange or red, PD+ yellow or orange); strain 2 (n = 8): usnic + salazinic + caperatic ± protocetraric (trace) acids (K+ yellow, orange or red, PD+ yellow or orange); strain 3 (n = 7): usnic acid (K–, PD–); strain 4 (n = 6): usnic + psoromic + 2'-*O*-demethylpsoromic acids (K– or K+ yellow, PD+ yellow). This is the only East Fennoscandian species with a psoromic acid strain. This chemotype is southern in *Usnea lapponica* in Europe (Clerc pers. comm.).

Remarks. *Usnea lapponica* is closely related to *U. substerilis*. The latter is distinguished by the superficial, tuberculate to slightly excavate soralia, which normally have granulose soredia and may also develop isidia. Furthermore, young soralia of *U. lapponica* are normally more widely arranged (later often becoming ± confluent) than young soralia of *U. substerilis* which usually are, especially near apical parts, arranged in clusters of minute soralia which become confluent forming larger soralia patches. There also are some chemical differences, since barbatic acid is not found in *U. lapponica* in East Fennoscandia, although the compound is very rarely present in British Columbia specimens (Halonen *et al.* 1998). On the other hand, *U. lapponica* may produce psoromic or caperatic acid which are not found in *U. substerilis*. These two species often are difficult to distinguish since some modifications of *U. lapponica*, especially compact morphs, may have tuberculate soralia with isidia-like spinules and the isidia may be abraded in *U. substerilis*. Furthermore, in a late stage soralia of *U. substerilis* may become confluent with eroded soredia, thus resembling soralia of *U. lapponica*. Specimens that cannot be determined with certainty could be named as *U. lapponica s. lato*.

Ecology. The species has been collected mainly from *Picea* (31%), *Betula* (22%) and *Alnus* (13%), and less frequently from *Sorbus*, *Pinus*, *Salix*, *Populus*, *Prunus*, *Quercus*, *Acer*, *Tilia*, *Larix*, *Juniperus* and lignum (in total 239 specimens). *Usnea lapponica* has a wide ecological amplitude occurring both in open and dense forests, in gardens and on roadside trees, but it avoids very dry sites.

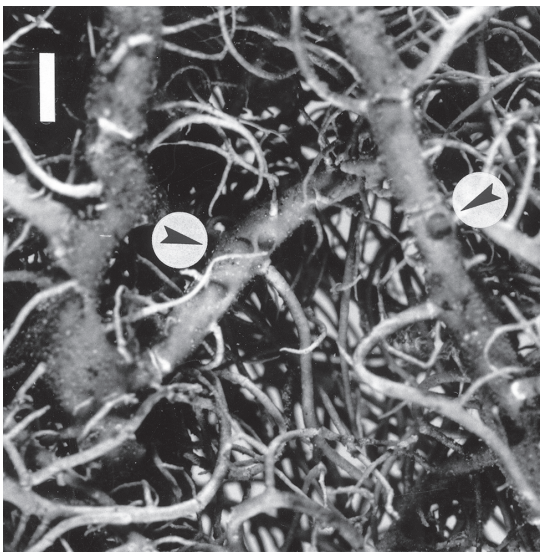

Fig. 6. Foveoles (pointed by arrows) on branches of *Usnea lapponica* Vain. From 1966 *Takala 2844* (H). Scale = 1.3 mm.

Distribution. Finland: 1–19, 21; Russia: 1–5, 8, 10–13, 17. World distribution: northern circumpolar, hemiarctic to temperate. According to Clerc (1992), *Usnea lapponica* has a continental distribution in Europe. The species has a wide range from the south coast to the northern parts of Lapland and the Kola Peninsula. *Usnea lapponica* seems to be locally the most common shrubby *Usnea* species in northern provinces, but it is rare in Åland and may have slightly eastern tendencies in its distribution.

Selected specimens examined. — **Finland**. Åland: Eckerö, Storby, Käringsund, 1949 *Häyrén* (H), strain 1. Etelä-Häme: Sääksmäki, Ikkala, Uotila, 1932 *Linkola* (H), strain 2. Laatokan Karjala: Saari, Honkakylä, Kiiveri, 1932 *Räsänen* (H), strain 1. Etelä-Pohjanmaa: Vaasa, 1957 *Bäck* (H), strain 4. Kainuu: Kuhmo, Siikasalmi, 1956 *Railonsala* (Räsänen, Lichenoth. Fenn. no. 960, H, OULU, S, TUR, *sub* "*U. sorediifera*"), strain 1. Koillismaa: Kuusamo, Toranginaho, 1960 *Ahti 11884* (H), strain 3. Kittilän Lappi: Kittilä, Uotivuoma, 1908 *Lång* (H), strain 1. Inarin Lappi: Inari, Kaunispää, 1936 *Ahlner* (S), strain 4. **Russia**. Leningrad Region. Karelia australis: Yashino (Vahviala), Hämeenvaa-

