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The lichen genus *Usnea* (lichenized Ascomycetes, *Parmeliaceae*) in Estonia with a key to the species in the Baltic countries

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Abstract: The occurrence of 12 *Usnea* species in Estonia is verified by investigating *c*. 1800 specimens. The known distribution and substratum preferences of *Usnea* taxa in Estonia are summarized. *Picea* is the main substratum for *Usnea* species in Estonia, but occasionally these species occur also on deciduous trees, wood, and exceptionally on rock. A key for identification of 16 taxa recorded in the three Baltic countries is provided and diagnostic morphological and chemical characters used in the key are discussed. A new chemotype of *U. fulvoreagens* has been identified. *U. wasmuthii* is reported as new to Lithuania.

Key words: chemotypes, diagnostic characters, distribution, substratum

Introduction

The lichen genus *Usnea* Dill. ex Adans. (*Parmeliaceae*) is a cosmopolitan genus which is represented in all continents and comprises *c*. 300–600 species, according to different authors (Kirk *et al*. 2001; Wirtz *et al*. 2006). Recognition of the genus is easy due to the beard-like morphology of the thallus, the yellowish colour caused by usnic acid in the cortex, and presence of a central axis. Identification of species, however, is much more complicated because of the variability in both morphology and chemistry of taxa, and numerous taxonomic uncertanties at the species level. Several recent treatments of *Usnea*, either taxonomic (Clerc 1992, 2006; Myllys 1994; Halonen & Puolasmaa 1995; Clerc & Herrera-Campos 1997; Halonen 1997, 2000; Halonen *et al*. 1998, 1999; Herrera-Campos *et al*. 1998; Fos & Clerc 2000; Ohmura 2001; James 2003) or phylogenetic (Clerc 1998; Ohmura 2002; Articus *et al*. 2002; Articus 2004, Wirtz *et al*. 2006), have reduced confusion in this genus. Nevertheless, there are still many regions even in Europe where the knowledge of *Usnea* is out of date or just insufficient; the Baltic countries belong to such a region.

The aims of the study reported here were to revise the list of *Usnea* species known from Estonia (Trass & Randlane 1994: 24 species; Randlane & Saag 1999: 12 species), to contribute to the identification of these significant lichens in all three Baltic states by compiling a classical key to species, and to summarize the known distribution and substratum preferences of *Usnea* taxa in Estonia.

Materials and Methods

A total of *c*. 1800 specimens collected from Estonia and deposited in H, ICEB, TALL, TAM, and TU have been studied. *Usnea* collections from Lithuania in BILAS and WI have also been partly revised and in addition a few specimens from Latvia and Lithuania have been collected.

Morphology and anatomy were examined under a stereomicroscope OLYMPUS SZ51; photographs were taken using Nikon DS camera head DS-Fi1 under Nikon stereoscopic zoom microscope SMZ1000. To identify secondary compounds, 225 specimens were analyzed chemically by TLC using solvent A (Culberson & Kristinsson 1970) and thin layer plates Macherey-Nagel SIL G-25 UV_{254}; a two-dimensional A × A TLC was carried out to attempt identification of an unknown substance in *Usnea fulvoreagens* (Culberson *et al.* 1981).

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The frequency of taxa was evaluated according to Randlane & Saag (1999) where Estonian lichens were divided into six frequency classes: very rare (1–2 localities), rare (3–5 localities), rather rare (6–10 localities), rather frequent (11–20 localities), frequent (21–50 localities), and very frequent (51 or more localities in Estonia). Distribution maps were compiled using the program DMAP (Morton 1999); recording units are equal to quadrangles with sides of 5′ (NS direction) × 10′ (EW direction). The maps are of illustrative character revealing only the general patterns of distribution; the number of dots on maps does not correspond to the actual number of localities.

Results

Twelve *Usnea* species are recognized in Estonia; two further species, *Usnea articulata* (L.) Hoffm. and *U. longissima* Ach., are considered doubtful as the herbarium material from Estonia has not been seen and the taxa are included in the list according to literature data only. Two species, *U. chaetophora* Stirt. and *U. diplotypus* Vain., not recorded in the second checklist of Estonian lichens (Randlane & Saag 1999) are reported here from Estonia for the first time. We also present the information about the occurrence of *Usnea* species in two other Baltic states as most of the taxa in the Estonian list have also been recorded both in Latvia (11 species) and Lithuania (12 species) (Table 1). One species, *U. wasmuthii* Räsänen, is new for Lithuania.

Altogether 16 *Usnea* species have now been recorded in the Baltic countries.

Key to the *Usnea* species occurring in the Baltic states

1 Main branches decorticated . . . . **U. longissima**
Main branches persistently corticated 2

2(1) Apothecia usually abundant; isidiomorphs and soralia absent . . . . **U. florida**
Apothecia usually lacking or a few, if present; isidiomorphs and/or soralia present 3

3(2) Medulla and central axis usually pink, C+ pale yellow . . . . . . **U. ceratina**
Medulla and central axis always white, C − 4

4(3) Thallus totally pendent, several times longer in length than in width 5
Thallus shrubby, main branches erect at base with only the apices sometimes pendent, more or less as wide as long 8

5(4) Branches are divided into segments by annular cracks almost throughout the thallus 6
Branches are not divided into segments or if cracked then only at the base . . 7

6(5) Older parts form sausage-like segments; medulla very loose; comma-like pseudocyphellae may be present . . . . **U. articulata**
Branches do not form sausage-like segments; medulla dense; pseudocyphellae absent . . . . **U. chaetophora**

7(5) Branches even in thickness, gradually narrowing towards the apices; without foveolae and/or ridges; fibrils usually numerous; isidiomorphs always present, usually abundant; medulla dense . . . . **U. filipendula**
Branches uneven in thickness, often with foveolae and/or ridges; fibrils sparse to numerous; isidiomorphs absent or sparse; medulla loose . . . . . **U. barbata**

8(4) Papillae absent on all branches 9
Papillae present on main or on terminal branches or on both 10

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9(8) Secondary branches are constricted at the base; main branch without foveolae; isidiomorphs absent . . . . **U. glabrata**
Secondary branches are not constricted at the base; main branches foveolate on basal parts; isidiomorphs abundant . . . . **U. hirta**

10(8) Isidiomorphs usually abundant **11**
Isidiomorphs absent or rarely present on young soralia **12**

11(10) Branches of uneven thickness, irregularly swollen, apical parts often sinuous; soralia punctiform and usually not expanding, bearing relatively tall isidiomorphs; contains salazinic acid . . . . **U. diplotypus**
Branches of even thickness, narrowing towards the apices, not swollen or sinuous; soralia punctiform to expanded, bearing relatively small isidiomorphs; contains squamatic or thamnolic acid . . . . **U. subfloridana**

12(10) Isidiomorphs occur on young soralia but are normally abraded on mature soralia **13**
Isidiomorphs totally absent **16**

13(12) Branching mostly anisotomic-dichotomous; branches of uneven thickness, sometimes with foveolae or depressions; soralia often tuberculate **14**
Branching mostly isotomic-dichotomous; branches even and without foveolae; soralia often plane or slightly excavate **15**

14(13) Thallus usually short, clearly shrubby; mature soralia enlarged, tuberculate to slightly excavate; soredia granulose . . . . **U. substerilis**
Thallus shrubby to subpendent, apical parts often sinuous; mature soralia punctiform, plane to tuberculate; soredia farinose . . . . **U. diplotypus**

15(13) Soralia oblong-cylindrical; contains barbatic acid (as a main substance) and salazinic acid (as an accessory) . . . . **U. wasmuthii**
Young soralia punctiform, later becoming rounded; contains norstictic acid (as a main substance) and salazinic acid (as an accessory) . . . . **U. glabrescens**

16(12) Young soralia punctiform, later becoming larger but always remaining distinctly rounded and discrete; fibrils sparse or absent . . . . **U. glabrescens**
Young soralia large, later becoming expanded; fibrils often abundant **17**

17(16) Branches often with foveolae or depressions; branching mainly anisotomic-dichotomous; contains salazinic acid (as a main substance) . . **U. lapponica**
Branches without foveolae and depressions; branching mainly isotomic-dichotomous; contains norstictic acid or an unidentified compound* (as a main substance) . . . . **U. fulvoreagens**

Characterization of some diagnostic characters used in the key

Most of the morphological characters commonly used for delimiting and identifying *Usnea* species such as thallus habit, branching, base, segments, fibrils, isidia/isidiomorphs, soralia, papillae, etc are discussed thoroughly in several papers (Clerc 1987*a*, 1987*b*, 1998; Clerc & Herrera-Campos 1997; Halonen *et al.* 1998; Herrera-Campos *et al.* 1998; Ohmura 2001). We add our observations based on the material examined from the Baltic region if they complement or differ from the standpoints described in the papers cited.

*For a description of this unidentified compound see p. 427.

TABLE 1. Usnea *species occurring in the Baltic states and the sources of information*

Species	Estonia	Latvia	Lithuania
U. articulata (L.) Hoffm.	Mereschkowski 1913	–	–
U. barbata (L.) F. H. Wigg.	Randlane & Saag 1999 (207*)	Piterāns 2001 (4)	Motiejūnaitė 1999
U. ceratina Ach.	–	Piterāns 2001	–
U. chaetophora Stirt.	Tõrra & Randlane 2005 (3)	–	–
U. diplotypus Vain.	Tõrra & Randlane 2005 (18)	–	Motiejūnaitė 2002 (2)
U. filipendula Stirt.	Randlane & Saag 1999 (354)	Piterāns 2001 (3)	Motiejūnaitė 1999
U. florida (L.) F. H. Wigg.	–	Piterāns 2001 (1)	Motiejūnaitė 1999
U. fulvoreagens (Räsänen) Räsänen	Randlane & Saag 1999 (30)	Piterāns 2001	Motiejūnaitė 1999 (3)
U. glabrata (Ach.) Vain.	Randlane & Saag 1999 (13)	–	Motiejūnaitė 1999 (1)
U. glabrescens (Nyl. ex Vain.) Vain.	Randlane & Saag 1999 (80)	Piterāns 2001	Motiejūnaitė 1999 (7)
U. hirta (L.) F.H. Wigg.	Randlane & Saag 1999 (536)	Piterāns 2001 (5)	Motiejūnaitė 1999
U. lapponica Vain.	Randlane & Saag 1999 (53)	Piterāns 2001	Motiejūnaitė 1999 (5)
U. longissima Ach.	Mereschkowski 1913	Piterāns 2001	–
U. subfloridana Stirt.	Randlane & Saag 1999 (446)	Piterāns 2001 (5)	Motiejūnaitė 1999
U. substerilis Motyka	Randlane & Saag 1999 (10)	Motiejūnaitė *et al.* 2006	Motiejūnaitė 2002 (1)
U. wasmuthii Räsänen	Randlane & Saag 1999 (20)	–	

*Number of herbarium specimens examined by the authors in parentheses.

Base (trunk)

The colour of the basal part of the thallus is a diagnostic character for some species (e.g. always black in *U. fulvoreagens*, *U. glabrescens*, *U. subfloridana* and *U. wasmuthii* or always non-pigmented in *U. glabrata* and *U. hirta*) but rather variable and therefore without diagnostic value in other species (e.g. *U. diplotypus*, *U. lapponica* and *U. substerilis*). The black base may have mainly transverse annular cracks (e.g. *U. glabrescens*, *U. subfloridana*) or both transverse and longitudinal cracks (*U. wasmuthii*).

Branches

The dominant branching pattern of the thallus can be (1) isotomic-dichotomous where the dividing branches are more or less equal in thickness or (2) anisotomic dichotomous where the dividing branches are of different thickness (Clerc 1987*b*). This character is usually recorded in the descriptions of the species but is of minor importance in the identification keys to separate large entities as both branching patterns may occur in the same thallus and determining the dominant pattern is not always easy. Nevertheless, the character may be of use in differentiating some similar species in the group of shrubby *Usnea* species (e.g. in the pairs *U. subfloridana*/*U. diplotypus* and *U. fulvoreagens*/*U. lapponica* branching is mainly isotomic-dichotomous in the first and anisotomic-dichotomous in the second taxon) (Clerc 1992).

The shape of branches in longitudinal and transverse sections is considered taxonomically important by Clerc (1998). In longitudinal sections branches may be either tapering or remain the same thickness almost the whole length or are clearly irregular. In transverse sections branches are usually terete but may also be irregular, with depressions, foveolae and ridges. Foveolate and irregular branches are especially characteristic in the taxa with a thick and loose medulla such as *U. barbata*, *U. glabrata* (Fig. 1A) and *U. hirta* but also occur on the species with variable density and thickness of medulla, for example *U. diplotypus*, *U. lapponica* and *U. substerilis*. Segmentation of branches by annular cracks is taxonomically significant only if the segmentation is regular throughout the whole thallus, for example in *U. articulata* (Fig. 1B) and *U. chaetophora* (Fig. 1C). Constriction of secondary branches at their base is an easily observable character which can be used as diagnostic for *U. articulata* and *U. glabrata* (Fig. 1A, B).

Fibrils

Fibrils are short branch-like projections which include a central axis as in branches but their central axis is not attached to the central axis of the branch on which they occur (Clerc & Herrera-Campos 1997). Fibrils are present on most *Usnea* species but their density varies. Numerous fibrils give a 'fish-bone like' appearance to the pendulous *U. filipendula* (Fig. 1D) and *U. longissima* while *U. articulata* and *U. chaetophora* almost lack fibrils (Fig. 1C). *Usnea glabrescens* is distinguished from the group of shrubby species is distinguished by having fibrils present on the basal parts but these are sparse or absent on apical parts.

Papillae, tubercles

Papillae are short cylindrical outgrowths of the cortex (Fig. 1E). They occur on main or secondary branches of most of the species treated here except *U. glabrata* and *U. hirta*. The density and number of papillae is considered to be influenced by environmental conditions and thus are not highly diagnostic (Clerc 1998). Tubercles are short outgrowths which are wider than papillae and with medulla inside. The presence of white coarse tubercles is characteristic of *U. ceratina*.

Isidia/isidiomorphs

Isidia are vegetative propagules of lichens having a spinulose habit, containing photobiont cells and being covered with cortex. Clerc declares that similar structures seen on soralia of *Usnea* species are not true isidia because they are not formed as outgrowths of the cortex but are initiated from the

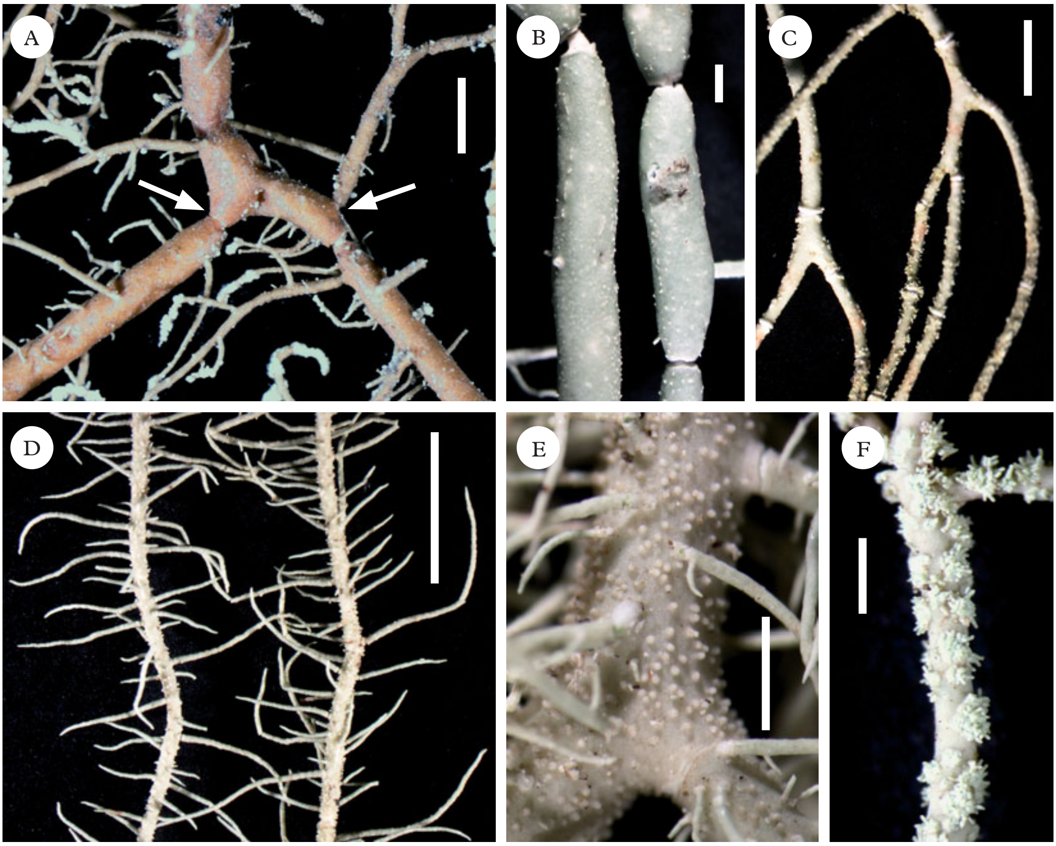

FIG. 1. *Usnea* species from Estonia showing characteristics of branches, fibrils, papillae and isidiomorphs. A, *U. glabrata*, foveolate branches (arrows mark constrictions of secondary branches at their base); B, *U. articulata*, inflated, sausage-like segments of branches; C, *U. chaetophora* normal branches without inflated segments (notice absence of fibrils); D, *U. filipendula*, fibrils giving the lichen a 'fish-bone like' appearance; E, *U. subfloridana*, papillae on branches; F, *U. subfloridana*, isidiomorphs. Scales: A, B & F=1·0 mm, C & D=3 mm, E=0·8 mm.

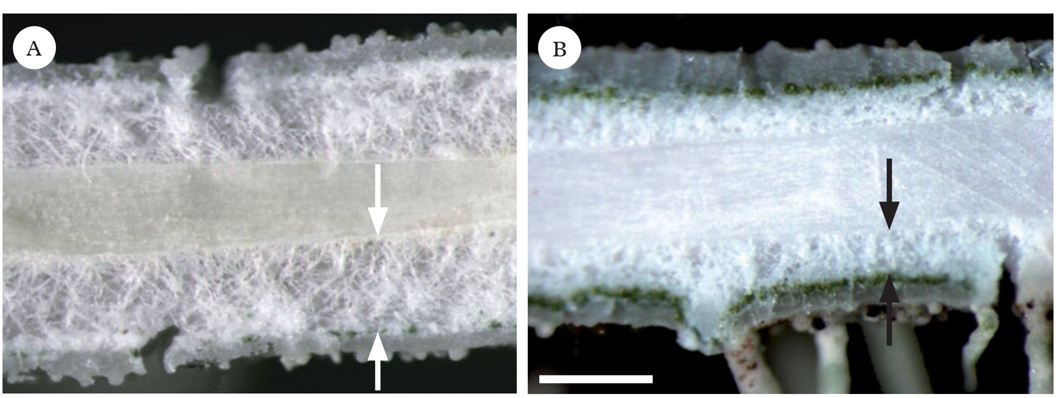

FIG. 2. *Usnea* species from Estonia; density of the medulla in longitudinal sections of the branches. A, *U. barbata*, loose medulla (notice relatively thick medulla marked with arrows, and thin central axis); B, *U. subfloridana*, dense medulla (notice relatively thin medulla marked with arrows, and thick central axis). Scale: B (also A)=0·5 mm.