ra, 1938 *Fagerström* (H), strain 1. Isthmus karelicus: Konevitsa, 1938 *Räsänen* (H), strain 2. Republic of Karelia. Karelia ladogensis: Hiitola, Mustolan hovi, 1933 *Räsänen* (H), strain 1. Karelia olonetsensis: Vedlozero (Vieljärvi), Pihtilahti, 1942 *Railonsala* (TUR), strain 1. Murmansk Region. Lapponia Imandrae: Zasheyek (Sascheika), 1861 *Fellman* (H), strain 1. Lapponia Varsugae: Ponoi River, Krasnoshchele, 1990 *Dudoreva* (KPABG), strain 3.

7. ***Usnea subfloridana*** Stirt.

Scott. Naturalist (Perth) 6: 294. 1882. — Type: Scotland. Perthshire, Killin, 1881 *Stirton* (BM!, holotype). Chemistry: usnic and thamnolic acids (TLC by D. L. Hawksworth) — *see* also Laundon (1965).

Lichen comosus Ach., Kongl. Svenska Vetenskapsakad. Handl. 1795: 209. 1795. — *Usnea comosa* (Ach.) Vain., Meddeland. Soc. Fauna Fl. Fenn. 48: 173. 1925 ('1924'), *nom. illeg.* (*non Usnea comosa* Pers.). — Type: Sweden (H-ACH 1857c!, lectotype designated by Clerc 1987a: 494). Chemistry: usnic, thamnolic and hypothamnolic acids.

Usnea comosa (Ach.) Vain. subsp. *similis* Motyka, Wydaw. Muz. Śląsk. Katowice, Dział 3, 2: 18. 1930. — *Usnea similis* (Motyka) Räsänen, Ann. Acad. Sci. Fenn., Ser. A4, 34(4): 19. 1931. — *Usnea subfloridana* subsp. *similis* (Motyka) Bystrek, Stud. Flechtengatt. *Usnea* Europa 48, 54. 1994, *nom. inval.* (basionym not cited). — Type: Poland. Silesia, Płaskowyż; Grabowa; Malinka; Barania Góra, 1928 *Motyka* (LBL, syntypes, *n.v.*, a lectotype should be designated among them). — The "type" in Motyka (1936: 270): "Polonia, Montes Lysogory, in m-te Lysica" cannot be regarded as the type, since it is not cited in the protologue. — *Usnea similis* clearly represents the thamnolic acid strain (K+) of *Usnea subfloridana*.

Usnea australis Vain. var. *wainioi* Räsänen, Ann. Acad. Sci. Fenn., Ser. A4, 34(4): 19. 1931. — *Usnea similis* (Motyka) Räsänen var. *wainioi* (Räsänen) Räsänen, in Cretzoiu, Rev. Bryol. Lichénol. 10: 28. 1937. — Type: Estonia. Võrumaa, Kurenurme-Vaabina, an *Picea excelsa*, *Reinthal* (holotype, not found). — Type: Russia. Leningrad Region, Isthmus karelicus, St. Petersburg City, Roshchino SW (formerly Uusikirkko, Raivola), *Larix sibirica*, 1924 *Kujala* (H!, neotype, here designated). Chemistry: usnic and thamnolic acids. — The specimen is labelled as *Usnea similis* var. *wainioi*, but it was commented by Motyka (1936: 304), and evidently thereafter the epithet '*australis*' on the label was changed to '*similis*' by Räsänen. The specimen apparently represents Räsänen's (1931) statement "im südlichen Finnland...".

Usnea comosa var. *stuppeiformis* Räsänen, Lich. Fenn. Exs. no. 16 (Schedae: 6). 1935. — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Heposaari, ad corticem *Pruni padi*, 1932 *Räsänen* (H!, lectotype, here designated; H!, KUO, S!, TUR!, isolectotypes). Chemistry: usnic and thamnolic acids.

Usnea comosa f. *albida* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 12(1): 48. 1939. — *Usnea albida* (Räsänen) Räsänen, Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja, Ser. A, 5: 63. 1951. — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Maasilta, ad corticem *Populi tremulae*, 1933 *Räsänen* (H!, holotype). Chemistry: usnic and squamatic acids.

Usnea comosa f. *perisidiosa* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 12(1): 48. 1939. — Type: Estonia. Virumaa, Simuna, Rohu, *Pinus silvestris* im Walde von Nõmme, 1869 *Bruttan*? (H!, holotype). Chemistry: usnic and thamnolic acids.

Usnea similis var. *peraspera* Räsänen, Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 20(3): 7. 1944. — Type: Estonia. Virumaa, Simuna, Rohu, ad ramos *Pini silvestris*, 1869 *Bruttan* (holotype, not found). — The taxon may be homotypic with *Usnea comosa* f. *perisidiosa*, i.e. the same specimen has been described twice under different names. — Type: Estonia. Viljandimaa, Puiatu, Nutru, ad cort. pini, 1934 *Rebane* (H!, neotype, here designated). Chemistry: usnic and thamnolic acids. — The label of the specimen is inscribed "original" by Räsänen.

Thallus erect, later occasionally becoming subpendent or rarely pendent, to ca. 12(–20) cm long, usually quite richly branched. Branching mainly isotomic-dichotomous. Branches normally slender, to ca. 1.3(–2) mm in diam. Annular cracks sparse to relatively abundant, occasionally with distinct medullary rings. Base distinctly blackened, rarely with longitudinal cracks. Cortex relatively thick, 10–*12*–15% ($n = 18$). Medulla dense, usually relatively thin, 7–*14*–21% ($n = 18$). Central axis relatively thick to thick, 32–*47*–66% ($n = 18$). Papillae short to more rarely cylindric, usually numerous. Fibrils relatively sparse to copious near basal portions, absent to sparse near apical parts. Soralia (Fig. 7) tuberculate to slightly excavate (especially near apices), minute to enlarged; soredia farinose. Isidia usually short and numerous but absent on excavate soralia.

Chemistry. Strain 1 ($n = 460$): usnic + squamatic acids (K–, PD–, UV+ whitish blue); strain 2 ($n = 396$): usnic + thamnolic acids (K+ yellow, PD+ yellow-orange, UV–); strain 3 ($n = 10$): usnic + squamatic + thamnolic acids (K+ yellow, PD+ yellow-orange, UV+ whitish blue). The thamnolic acid strain is the main chemotype only in three southern-coastal provinces, namely Åland (18 of 23 studied specimens), Karjalan kannas (22 of 36 studied specimens) and Laatokan Karjala (71 of 106 studied specimens). The strains are approximately equal in frequency in Varsinais-Suomi and Uusimaa on the southern coast and along the coast of the Gulf of Bothnia. In the other regions the

squamatic acid strain is more frequent. However, there are only sparse collections from northern Lapland and from most Russian regions. The chemotype with both squamatic and thamnolic acids has been found from many provinces, but relatively many of them (four) have been collected from Laatokan Karjala. Small amounts of squamatic acid in addition to thamnolic acid, or *vice versa*, would presumably be found more frequently in HPLC analyses. The strain containing thamnolic and ± alectorialic acids is the main chemotype of *Usnea subfloridana* in most parts of Europe, e.g., in Estonia (P. Halonen & T. Randlane, unpubl.), Norway (Krog *et al.* 1994), and the British Isles (James *et al.* 1992).

Remarks. *Usnea subfloridana* is close to *U. wasmuthii*, but the latter has more often longitudinal cracks at the base and its soralia become more frequently slightly excavate and elongated. Furthermore, *U. wasmuthii* has on average a thinner medulla and a thicker central axis, and it has a different chemistry with barbatic and/or salazinic acids or very rarely usnic acid alone. However, Clerc (1991) did not find any differences in the thickness of the medulla between these two species.

Ecology. The species has been collected mainly from *Betula* (34%), *Picea* (25%) and *Alnus* (11%), and less frequently from *Pinus*, *Sorbus*, *Salix*, *Populus*, *Prunus*, *Tilia*, *Quercus*, *Acer*, *Larix*, *Juniperus*, lignum and rocks (in total 548 specimens). *Usnea subfloridana* has a wide ecological amplitude from humid and relatively shady forests to open inhabited sites, although it avoids very dry localities.

Distribution. Finland: 1–21; Russia: 1–8, 10–12. World distribution: widespread from northern boreal to temperate areas (Halonen *et al.* 1998). *Usnea subfloridana* is the most common shrubby *Usnea* in mesic and moist forests in most regions of East Fennoscandia. The species occurs in every province of Finland, but it has not been found in northernmost parts of the Murmansk Region.