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hyphae of the medulla, and he proposes to call them 'isidiomorphs' (Clerc 1998; Halonen *et al*. 1998). James (2003) described soredia in a soralium that may become secondarily corticate and also look like isidia. The term 'isidium' is traditionally much used in identification keys for *Usnea* species as all these structures are externally very similar. Their presence/absence is diagnostic for many species (see under soralia) but the taxonomic importance of distinguishing between true isidia, isidiomorphs and soredia which are secondarily covered with cortex needs further studies. In this paper we use the term 'isidiomorph' for all isidia-like spinules which are in connection with soralia.

Soralia

Soralia are considered a most important character in the taxonomy of *Usnea* (Clerc 1998, Herrera-Campos *et al*. 1998). Not only the presence/absence and the shape and size of soralia are significant but also their ontogeny—both young and mature soralia should be considered. Young soralia bear isidiomorphs in many species while mature soralia often lack them. For instance, isidiomorphs are totally absent in *U. glabrata*, *U. lapponica* and *U. fulvoreagens*, but may occur on young soralia of *U. glabrescens*, *U. substerilis* and *U. wasmuthii*, and are commonly present on *U. diplotypus*, *U. hirta* and *U. subfloridana* (Fig. 1F). The following features of soralia are diagnostically valuable: (1) flatness compared to the cortex of branches (tuberculate, flat, concave) (Fig. 3A); (2) shape (rounded, oblong-cylindrical, surrounding the branch, bracelet-like, irregular) (Fig. 3B–F); (3) size (punctiform, enlarged) (Fig. 3A–F). Characters of soralia are essential in the group of shrubby species and not so significant among pendulous *Usnea* species treated here. Typically characteristic soralia can be described for most species (see descriptions in the taxonomic section), but unfortunately atypical soralia also often occur.

Anatomical characters

The colour of the medulla is an easily observed character in longitudinal sections of branches. All *Usnea* species recorded in the Baltic countries except one (*U. ceratina*) have a white medulla. The medulla and outer surface of the central axis of the latter species are light pink to dark rose and can usually be easily checked in the field by stretching the branch. This diagnostic character is caused by the presence of an unidentified pink pigment with distinct spot tests C+ yellow and CK+ deep yellow or orange. Thus the colour of the medulla should rather be classified under the chemical characters.

The consistency of the medulla can also be observed on longitudinal sections of branches using a stereomicroscope. Three types have been distinguished: (1) loose with a few separated and conspicuous hyphae; (2) dense with agglutinated and individually visible hyphae; (3) compact with agglutinated but not individually visible hyphae (Clerc 1987*b*; Clerc & Herrera-Campos 1997; Herrera-Campos *et al.* 1998). Species with truly compact medulla are not known in the Baltic area. As the density of the medulla varies greatly in many species (such as *U. diplotypus*, *U. fulvoreagens*, *U. glabrescens*, *U. lapponica* and *U. substerilis*), it is used as a diagnostic character in only a few cases, for example, loose medulla in *U. articulata*, *U. barbata* and *U. glabrata* (Fig. 2A); dense medulla in *U. chaetophora* and *U. filipendula* (Fig. 2B).

Comparison of the thickness of the inner layers of branches is another widely used anatomical character which has been consistently applied by Clerc (1987*b*; etc). This character is quantitative and can be objectively measured. The ratio is recorded as a percent of the radius of the cortex and the medulla, and as a percent of the diameter of the axis (%C/%M/%A). Even so, these ratios can be rather similar in different species, especially in the group of taxa with foveolate branches [e.g. 9/22/40 for *U. diplotypus*, 9/20/42 for *U. substerilis* and 9/19/45 for *U. lapponica*, after Halonen *et al.* (1999)].

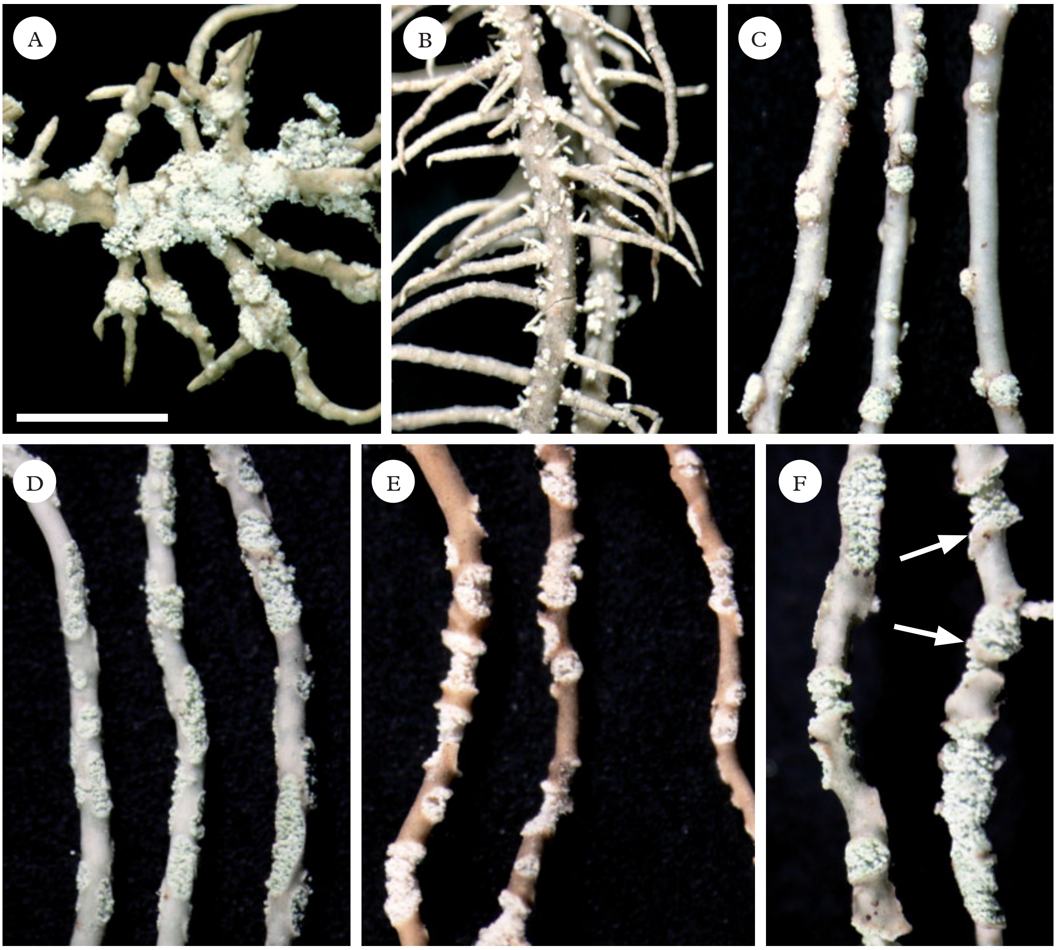

FIG. 3. *Usnea* species from Estonia, soralia. A, *U. substerilis*, slightly tuberculate soralia; B, *U. diplotypus*, punctiform soralia; C, *U. glabrescens*, rounded and discrete soralia; D, *U. wasmuthii*, oblong soralia; E, *U. fulvoreagens*, bracelet-like soralia; F, *U. lapponica*, irregular and expanded, occasionally also bracelet-like soralia (notice torn cortex around the soralia marked with arrows). Scale: A (also for B–F) = 1·5 mm.

General description of the thickness of inner layers is also often used instead of presenting percentages as precise measurements are time consuming. The thickness of the medulla is usually correlated with its consistency i.e. a loose medulla is usually thick (e.g. 32–39% in *U. glabrata*) and a dense medulla is thin (e.g. 5–16% in *U. wasmuthii*).