Selected specimens examined. — **Finland**. Uusimaa. Lapinjärvi (Lappträsk), Hardom, Lindnäs, 1956 *Klingstedt* (H), strain 1. Etelä-Savo: Hirvensalmi, Kirjala, 1917 *Linkola* (H), strain 2. Etelä-Pohjanmaa: Raippaluoto (Replot), Norra Vallgrund, 1957 *Bäck* (H), strain 2. Pohjois-Savo: Pielavesi, Säviä, Kallioselkä, 1947 *Huuskonen* (Räsänen, Lichenoth. Fenn. no. 244, H, OULU), strain 1. Oulun Pohjanmaa: Oulu, Välivainio (Siirtola), 1911 *Huumonen* (OULU), strain 3. Sompion Lappi: Sodankylä, Riesto 3.5 km WSW, Jäkälämaa, 1959 *Ahti 10192* (H), strain 2. Enontekiön Lappi: Enontekiö, Muotkajärvi, 1992 *Puolasmaa* (TUR), strain 1. Inarin Lappi: Inari, Ivalo, E of the village, 1936 *Ahlner* (S), strain 2. **Russia**. Leningrad Region. Isthmus karelicus: Zelenogorsk (Terijoki), Puhtula, 1938 *Fagerström* (H), strain 2. Republic of Karelia. Karelia ladogensis: Kurkijoki, Otsanlahti, 1932 *Räsänen* (Räsänen, Lich. Fenn. Exs. no. 13, TUR, *sub U. fulvoreagens*), strain 1. Karelia transonegensis: Vodlozero National Park, Lake Vodlozero NE, 1991 *Vitikainen 12529* (H), strain 1. Murmansk Region. Regio kuusamoënsis: Kutsa Nature Reserve, Nivajärvi, 1994 *Halonen* (OULU), strain 1. Lapponia Imandrae: Kumzha River, near Kaita Mt., 1996 *Petrova* (KPABG), strain 1.

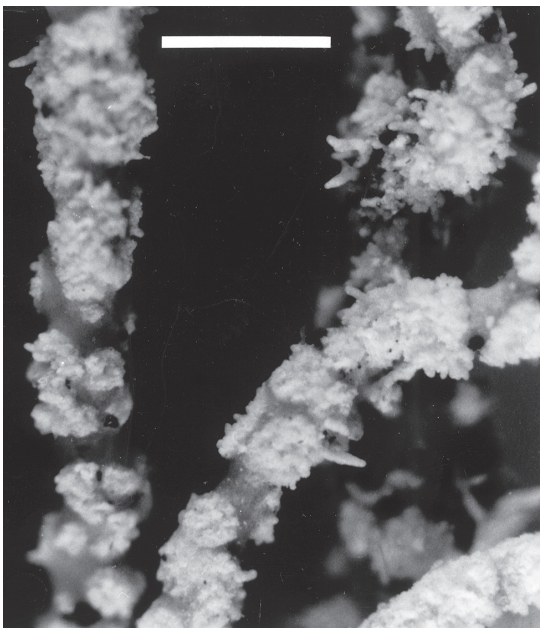

Fig. 7. Expanded soralia of *Usnea subfloridana* Stirt. with some isidia. From 1994 *Halonen* (OULU). Scale = 0.5 mm.

8. ***Usnea substerilis*** Motyka

Wydaw. Muz. Slask. Katowicach, Dzial 3, 2: 24. 1930. — Type: Italy ('Austria'). Bolzano (Bozen), Gröden (Groeden), St. Ulrich, above Unterkoffel, 1899 *Arnold*, Lich. Exs. no. 1538b (W, lectotype, *n.v.*, designated by Motyka 1936:291; H!, H-NYL p.m. 1371!, isolectotypes). Chemistry: usnic, salazinic, barbatic and 4-*O*-demethylbarbatic acids (isolectotype in H).

Usnea sorediifera Motyka, Wydaw. Muz. Śląsk. Katowice, Dział 3, 2: 24. 1930, *nom. illeg.* [*non Usnea sorediifera* (Arnold) Lynge 1921, see *Usnea glabrata*]. — Type: Italy. Bocche, on *Larix*, *Zopf*, Krypt. Exs. Mus. Vindob. no. 1555 (UPS!, lectotype, here designated; B, BP, W, iso-

lectotypes). Chemistry: usnic, salazinic, barbatic and 4-*O*-demethylbarbatic (trace) acids.