Medullary chemistry

A great variety of medullary compounds occurs in the species recorded in the Baltic countries such as β-orcinol depsidones (norstictic, salazinic, fumarprotocetraric, protocetraric and psoromic acids) and depsides (thamnolic, squamatic, barbatic and alectorialic acids) as well as fatty acids (murolic acid complex). Most of the species (except *U. ceratina* and *U. diplotypus*) are represented by more than one chemotype with different main substances (Table 2). Furthermore, accessory substances which may occur in some specimens have only been detected in very low quantities add more complexity. For example, six different

TABLE 2. *Chemotypes of Estonian* Usnea *species*

			Depsidones						Depsides					—	Higher aliphatic acids	
Taxon	Chemotype number*	Recorded in Estonia	Fumarprotocetraric acid	Protocetraric acid	Salazinic acid	Norstictic acid	Stictic acid	Psoromic acid	Barbatic acid	Diffractaic acid	Squamatic acid	Thamnolic acid	Alectorialic acid	Unkown	Caperatic acid	Murolic acid
U. barbata	(1)	+		±	+											
	(2)	–														
U. chaetophora	(1)	+			+											
	(2)	+														
U. diplotypus	(1)	+		±	+				±				±			
U. filipendula	(1)	+		±	+											
	(2)	–														
U. fulvoreagens	(1)	+		±		+	±			±						
	(2)	+		±	+	+	±									
	(3)	–				+					+					
	(4)	+												+		
	(5)	+														
U. glabrata	(1)	+	+	+												
	(2)	–		±	+	+	±									
	(3)	–														
U. glabrescens	(1)	+		±	+	+	±									
	(2)	+				+	±									
	(3)	–						+								
	(4)	–														
U. hirta	(1)	+				±										+
	(2)	+														
U. lapponica	(1)	+		±	+				±						±	
	(2)	–						+								
	(3)	+														
U. subfloridana	(1)	+									+					
	(2)	+										+	±			
	(3)	–									+	+				
U. substerilis	(1)	+		±	+				±							
	(2)	+														
U. wasmuthii	(1)	+		±				±	+							
	(2)	–			+											
	(3)	+		±	+				+							
	(4)	–									±	+				
	(5)	–														

*Chemotype identification numbers correspond to those in the text; + = main substance, ± = accessory substance.

secondary compounds have been reported in *U. fulvoreagens* and five in *U. glabrescens* and *U. lapponica*. Therefore it is important to determine which of these medullary substances might be of diagnostic importance. Usual spot tests with K and Pd are of limited value as some diagnostic substances (e.g. squamatic acid in *U. subfloridana* chemotype 1 or barbatic acid in *U. wasmuthii* chemotype 1) have negative tests while colour tests of different compounds may be rather similar (e.g. norstictic acid causes K+ red and Pd+ orange spot tests while salazinic acid gives K+ yellow, orange or red and Pd+ yellow to orange reactions). Ultimately, TLC is necessary for identification of medullary substances if they are considered to be diagnostic.

Chemistry is not always useful in the group of pendulous species. First, the taxa which have diagnostic main medullary substances such as fumarprotocetraric acid in *U. articulata* or diffractaic acid in *U. ceratina*, often have easily recognizable morphological characters. Second, species which may sometimes be confused, such as *U. barbata*, *U. chaetophora* and *U. filipendula*, have exactly the same chemotypes with chemotype (1) containing salazinic acid as a main substance and protocetraric acid as an accessory, and chemotype (2) without medullary compounds.

In the group of shrubby species identification of secondary compounds is important in some cases. The presence of fumarprotocetraric acid distinguishes *U. glabrata* (chemotype 1), the presence of thamnolic and/or squamatic acids differentiates *U. subfloridana* (chemotypes 1–3), and the presence of psoromic acid indicates *U. glabrescens* (chemotype 3) or *U. lapponica* (chemotype 2). Other depsides and depsidones often occurring in this group have little diagnostic value. For instance, the chemotype with salazinic acid as a main substance is known in *U. diplotypus*, *U. glabrescens* (together with norstictic acid), *U. lapponica*, *U. substerilis* and *U. wasmuthii*. Norstictic acid is the main substance in *U. fulvoreagens*, *U. glabrata* and *U. glabrescens*, and an accessory in *U. hirta* and *U. substerilis*; barbatic acid is the main substance in *U. wasmuthii* and an accessory in *U. diplotypus*, *U. lapponica* and *U. substerilis*. Thus the identification of these substances helps to exclude some species rather than unambiguously determine the taxon. Nevertheless in some cases chemistry is very useful to separate morphologically similar taxa in terminal parts of the key. For instance, *U. fulvoreagens* and *U. lapponica* both have large, expanded soralia and lack isidiomorphs. They can be separated by the branching pattern or shape of branches (see above) but these characters are sometimes indistinct while norstictic acid is predominantly the main substance in *U. fulvoreagens* and is always absent in *U. lapponica*.

The species occurring in Estonia

U. barbata (L.) Weber ex F. H. Wigg. emend. Jørgensen *et al.*

Brit. Fl. **1:** 206 (1780); *Bot. J. Linn. Soc.* **115:** 280 (1994).—*Lichen barbatus* L., *Spec. Plant.* **2:** 1155 (1753).—*Usnea scabrata* Nyl., *Flora* **58:** 103 (1875).

U. prostrata Vain. ex Räsänen, *Medd. Soc. Fauna Fl. Fenn.* **46:** 160 (1921).

(Fig. 2A)

This species is very polymorphic and may represent a collection of intergrading taxa; several characters (e.g. presence of fibrils, papillae, isidiomorphs; degree of depressions and ridges) vary greatly as seen from the following synopsis.

Thallus pendulous, may be partly divided into irregular segments by annular cracks; branches uneven in thickness, often with depressions and/or ridges; fibrils short, few to numerous; *isidiomorphs* few or absent [abundant in North America according to Brodo *et al.* (2001)]; papillae abundant, sparse or absent; *soralia* punctiform and irregular, few to abundant, developing on the top of eroded papillae, tubercules or ridges. *Cortex* thin; *medulla* thick and loose.

For a detailed description, see Halonen *et al.* (1998) and Herrera-Campos *et al.* (1998) under the name *U. scabrata*.

Medullary chemistry. Two chemotypes have been recorded: (1) with salazinic acid as a main substance (K+ yellow, orange or red, Pd+ yellow to orange) and protocetraric acid as an accessory substance; (2) without medullary substances (K−, Pd−) (Halonen *et al.* 1998). In Estonia only the first chemotype is known (n=12).

Remarks. Some specimens which have numerous fibrils may be confused with *U.*

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filipendula in which case the consistency of medulla should be checked (loose medulla in *U. barbata*, and dense in *U. filipendula*).

Ecology and distribution. Grows mainly on conifers (44% of specimens examined on *Picea*, 22% on *Pinus*), sometimes on *Betula* (17%) and rarely on other substrata (lignum, *Alnus glutinosa*) in coniferous or mixed forests, occasionally in wooded meadows. Very frequent in Estonia, found in all regions (Fig. 4A).

Selected specimens examined. **Estonia:** *Harjumaa*: Anija, Põhja-Kõrvemaa Landscape Reserve, 59°19′N, 25°41′E, on *Picea*, 2005, *Tõrra* (TU 32687). *Ida-Virumaa*: Illuka, Kivinõmme Landscape Reserve, 59°15′N, 27°33′E, on *Picea*, 2005, *Tõrra* (TU 32686). *Põlvamaa*: Vastse-Kuuste, 58°10′N, 26°57′E, on *Picea*, 2005, *Tõrra* (TU 41771). *Pärnumaa*: Kanaküla, 58°15′N, 25°11′E, on *Picea*, 2005, *Tõrra* (TU 41765). *Valgamaa*: Taheva, Koiva wooded meadow, 57°41′N, 26°11′E, on *Quercus robur*, 2005, *Suija* (TU 32767).

U. chaetophora Stirt.

Scott. Naturalist Nov. Ser. **1:** 76 (1883).

(Fig. 1C)

Thallus pendulous, with numerous and smooth branches; most branches are divided by annular cracks into regular segments almost up to the terminal parts; fibrils, *isidiomorphs* and papillae absent or scarce; *soralia* few, punctiform. *Cortex* rather thick; *medulla* thin and dense.

For a detailed description, see Halonen *et al.* (1998).

Medullary chemistry. Two chemotypes have been recorded by Halonen *et al.* (1998) from Canada (British Columbia): chemotype (1) with salazinic acid as a main substance (K+ yellow, orange or red, Pd+ yellow to orange) is more common; chemotype (2) without medullary substances (K −, Pd −) occurs occasionally. In Estonia both chemotypes are known (n=1 for each chemotype).

Remarks. A pendulous thallus, absence (or sparse presence) of fibrils and isidiomorphs, and annulation of branches throughout the thallus (not only at the base) are the diagnostic characters of this species. Sometimes it may resemble *U. barbata* and then the consistency of the medulla should be checked again (dense medulla in *U. chaetophora*, and loose in *U. barbata*).

Ecology and distribution. Grows on branches of *Picea* in fresh boreal forests. Very rare in Estonia, recorded twice in southern and south-eastern regions (Fig. 4B); not known from Latvia or Lithuania.

Specimens examined. **Estonia:** *Tartumaa*: Peipsiääre, 58°32′N, 27°07′E, on *Picea*, 2005, *Tõrra* (TU 33516). *Valgamaa*: Puka, Purtsi, 58°03′N, 26°06′E, on *Picea*, 2005, *Tõrra* (TU 32100).

U. diplotypus Vain.

Medd. Soc. Fauna Fl. Fenn. **48:** 172 (1925).

(Fig. 3B)

Thallus shrubby, often subpendent; base pale or blackened; branching mainly anisotomic-dichotomous; branches of uneven thickness, may be irregularly swollen and with depressions, branch tips often twisted; fibrils and papillae present but their number is variable; *isidiomorphs* frequently numerous and relatively long; *soralia* punctiform and usually not expanding, *soredia* farinose. *Cortex* thin; *medulla* variable both in density and thickness.

For a detailed description, see Halonen *et al.* (1998, 1999).

Medullary chemistry. Salazinic acid (K+ yellow, orange or red, Pd+ yellow to orange) is present as a main substance, and protocetraric, barbatic, 4-*O*-demethylbarbatic and alectorialic acids occur as accessory substances in this species from Europe and North America (Clerc 1987*b*; Halonen *et al.* 1998). This chemotype is common in Estonia (n=18).