Usnea cinchonarum (Fée) Vain. var. *borealis* Räsänen., Ann. Acad. Sci. Fenn., Ser. A4, 34(4): 18. 1931. — Type: Estonia. Harjumaa, Keila, ad corticem *Laricis*, 1929 *Räsänen* (H!, lectotype, here designated). Chemistry: usnic, salazinic, protocetraric, barbatic and 4-*O*-demethylbarbatic acids. — Syntypes (not found): Estonia. Tartumaa, Kastre-Peravalla, an Hainfichte, *Linkola*; Võrumaa, Vaabina, Kurenurme, an Fichte, *Reinthal*.

Usnea comosa (Ach.) Vain. var. *stuppea* Räsänen, Ann. Missouri Bot. Garden 20: 9. 1933. — *Usnea stuppea* (Räsänen) Mot., Usnea 1: 262. 1936. — Type: Canada. British Columbia, Hazelton, ad corticem *Pini murrayani*, 1931 *Kujala* (H!, lectotype designated by Halonen *et al.* 1998: 57; Gyelnik, Lichenoth. no. 17; H!, LBL!, isolectotypes). Chemistry: usnic and salazinic acids.

Usnea hirta (L.) F. H. Wigg. var. *romanica* Räsänen, Acta Fauna Fl. Universali, Ser. 2, Bot., 2(1): 4. 1935. — Type: Romania. Buzau District, Mt. Buzau, Valea Tigva, 1933 *Chirila* (H!, holotype?). Chemistry: usnic and salazinic acids. — The specimen was misidentified as *Usnea lapponica* by Halonen and Puolasmaa (1995: 134).

Usnea monstruosa Vain. var. *balcanica* Räsänen, Acta Fauna Fl. Univ. Bukarest, Ser. 2, Bot., 2(1): 4. 1935. — Type: Romania. Distr. Muscel, Cretisoara by Câmpulung, *Quercus*, 1935 *Bordusanu* (H!, holotype?). Chemistry: usnic acid. — The thalli are strongly modified and compact representing probably *Usnea substerilis*.

Thallus erect, rarely subpendent, to ca. 8(–12) cm long, usually richly branched. Branching isotomic-dichotomous or anisotomic especially near the extremities. Branches normally slender, to ca. 1.3(–1.8) mm in diam., often with foveoles or depressions. Annular cracks often slightly constricted, rarely with everted medullary tissues. Base pale or shortly brown black to distinctly blackened. Cortex usually relatively thin, 6–*9*–13% ($n = 12$). Medulla normally lax and relatively thin, 10–*20*–28% ($n = 12$). Central axis usually relatively thick, 31–*42*–54% ($n = 12$). Papillae low to more often cylindric, generally numerous. Fibrils fairly sparse to more often abundant, commonly present also near apical parts. Soralia (*see* Clerc 1987b: 101, Halonen *et al.* 1998: 39) tuberculate to slightly excavate (especially old soralia near apices) and often irregular in shape, developing mainly on tubercles and low pustules; soredia usually ± granulose. Isidia short, quite common on young soralia but normally abraded on mature soralia.

Chemistry. Strain 1 ($n = 35$): usnic + salazinic ± protocetraric (trace) acids ± unknown fatty acid A2/B3 (K+ yellow, orange or red, PD+ yellow or orange); strain 2 ($n = 8$): usnic acid (K–, PD–); strain 3 ($n = 5$): usnic + salazinic + barbatic ± 4-*O*-demethylbarbatic ± protocetraric (trace) acids (K+ yellow, orange or red, PD+ yellow or orange); strain 4 ($n = 1$): usnic + salazinic + norstictic acids (K+ red, PD+ orange). The specimen containing norstictic acid is morphologically a typical representative of *Usnea substerilis*, but it may be a hybrid, since norstictic acid is not known before in *U. substerilis* and its close species.

Remarks. *Usnea substerilis* is close to *U. diplotypus* and *U. lapponica* (*see* the comments under the species). Soralia of *U. substerilis* are only rarely abundantly isidiate in the East Fennoscandian material, while the species often has abundant isidia in Central Europe and British Columbia, for instance. Because of the minor morphological differences between *U. lapponica* and *U. substerilis*, and the intermediate morphs, a more suitable taxonomical status for *U. substerilis* may rather be a subspecies of *U. lapponica*.

Ecology. The species has been collected mainly from *Picea* (23%), *Betula* (18%) and *Pinus* (10%), and less frequently from *Sorbus*, *Prunus*, *Salix*, *Populus*, *Alnus*, *Tilia*, *Acer*, *Fraxinus*, *Malus*, *Larix* and lignum (in total 62 specimens). *Usnea substerilis* occurs relatively more often in inhabited areas than *U. lapponica*.