Remarks. Close to *U. lapponica* and *U. substerilis:* all these taxa have a more or less shrubby thallus, anisotomic-dichotomous branching, branches of uneven thickness, with occasional foveolae and depressions. *Usnea diplotypus* often has a subpendent thallus, twisted branch tips and comparatively long isidiomorphs, while on *U. substerilis* short isidiomorphs are present only on young soralia, and on *U. lapponica* they are totally absent. All three species have similar chemotypes (with salazinic acid as a main substance) and therefore identification of medullary compounds is of little value for distinguishing these taxa.

Ecology and distribution. Usnea diplotypus grows mainly on *Picea* (39% of specimens examined) and *Betula* (20%), more rarely on other deciduous trees (e.g. *Acer*) (7%), and *Pinus* (7%) or lignum (7%) in coniferous or mixed forests. Rather frequent in Estonia (18 specimens), found mainly along the northern coast (Fig. 4C); not known in Latvia.

Selected specimens examined. **Estonia:** *Harjumaa*: Anija, Põhja-Kõrvemaa Landscape Reserve, 59°19′N, 25°39′E, on *Salix caprea*, 2005, *Tõrra* (TU 32700); Harku, near Vääna river, 59°24′N, 24°21′E, on *Larix*, 2005, *Tõrra* (TU 32699). *Lääne-Virumaa*: Vihula, NE of road between Karula and Kandle, 59°30′N, 26°14′E, on *Picea*, 2005, *Tõrra* (TU 33519). *Põlvamaa*: Värska, Verhulitsa, 57°56′N, 27°39′E, on *Betula*, 2005, *Tõrra* (TU 33518). *Saaremaa*, Kihelkonna, 58°21′N, 22°02′E, on *Acer platanoides*, 1984, *Trass* (TU 32095).

U. filipendula Stirt.

Scott. Naturalist **6:** 104 (1881).

U. sublaxa Motyka, *Ann. Univ. Marie Curie-Sklodowska Sect. 3, Biol.* **1**(9)**:** 217 (1936).

U. dasypoga (Ach.) Röhl., *Deutschl. Flora* **3:** 144 (1813).

(Fig. 1D)

Thallus pendulous; base blackened; branches gradually tapering; fibrils and *isidiomorphs* conspicuous and numerous; papillae sparse to abundant, mostly on main branches; *soralia* punctiform, rarely enlarging, often bearing isidiomorphs. *Cortex* thick; *medulla* rather thick, dense.

For a detailed description this variable taxon, see Halonen *et al.* (1998) and Herrera-Campos *et al.* (1998).

Medullary chemistry. Chemotype (1) with salazinic acid as a main substance (K+ yellow, orange or red, Pd+ yellow to orange) and protocetraric acid as an accessory substance is known from Europe and North America; chemotype (2) without medullary substances (K−, Pd−) has been reported from Europe (Halonen *et al.* 1998). In Estonia only the chemotype (1) with salazinic acid has been identified (n=13).

Remarks. For distinction from *U. barbata* see under that species.

Ecology and distribution. Half (50%) of the specimens examined grew on *Picea*, 25% on *Pinus*, and 19% on *Betula*; other substrata are only of minor importance. Very frequent in Estonia, mainly in fresh boreal forests, and found in all regions (Fig. 4D).

Selected specimens examined. **Estonia:** *Harjumaa*: Anija, Põhja-Kõrvemaa Landscape Reserve, 59°19′N, 25°41′E, on *Picea*, 2005, *Tõrra* (TU 32762); Harku, Viti, 59°25′N, 24°20′E, on *Picea*, 2005, *Tõrra* (TU 32764). *Põlvamaa*: Kõlleste, 1 km N of Palojärv, 58°5′N, 26°55′E, on *Picea*, 2005, *Tõrra* (TU 33523). *Valgamaa*; Taheva, Koiva wooded meadow, 57°41′N, 26°11′E, on *Quercus robur*, 2005, *Leppik* (TU 32766).

U. fulvoreagens (Räsänen) Räsänen

Lich. Fenn. Exs. no **13** (1935).—*U. glabrescens* (Nyl. ex Vain.) Vain. var. *fulvoreagens* Räsänen, *Ann. Acad. Sci. Fenn. Ser.* A4, **34**(4)**:** 20 (1931).

(Fig. 3E)

Thallus shrubby, usually richly branched; branching mainly isotomic-dichotomous, branches gradually tapering; base distinctly blackened; annular cracks often abundant and with thick white medullary rings; fibrils numerous; *isidiomorphs* always absent; papillae abundant on main branches; *soralia* excavate when mature and may totally surround the terminal branches. *Cortex* thick; *medulla* rather thin, loose to dense.

For a detailed description, see Halonen *et al.* (1999).

Medullary chemistry. The chemistry of this species is very variable but in many cases the presence of norstictic acid can be used as a diagnostic character. The treatment of chemotypes also varies by different authors (Purvis *et al.* 1992; Halonen *et al.* 1999; Fos & Clerc 2000). The following chemotypes are recognized here: (1) with norstictic acid (K+ red, Pd+ orange) as the main substance and different accessory substances such as other compounds of the stictic acid complex, protocetraric and diffractaic acids is the most common in Europe (Purvis *et al.* 1992; Halonen *et al.* 1999); (2) with salazinic and norstictic acids (K+ red, Pd+ yellow to orange) plus accessory substances has been reported from Fennoscandia (Halonen *et al.* 1999); (3) with norstictic and squamatic acids as main compounds has been recently reported from Spain (Fos & Clerc 2000). Two further chemotypes are reported here: (4) with an unidentified substance (Rf class 2 in A, dark fingerprint-like spot in UV 254, blue in UV 366, dark yellow after treatment with H_2SO_4, dark blue in UV 366 after acid and heating, and not belonging to the stictic acid complex as checked using two-dimensional TLC compared to *Parmotrema crinita*) as a main substance (K−, Pd−); (5) without medullary substances (K−, Pd−). In Estonia chemotype (4) is the most widespread (n=12) and chemotypes (1) and (2) are not rare (both n=5) while chemotype (5) has been recorded only once.

Remarks. This species shares with *U. glabrescens* and *U. wasmuthii* a shrubby thallus, isotomic-dichotomous branching, and branches without foveolae or depressions. *Usnea fulvoreagens* always lacks isidiomorphs and is often characterized by bracelet-like soralia which may totally surround the terminal branches, becoming excavate when mature. Both *U. glabrescens* and *U. wasmuthii* may have isidiomorphs on young soralia but their soralia are somewhat different in shape. *Usnea glabrescens* has young punctiform soralia, later becoming regularly rounded but still staying discrete while *U. wasmuthii* has typically oblong-cylindrical soralia. The identification of medullary compounds usually helps to distinguish *U. wasmuthii* which is represented in Estonia by two chemotypes (one with barbatic acid as a main substance, and the other with barbatic and salazinic acids as main substances). *Usnea fulvoreagens* usually contains either norstictic acid or an unidentified substance as a main compound, and *U. glabrescens* contains either norstictic only or both norstictic and salazinic acids as main compounds.

Ecology and distribution. The majority of specimens examined grew on conifers (55% on *Pinus*, 33% on *Picea*), and were rarely recorded on *Betula* (8%) or other deciduous trees (4%). These contrast with the main phorophytes recorded for *U. fulvoreagens* in East Fennoscandia where 35% of specimens grew on *Alnus*, 18% on *Betula* and 13% on *Picea* (Halonen *et al.* 1999). A frequent species in Estonia (30 specimens), known mainly from the north coast and south-eastern part of the mainland (Fig. 4E).

Selected specimens examined. **Estonia:** *Harjumaa*: Viimsi, on *Picea abies*, 1941, *Seim* (TU 31453). *Lääne-Virumaa*: Lahemaa National Park, 59°34′N, 26°02′E, on *Pinus sylvestris*, 2004, *Randlane* (TU 31460). *Põlvamaa*: Taevaskoja, 58°06′N, 27°02′E, 1959, *Trass* (TU 31449). *Valgamaa*, Kääriku-Mustametsa, 58°00′N, 26°23′E, on *Betula pubescens*, 1964, *Trass* (TU 31443).

U. glabrata (Ach.) Vain.

Ann. Acad. Sci. Fenn., Ser. A4, **6**(7)**:** 7 (1915).—*Usnea plicata* (L.) F.H. Wigg. var. *glabrata* Ach., *Lichenogr. Univ.*: 624 (1810).

Usnea sorediifera (Arnold) Lynge, *Skr. Vidensk.-Selsk. Christiania, Math.-Naturvidensk. Kl.* **1921**(7)**:** 229 (1921).

(Fig. 1A)

Thallus shrubby, small (not exceeding 5 cm, often less); branches somewhat inflated, foveolate and constricted at ramification points; base not blackened, of the same colour as the rest of the thallus; fibrils numerous; *isidiomorphs* absent; papillae usually absent; conspicuous *soralia* mostly near the apices of branches and fibrils, large and may become confluent. *Cortex* thin, shiny; *medulla* thick, very loose; central axis thin.

For a detailed description, see Myllys (1994) and Halonen *et al*. (1998, 1999).

Medullary chemistry. Chemotype (1) with protocetraric and fumarprotocetraric acids as main compounds (K± brownish, Pd+ red) and several accessory substances is known in Europe and North America; chemotype (2) with salazinic and norstictic acids as main substances (K+ red, Pd+ yellow to orange) and with different accessory compounds has been reported from Fennoscandia (Halonen *et al*. 1999); a third acid deficient chemotype (3) without medullary substances (K−, Pd−) has also been reported (Clerc 1987*b*; Myllys 1994; Brodo *et al*. 2001). In Estonia chemotype (1) is common (*n*=7).