Distribution. Finland: 1–3, 5–7, 9–17, 19; Russia: 1, 3, 6, 10, 13, 16. World distribution: seemingly circumpolar from boreal to southern temperate regions (Halonen *et al.* 1998). *Usnea substerilis* has a wide range in East Fennoscandia, but it is distinctly less common than *U. lapponica* in most regions. Based on preliminary studies by the first author, Vitikainen *et al.* (1997) reported *Usnea substerilis* also from Inarin Lappi. The specimens cannot be determined with certainty, however, but they represent *U. lapponica s. lato*.

Selected specimens examined. — **Finland**. Varsinais-Suomi: Raisio, 1931 *Auer* (TUR), strain 1. Etelä-Häme: Hattula, Lepaa, Vahopää, 1935 *Räsänen* (H), strain 1. Pohjois-Häme: Äänekoski, Pukkimäki, 1947 *Klingstedt* (H), strain 2. Keski-Pohjanmaa: Sievi, Korhonen, 1967 *Kosonen* (OULU), strain 1. Kainuu: Paltamo, Melalahti, Viilonkallio, 1959 *Huuskonen* (H), strain 1. Oulun Pohjanmaa: Oulu, Sankivaara, 1988 *Halonen* (OULU), strain 3. Sompion Lappi: Sodankylä, Korvanen, Vuollosvaara, 1958 *Ulvinen* (OULU), strain 3. **Russia**. Leningrad Region. Karelia australis: Yashino (Vahviala), Hämeenvaara, 1938 *Fagerström* (H),

strain 1. Republic of Karelia. Karelia ladogensis: Kurkijoki, Vossina, 1936 *Räsänen* (H), strain 1. Karelia onegensis: ca. 7 km W of Medvezhyegorsk, 1942 *Laurila* (H), strain 4.

9. ***Usnea wasmuthii*** Räsänen

Ann. Acad. Sci. Fenn., Ser. A4, 34(4): 19. 1931. — Type: Estonia. Harjumaa, Tallinn, Kakumäe (Kakkomägi), *Picea*, 1908 *Wasmuth* (H!, holotype), fertile, %C/%M/%A: 11/12/53, upper left-hand specimen. Chemistry: usnic and barbatic acids.

Usnea glabrescens (Nyl. ex Vain.) Vain. ex Räsänen var. *sanguinea* Räsänen, Acta Fauna Fl. Universali, Ser. 2, Bot., 2(1): 3. 1935. — Type: Romania. Distr. Gorj, Mt. Cioclovina, ad ram. *Fagi silvatici*, 1933 *Cretzoiu* (H!, holotype?). Chemistry: usnic, salazinic, barbatic and 4-*O*-demethylbarbatic acids.

Thallus erect to rarely subpendent, to ca. 10(–13) cm long, usually quite richly branched. Branching mostly isotomic-dichotomous. Branches slender, to ca. 1(–1.5) mm in diam. Annular cracks sparse to relatively abundant, quite often with white medullary rings. Base distinctly blackened, often with ± numerous longitudinal cracks (Fig. 8). Cortex relatively thick, 10–*12*–15% (n = 18). Medulla dense, thin to relatively thin, 5–*10*–16% (n = 18). Central axis usually thick, 44–*55*–65% (n = 18). Papillae small and verrucous, more rarely cylindric, normally fairly densely arranged. Fibrils relatively sparse to abundant, usually not present near apical parts. Soralia (*see* Clerc 1987b: 101) tuberculate to often slightly excavate and ± elongated (especially near apices), minute to enlarged, developing from plane cortex or from tubercles; soredia farinose. Isidia short but often absent on mature soralia.

Chemistry. Strain 1 (n = 29): usnic + barbatic ± 4-*O*-demethylbarbatic ± protocetraric (trace) acids (K–, PD–); strain 2 (n = 8): usnic + salazinic + barbatic ± 4-*O*-demethylbarbatic ± protocetraric (trace) acids (K+ yellow, orange or red, PD+ yellow or orange); strain 3 (n = 2): usnic + salazinic acids (K+ orange or red, PD+ yellow or orange); strain 4 (n = 1): usnic acid (K–, PD–). Strain 2 has eastern tendencies in East Fennoscandia since we have seen only two specimens from western Finland (Varsinais-Suomi: Kemiö, and Oulun Pohjanmaa: Oulu). According to Krog *et al.* (1994), strain 1 is rare in Norway. Bystrek *et al.* (1981) described *Usnea wasmuthii* f. *negativa* Bystrek for a chemotype in Poland (type specimen not seen) which reacts K– and PD–. However, these colour reactions are typical for the type strain.