Remarks. *Usnea glabrata* is easily recognized by morphological (small shrubby thallus, constriction of secondary branches at their base, presence of rather large soralia, and absence of both papillae and isidiomorphs) as well as by chemical characters (fumarprotocetraric and protocetraric acids as main substances in the chemotype represented in Estonia).

Ecology and distribution. Most specimens examined (78%) grew on *Picea*, and 11% on both *Pinus* and on *Betula*; other substrata are not known for this *Usnea* species in Estonia while in Finland and the Russian part of East Fennoscandia the predominant phorophyte is *Alnus* (Myllys 1994). A rather frequent species (13 specimens), reported mainly from paludified forests in southern and south-eastern regions of Estonia (Fig. 4F); the latest collection dates back to 1959. Not recorded in Latvia, and in Lithuania only one verified locality is known (Motiejūnaitė 2002).

Selected specimens examined. **Estonia:** *Tartumaa*: lake Vissi, 58°15′N, 26°26′E, on *Picea*, 1932, Lippmaa (TU 31463); Järvselja, 58°16′N, 27°18′E, on *Picea abies*, 1959, *Trass* (TU 31472). *Põlvamaa*: Hatiku, 58°5′N, 26°58′E, on *Pinus sylvestris*, 1959, *Golubkova & Trass* (TU 31473). *Viljandi*: park Heimtali, 58°19′N, 25°31′E, 1958, *Trass* (TU 31470).

U. glabrescens (Nyl. ex Vain.) Vain.

Medd. Soc. Fauna Fl. Fenn. **48:** 173 (1925).—*Usnea barbata* (L.) F. H. Wigg. var. *glabrescens* Nyl. ex Vain., *Meddel. Soc. Fauna Fl. Fenn*. **2:** 46 (1878).

(Fig. 3C)

Thallus initially shrubby, later may become subpendent; branching mainly isotomic-dichotomous; base distinctly blackened, often with transverse annular cracks; fibrils present on basal parts and sparse to absent at apical parts; *isidiomorphs* rarely present only on young soralia; papillae present on main branches and absent on secondary branches; young *soralia* punctiform, later becoming larger but usually staying distinctly rounded and discrete. *Cortex* rather thick; *medulla* variable.

For a detailed description, see Halonen *et al*. (1998, 1999).

Medullary chemistry. Variable, with several chemotypes reported: chemotype (1) with norstictic and salazinic acids (K+ red, Pd+ yellow to orange) as main compounds plus other compounds of the stictic acid complex and protocetraric acid as accessory substances is the most common in Fennoscandia; chemotype (2) with norstictic acid as main substance (K+ red, Pd+ orange) plus the stictic acid complex as accessories is widely known in Fennoscandia (Halonen *et al*. 1999) and Great Britain (James 2003); chemotype (3) with psoromic acid (K−, Pd+ yellow) and accessory substances is rare in Great Britain (Clerc 1992; James 2003); chemotype (4) without medullary substances (K−, Pd−) has been reported as rare in East Fennoscandia (Halonen *et al*. 1999). In Estonia chemotype (1) is common (*n*=20) and chemotype (2) is rare (*n*=3).

Remarks. For distinction from closely related taxa see under *U. fulvoreagens*.

Ecology and distribution. The majority (72%) of specimens examined grew on coniferous trees (*Picea* and *Pinus*) and 21% on

Betula; other phorophytes are of less importance. Very frequent in Estonia (80 specimens), reported mainly on the northern coast and in south-eastern regions (Fig. 5A).

Selected specimens examined. **Estonia:** *Põlvamaa*: Kõlleste, 1 km N of Palojärv, 58°05′N, 26°55′E, on *Picea* and *Betula*, 2005, *Tõrra* (TU 32772); Veriora, Ilumetsa, 57°58′N, 27°24′E, on *Picea*, 2005, *Tõrra* (TU 32771); Värska, Mustoja Landscape Reserve, 57°55′N, 27°39′E, on *Betula*, 2005, *Tõrra* (TU 32773). *Valgamaa*: Otepää, Kirikuküla, 58°04′N, 26°25′E, on *Picea*, 2005, *Tõrra* (TU 32777); Puka, Purtsi, 58°03′N, 26°06′E, on *Picea*, 2005, *Tõrra* (TU 32170).

U. hirta (L.) F.H. Wigg.

Prim. Fl. Hols.: 91 (1780)—*Lichen hirtus* L., *Spec. Plant.* **2:** 1155 (1753).

Thallus shrubby, richly branched; branching mainly anisotomic-dichotomous; main branches slightly deformed and foveolate, constrictions may also occur; base pale; fibrils abundant; *isidiomorphs* numerous, scattered or in clusters, more abundant on the terminal parts; papillae absent; *soralia* punctiform and develop on the scars where isidiomorphs have broken off. *Cortex* thin; *medulla* thick and usually loose.

For a detailed description, see Halonen & Puolasmaa (1995) and Halonen *et al.* (1998).

Medullary chemistry. Chemotype (1) with fatty acids (of the murolic acid complex) (K−, Pd−) is widely distributed both in Europe and North America; the presence of norstictic acid (K+ red, Pd+ orange) as an accessory substance has been reported in Great Britain and East Fennoscandia (Purvis *et al.* 1992; Halonen & Puolasmaa 1995). Chemotype 2 without any medullary substances is known from North America (Halonen *et al.* 1998). In Estonia both chemotypes are known (n=8 and n=6, respectively).

Remarks. Shrubby thallus and presence of numerous isidiomorphs of *U. hirta* are similar to those of *U. subfloridana* but it can be distinguished by its slightly deformed main branches and lack of any papillae.

Ecology and distribution. Since *U. hirta* prefers acid bark (Fos & Clerc 2000), it grows mainly on conifers (36% of specimens examined on *Pinus*, 34% on *Picea*, 10% on other) and lignum (9%); deciduous trees are seldomly colonized by this species. Very frequent in Estonia being found in all regions (Fig. 5B), both in forests, open landscapes (wooded meadows, bogs, alvars, seashore areas) and in areas of human activity.

Selected specimens examined. **Estonia:** *Harjumaa*: Naissaar, 59°32′N, 24°32′E, on *Betula pendula*, 1995, *Randlane & Jüriado* (TU 31582). *Ida-Virumaa*: Sonda, Uljaste, 59°21′N, 26°47′E, on *Pinus*, 2005, *Tõrra* (TU 32787). *Lääne-Virumaa*: Vihula, 59°30′N, 26°14′E, on *Picea*, 2005, *Tõrra* (TU 32795). *Pärnumaa*: Häädemeeste, Nigula Nature Reserve, 58°02′N, 24°39′E, on *Picea*, 2005, *Tõrra* (TU 32789). *Saaremaa*: Tagamõisa wooded meadow, 58°28′N, 22°02′E, on *Picea abies*, 1986, *Randlane* (TU 33546).

U. lapponica Vain.

Medd. Soc. Fauna Fl. Fenn. **48:** 173 (1925).

(Fig. 3F)

Thallus shrubby, richly branched; branching mainly anisotomic-dichotomous; branches often with depressions and foveolae; base pale to blackened; fibrils abundant; *isidiomorphs* always absent; papillae numerous; *soralia* large, becoming expanded and irregular or bracelet-like, flat to deeply concave, cortex around soralia is often torn. *Cortex* thin; *medulla* variable in thickness, loose to dense.

For a detailed description, see Halonen *et al.* (1998, 1999).

Medullary chemistry. The main chemotype (1) contains salazinic acid (K+ red, Pd+ yellow to orange) with different accessory substances (protocetraric, barbatic and caperatic acids) (Halonen et al. 1998); chemotype (2) with psoromic acid (K−, Pd+ yellow) is the rarest (Halonen *et al.* 1999); chemotype (3) without medullary compounds (K−, Pd−) is known both in Europe and North America. In Estonia chemotypes (1) and (3) are reported (n=12 and n=5, respectively).

Remarks. For distinction from closely related taxa see under *U. diplotypus*.

Ecology and distribution. Usnea lapponica grows mainly on conifers (37% of specimens examined on *Picea*, 24% on *Pinus*, 22% on other), *Betula* (15%) and on lignum (7%). Very frequent in Estonia (53 specimens), being found mainly on the northern coast and in south-eastern regions (Fig. 5C).

Selected specimens examined. **Estonia:** *Harjumaa*: Harku, near Vääna river, 59°24′N, 24°21′E, on *Larix* and *Picea*, 2005, *Tõrra* (TU 32849). *Jõgevamaa*: Kasepää, Tossumetsa, 58°46′N, 26°58′E, on *Betula*, 2005, *Tõrra* (TU 32844). *Põlvamaa*: Vastse-Kuuste, 58°12′N, 27°02′E, on *Larix* branches, 2005, *Tõrra* (TU 32841); Ahja, Kosova, 58°13′N, 27°02′E, on *Picea*, 2005, *Tõrra* (TU 32840).

U. subfloridana Stirt.

Scott. Naturalist **6:** 294 (1882).

(Figs 1E & F, 2B)

Thallus shrubby to subpendent, richly branched; branching mainly isotomic-dichotomous; base clearly differentiated and blackened, often with transverse annular cracks; fibrils present, abundant near the base and sparse terminally; *isidiomorphs* and papillae usually numerous; *soralia* vary from punctiform to enlarged and typically bear short isidiomorphs. *Cortex* rather thick; *medulla* thin and dense.

For a detailed description, see Halonen *et al.* (1998, 1999).