Fig. 8. Longitudinal cracks at the blackened base of *Usnea wasmuthii* Räsänen. Two annular cracks are pointed by arrows. From 1946 *Railonsala* (OULU). Scale = 0.5 mm.

Remarks. *Usnea wasmuthii* is closely related to *U. subfloridana* (*see* the comments under the latter species).

Ecology. The species has been collected mainly from *Alnus* (n = 8), *Betula* (n = 7), *Sorbus* (n = 5) and *Picea* (n = 4), and less frequently from *Quercus*, *Salix*, *Populus*, *Malus*, *Larix*, *Juniperus* and lignum (in total 36 specimens). *Usnea wasmuthii* is most common in moderately open mixed forests and it occurs often in inhabited areas.

Distribution. Finland: 1–3, 6, 9–11, 13–15, 17, 19; Russia: 2, 3, 6. World distribution: northern boreal to temperate. The species has been found in Eurasia (Motyka 1936) and recently in North America (Halonen 2000), though Halonen *et al.* (1998) rejected some earlier North American records. *Usnea wasmuthii* is rare to scattered in southern parts of East Fennoscandia and very rare in northern Finland (Fig. 9). The species will be added to the list of threatened lichens of Finland

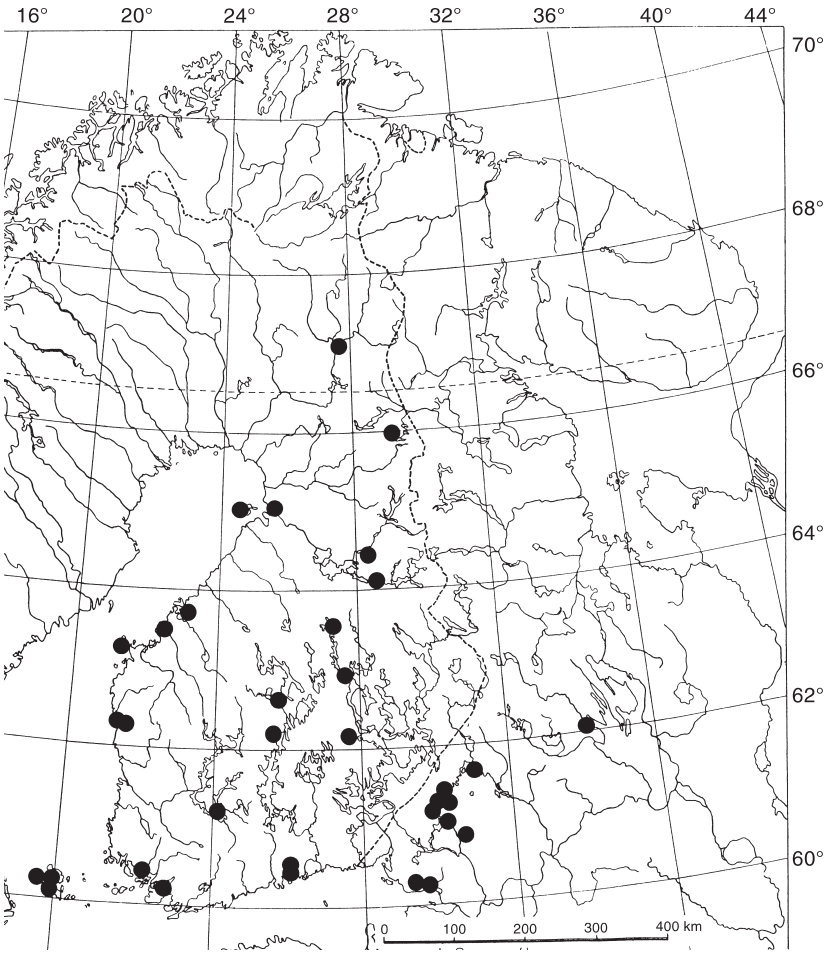

Fig. 9. Known distribution of *Usnea wasmuthii* Räsänen in East Fennoscandia.

(categories "Near Threatened" and "in need of monitoring"), since there are only a few collections from Finland from last decades.