Medullary chemistry. Three chemotypes are reported: (1) with squamatic acid (K−, Pd−, UV+ whitish blue) as a main substance; (2) with thamnolic acid (K+ yellow, Pd+ orange) as a main substance; (3) with both squamatic and thamnolic acids (Halonen *et al.* 1998, 1999). Alectorialic acid may occur as an accessory substance. In Estonia the first two chemotypes are known (n=37 and n=31, respectively).

Remarks. Usnea subfloridiana is usually easily recognized by the presence of numerous isidiomorphs. Sometimes it may be confused with *U. diplotypus* or with *U. wasmuthii*, but can then be distinguished using the medullary substances; squamatic or thamnolic acids which are the main compounds in *U. subfloridana* and are usually absent in *U. diplotypus* and *U. wasmuthii* [except the chemotype (4) of the latter].

Ecology and distribution. Usnea subfloridiana grows mainly on conifers (35% of examined specimens on *Picea*, 18% on *Pinus*, 14% on other), on *Betula* (22%), and rarely on other deciduous trees (7%) and lignum (4%); it has been reported also on rocks (0·3%). Very frequent being found in all regions of Estonia (Fig. 5D).

Selected specimens examined. **Estonia:** *Harjumaa*: Anija, Põhja-Kõrvemaa Landscape Reserve, 59°19′N, 25°41′E, on *Picea*, 2005, *Tõrra* (TU 33314). *Järvamaa*: Koeru, Võlingi wooded meadow, 58°51′N, 26°03′E, on *Picea*, 2005, *Tõrra* (TU 41770). *Põlvamaa*, Kanepi, Vähkjärve, 58°00′N, 26°46′E, on *Betula*, 2005, *Tõrra* (TU 33308). *Tartumaa*: Peipsiääre, 58°32′N, 27°07′E, on *Salix caprea* and *Picea*, 2005, *Tõrra* (TU 33316). *Valgamaa*, Puka, Purtsi, 58°03′N, 26°06′E, on *Picea*, 2005, *Tõrra* (TU 32172).

U. substerilis Motyka

Wydaw. Muz. Slask. Katowic. **3**(2)**:** 24 (1930).

(Fig. 3A)

Thallus shrubby, usually short, richly branched; branching mainly anisotomic-dichotomous; base pale to blackened; branches of uneven thickness, may be irregularly deformed, swollen and foveolate, with annular cracks which may have white medullary rings; fibrils present, sometimes also abundant terminally; *isidiomorphs* short, present at least on young soralia (and abraded on mature soralia); papillae numerous; *soralia* irregular, slightly tuberculate to slightly excavate, with granulose soredia. *Cortex* thin; *medulla* variable in thickness and density.

For a detailed description, see Halonen *et al.* (1998, 1999).

Medullary chemistry. The main chemotype (1) contains salazinic acid (K+ red, Pd+

yellow to orange) with different accessory substances (protocetraric barbatic and 4-*O*-demethylbarbatic acids); chemotype (2) without medullary compounds (K −, Pd −) is also known (Halonen *et al.* 1998). In Estonia both chemotypes are recorded (n=6 and n=4, respectively), but chemotype (1) is the most frequent.

Remarks. For distinction from closely related taxa see under *U. diplotypus.*

Ecology and distribution. Usnea substerilis grows mainly on deciduous trees (17% of specimens examined on *Betula*, 33% on other deciduous trees); conifers are colonized less often (*Picea* 17%, *Pinus* 8%, other tree species 15%) than by most *Usnea* species. Rather rare in Estonia (10 specimens), found scattered in all regions (Fig. 5E).

Selected specimens examined. **Estonia:** *Hiiumaa*: Saarnaki, 58°07′N, 23°00′E, on *Alus glutinosa*, 1974, *Sander* (TU 32062): *Ida-Virumaa*, Ereda-Puru, 59°20′N, 27°20′E, on wood, 1961, *Piin* (TU): *Lääne-Virumaa*, Lahemaa National Park, 1974, *Sander*, (TU 32066). *Tartumaa*: Vara, Välgi, 58°35′N, 26°52′E, on *Betula*, 2005, *Tõrra* (TU 32972).

U. wasmuthii Räsänen

Ann. Acad. Sci. Fenn., Ser. A4, **34**(4)**:** 19 (1931).

(Fig. 3D)

Thallus shrubby or rarely subpendent, rather richly branched, branches gradually tapering; branching mainly isotomic-dichotomous; base distinctly blackened, often with both transverse and longitudinal cracks; fibrils present, but usually few near apices; *isidiomorphs* short, present at least on young soralia (and abraded on mature soralia); papillae present; *soralia* small to enlarged, oblong-cylindrical, slightly excavate. Cortex thick; medulla thin, dense.

For a detailed description, see Clerc (1992) and Halonen *et al.* (1999).

Medullary chemistry. Altogether five chemotypes have been recorded in *U. wasmuthii* (Clerc 1992; Halonen *et al.* 1999; Fos & Clerc 2000; Ohmura 2001). Chemotype (1) with barbatic acid (K −, Pd −) as the main substance; chemotype (2) with salazinic acid (K+ red, Pd+ yellow to orange) as the main substance; chemotype (3) with both barbatic and salazinic acids (K+ red, Pd+ yellow to orange) as main substances; chemotype (4) with thamnolic acid (K+ yellow, Pd+ orange); chemotype (5) without medullary compounds (K −, Pd −). Different accessory compounds (protocetraric, 4-*O*-demethylbarbatic, psoromic acids) may occur in chemotypes (1) and (2), and in addition squamatic acid in chemotype (4). The latter (recorded in Japan and Spain) has also been considered a possible hybrid since thamnolic and squamatic acids are typical compounds for *U. subfloridana*. In Estonia chemotype (1) is common (n=15) and chemotype (3) is rare (n=3).

Remarks. Veli Räsänen named this taxon after the German, Paul Wasmuth (1874–1934), an estate owner in Russia, who lived and worked as a journalist in Tallinn, Estonia. He was mainly interested in birds and plants but also collected lichens and sent unusual specimens to Räsänen for identification. The type specimen (Estonia, Harjumaa, Tallinn, Kakumäe; preserved in H) was collected by him in 1908.

For distinction from closely related taxa see under *U. fulvoreagens.*

Ecology and distribution. Usnea wasmuthii grows mainly on *Picea* (29% of specimens examined) and on *Betula* (29%), while on *Pinus* it has been observed only occasionally (6%). A third (33%) of the specimens examined grew on other conifers and 11% on other deciduous trees. Rather frequent in Estonia (20 specimens), being found on the northern coast, south-eastern region of the mainland and the western islands (Fig. 5F).

Selected specimens examined. **Estonia:** *Harjumaa*: Harku, near Väana river, 59°24′N, 24°21′E, on *Larix* and *Picea*, 2005, *Tõrra* (TU 32928). *Lääne-Virumaa*: Väsu, 59°34′N, 25°57′E, on *Alnus glutinosa*,1958, *Trass* (TU 32077). *Põlvamaa*: Vähkjärv, 58°00′N, 26°46′E, on *Betula*, 2005, *Tõrra* (TU 32931); Vastse-Kuuste, 58°12′N, 27°02′E, on *Larix* branches, 2005, *Tõrra* (TU 32934). *Tartumaa*: Vara, Välgi, 58°35′N, 26°52′E, on *Betula*, 2005, *Tõrra* (TU 32929).

Species doubtful or potential for Estonia

U. articulata (L.) Hoffm.

Deutschl. Fl. **2:** 133 (1796).—*Lichen articulatus* L., *Spec. Plant.* **2:** 1156 (1753).

(Fig. 1B)

Thallus pendulous with inflated sausage-like segments which are conspicuous in the older part of the thallus; fibrils scarce or absent; *isidiomorphs* present or absent; *soralia* absent but soredia-like propagules may be produced by pseudocyphellae; pseudocyphellae usually present, punctiform, sometimes enlarged. *Cortex* thin; *medulla* thin and extremely loose.

For a detailed description, see Swinscow & Krog (1976).

Medullary chemistry. Five chemotypes have been identified in East Africa (Swinscow & Krog 1976), one with fumarprotocetraric acid as a main and protocetraric acid as an accessory substance is also known in Europe.

Ecology and distribution. The record of *U. articulata* from Estonia is based on a single specimen, collected by Wasmuth at the beginning of the 20th century in the vicinity of Tallinn, on the southern coast of the Baltic Sea (Mereschkowski 1913); no herbarium specimen has been found. Its occurrence in Estonia is most doubtful as the species is generally distributed in western, central and southern areas of Europe (e.g. Great Britain, Poland, Germany, France, Italy) where it grows on the branches of deciduous or coniferous trees but may also scramble over low scrub vegetation in coastal sites (James 2003). It is not recorded from Latvia or Lithuania.

U. ceratina Ach.

Lichenogr. Univ.: 610 (1810).

Thallus shrubby to pendulous, course and tough; fibrils and papillae sparse to numerous; wart-like tubercles numerous on larger branches, becoming white at the top and bearing *soralia* and/or *isidiomorphs*. *Cortex* thick and glossy; *medulla* thick and dense, light pink to pink, occasionally white; central axis pink to almost red, rarely white or yellow.

For a detailed description, see Halonen *et al.* (1998) and Herrera-Campos *et al.* (1998).

Medullary chemistry. Diffractaic acid (K −, Pd −, C+ pale yellow, CK+ yellow to yellow-orange) is present as a main substance and barbatic and squamatic acids as accessory substances; the amounts of an unidentified pink and/or yellow pigments vary.