Selected specimens examined. — **Finland**. Åland: Maarianhamina (Mariehamn), Ytternäs, 1935 *Räsänen* (H), strain 4. Etelä-Häme: Sääksmäki, Ikkala, Uotila, 1932 *Linkola* (H), strain 1. Etelä-Pohjanmaa: Kristiinankaupunki, Skatan, 1946 *Railonsala* (TUR), strain 1. Pohjois-Savo: Kuopio, Laivonsaari, 1942 *Räsänen* (Räsänen, Lich. Fenn. Exs. no. 735, H, *sub U. comosa*), strain 2. Kainuu: Sotkamo, *Chydenius* (H), strain 1. Oulun Pohjanmaa: Hailuoto, Marjaniemi, 1990 *Väre 328* (OULU), strain 1. Koillismaa: Kuusamo village, Kuusela, 1973 *Ahti 29504* (H), strain 1. Sompion Lappi: Pelkosenniemi, 1994 *Soppela* (OULU), strain 3. **Russia**. Leningrad Region. Isthmus karelicus: Roshchino SW (formerly Uusikirkko, Raivola), 1924 *Kujala* (H), strain 2; Konevitsa, 1938 *Räsänen* (H), strain 1. Republic of Karelia. Karelia ladogensis: Kurkijoki, Vossina, 1936 *Räsänen* (H), strain 1; Hiitola, Kyläjärvi, 1931 *Räsänen* (H), strain 2.

EXCLUDED TAXA

Usnea florida (L.) F. H. Wigg. var. *subcomosa* Vain., Acta Soc. Fauna Fl. Fenn.7: 3. 1890. — *Usnea subcomosa* (Vain.) Vain., Kgl. Danske Vidensk.-Selsk. Skr., Naturwidensk. Math., B, 6: 392. 1924. — Type: Brazil. Minas Gerais (Minas Geraës), Antônio Carlos (Sítio), ad corticem et ramulos arborum, 1885 *Vainio*, Lich. Brasil. Exs. no. 387 (TUR-V 783!, lectotype, here designated; TUR-V 784!, 785, isolectotypes). Chemistry: usnic (trace), diffractaic, barbatic and 4-*O*-demethylbarbatic acids and probably a low amount of squamatic acid. The lectotype is *Usnea ceratina* Ach., but the other isolectotype, which contains usnic, norstictic (trace), stictic, cryptostictic, constictic and protocetraric (trace) acids, seemingly represents *Usnea rubicunda* Stirt. The East Fennoscandian material named as *U. subcomosa* mainly contains *U. subfloridana* specimens.

Usnea laricina Vain. ex Räsänen, Ann. Acad. Sci. Fenn., Ser. A4, 34 (4): 17. 1931. — Type: Estonia. Harjumaa, Keila, ad corticem *Laricis*, 1929 *Räsänen* (H!, lecto-

type, here designated). Chemistry: usnic and salazinic acids. The specimen is a terminal part of a thallus which probably represents *Usnea filipendula*. The syntype from Estonia, Saaremaa, Kihelkonna was not found. The "type" (incorrect since not syntype) used by Motyka (1936: 280) for *U. laricina* [Russia, Republic of Karelia, Karelia ladogensis, Valaam (Valamo), 1923 *Hiitonen*, H!, chemistry: usnic and thamnolic acids] represents *Usnea subfloridana*.

Usnea leucostictoides Räsänen, Memoranda Soc. Fauna Fl. Fenn. 8: 187. 1933. — *Usnea diplotypus* var. *leucostictoides* (Räsänen) Räsänen, Lich. Fenn. Exs. no. 9 (Schedae: 3). 1935. — Type: Russia. Republic of Karelia, Karelia ladogensis, Kurkijoki, Majasaari, on rock (kalliolla), 1931 *Räsänen* (H!, lectotype, here designated; H! isolectotype), fertile. Chemistry: usnic and salazinic acids. The thalli are ± pendent and have abundant foveoles. They represent aberrant thalli of the pendent species *Usnea scabrata s. lato.*

Usnea monstruosa Vain., Meddeland. Soc. Fauna Fl. Fenn. 48: 173. 1925 ('1924'). — Type: Finland. Nurmijärvi, Numlahti (Numlaks), ad corticem arboris, 1907 *Vainio* (TUR-V 835!, lectotype, here designated; isolectotype TUR-V 834!). Chemistry: salazinic and protocetraric acids, and an unknown fatty acid A4/B5/C5 (lectotype, TLC by P. Clerc). P. Clerc (in litt.) has concluded that the type material represents strongly modified thalli of an unidentified pendent species. We agree with his conclusion. Also Klingstedt (1965: 13) noted that no other material he had seen in the Finnish *Usnea* collections exactly matches Vainio's original material and that the other Finnish material is not conspecific. He also reports that part of the type material in TUR-V was lost during World War II.

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