Ecology and distribution. This species is widely distributed both in the Northern and Southern Hemispheres. It is not known in Estonia or Lithuania but has been reported on conifers in Donikava, north-eastern Latvia (Piterāns 1982, 2001). It is perhaps likely to occur in southern Estonia.

U. florida (L.) Weber ex F.H. Wigg.

Prim. Fl. Holsat. **2:** 7 (1780).—*Lichen floridus* L., *Spec. Plant.* **2:** 1156 (1753).

Thallus shrubby; base blackened; fibrils numerous, becoming curved at the tips; *isidiomorphs* absent, papillae abundant, low, mostly on main branches; *soralia* absent; *apothecia* frequent, arising at apices of primary and secondary branches, with long (up to 5 mm) marginal projections. *Cortex* rather thick; *medulla* thin, dense.

For a detailed description, see Clerc (1984), Purvis *et al.* (1992).

This taxon is considered to be the primary, fertile counterpart in a species pair where *U. subfloridana* is the sterile, secondary counterpart (Clerc 1984). Even so, phylogenetic analyses have demonstrated that the specimens of these two taxa do not form two monophyletic clades according to their reproductive mode but fall into one intermixed group (Articus *et al.* 2002).

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Medullary chemistry. Two chemotypes are known: (1) with thamnolic acid as a major substance (K+ yellow, Pd+ orange) and alectorialic acid as an accessory substance; (2) with squamatic acid (K −, Pd −) (Clerc 1984; Articus *et al.* 2002).

Ecology and distribution. This species is found in Europe growing on old deciduous trees in areas with high atmospheric humidity. It is not known in Estonia, but has been recorded in Latvia (Piterāns 1982, 2001) and Lithuania (Motiejūnaitė 1999) and likely to be found in south-western Estonia.

U. longissima Ach.

Lichenogr. Univ.: 626 (1810).

Thallus pendulous, long to extremely long (up to 3 m); base blackened; the main stem only a few mm long, numerous primary branches are almost undivided, with numerous perpendicular fibrils; papillae absent; *isidiomorphs* and *soralia* occasionally occur on side branches or fibrils. *Cortex* disintegrated on the primary branches exposing the thin compact *medulla*; central axis very thick, originally white but becoming pink to almost red or brown in decorticated branches. I+ blue reaction on the central axis is useful for the identification of juvenile specimens.

For a detailed description, see Halonen *et al.* (1998).

Medullary chemistry. Several chemotypes have been reported; diffractaic, evernic and barbatic acids (all react K −, Pd −) seem to be the most common substances in *U. longissima* in Europe and North America (Halonen *et al.* 1998) while salazinic and fumarprotocetraric acids and atranorin are additionally known in Japan (Asahina 1967).

Ecology and distribution. This species is distributed in the Northern Hemisphere, having a circumboreal distribution pattern and occurring in humid forests, often near lakes or streams (Nimis 1993; Brodo *et al.* 2001); in eastern Fennoscandia it has been reported on *Picea* and *Betula* (Halonen 1997). The listing in Estonia is based on a record from Aegviidu (Charlottenhof), in the vicinity of Tallinn, at the beginning of the 20th century (Mereschkowski 1913), but no herbarium specimens have been found. It has been reported from Mazsalaca in the northern region of Latvia (Piterāns 1982, 2001) but is not known from Lithuania.

Discussion

Frequency and distribution patterns

Of the 12 *Usnea* species now reported from Estonia, one, *U. chaetophora* (Fig. 4B), is very rare, with only two known localities in the south-eastern part of the mainland and another species, *U. substerilis* (Fig. 5E), is rather rare, recorded from only ten localities. Three species, *U. diplotypus* (Fig. 4C), *U. glabrata* (Fig. 4F), and *U. wasmuthii* (Fig. 5F), known from more than ten localities are considered to be rather frequent, (however *U. glabrata* has not been recorded since 1959). *Usnea fulvoreagens* (Fig. 4E) is known from more than 20 localities and is considered to be frequent, while the remaining six species, *U. barbata* (Fig. 4A), *U. filipendula* (Fig. 4D), *U. glabrescens* (Fig. 5A), *U. hirta* (Fig. 5B), *U. lapponica* (Fig. 5C), and *U. subfloridana* (Fig. 5D), known from more than 50 localities are very frequent (Table 1).

Four principal local distribution patterns can be distinguished. (1) very frequently reported *Usnea* species which are distributed more or less over the whole the of Estonia. This pattern is characteristic of *U. barbata*, *U. filipendula*, *U. hirta*, and *U. subfloridana* (Figs 4A & D, 5B & D) and is also evident, but less clearly, on the maps of *U. glabrescens* and *U. lapponica* (Fig. 5A & C). The rather rare species, *U. substerilis* (Fig. 5E), shows a similar pattern. (2) a fragmentary pattern where localities are known mainly from two separate parts of Estonia, the northern coast (and occasionally also in the western islands) and the south-eastern region, is characteristic of *U. fulvoreagens* and *U. wasmuthii* (Figs 4E & 5F). (3) a distribution with all known localities situated in the south-eastern part of Estonia, which is typified by

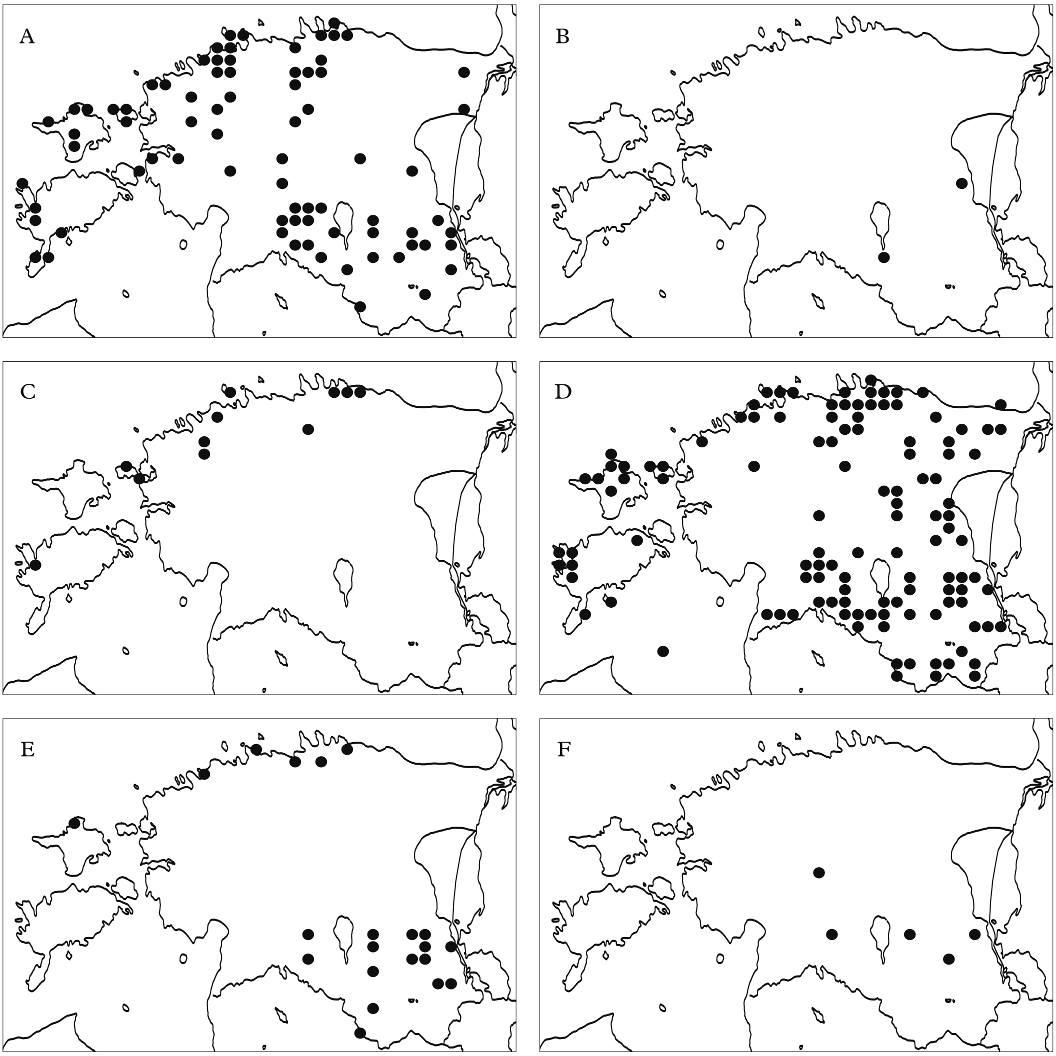

FIG. 4. Distributions of *Usnea* species in Estonia. A, *U. barbata*; B, *U. chaetophora*; C, *U. diplotypus*; D, *U. filipendula*; E, *U. fulvoreagens*; F, *U. glabrata*.

the distributions of *U. chaetophora* and *U. glabrata* (Fig. 4B, F). (4) a distribution confined to the northern coast and western islands as typified by that of *U. diplotypus* (Fig. 4C).

The distribution maps reveal that the south-eastern region in Estonia is the richest in *Usnea* species, while the extensive forested areas in the south-western and north-eastern parts of the mainland are rather poor in species. The north-eastern region of Estonia has been seriously polluted by both sulphur dioxide and alkaline emissions (ash and cement dust) originating from electricity power stations and a cement works, respectively. It has been shown that epiphytic lichen communities close to these pollution sources have changed when compared to the natural communities (Martin & Nilson 1992). In more distant localities (*c.* 30–40 km from the power plants), there is a greater abundance in the forests of lichen species which favour

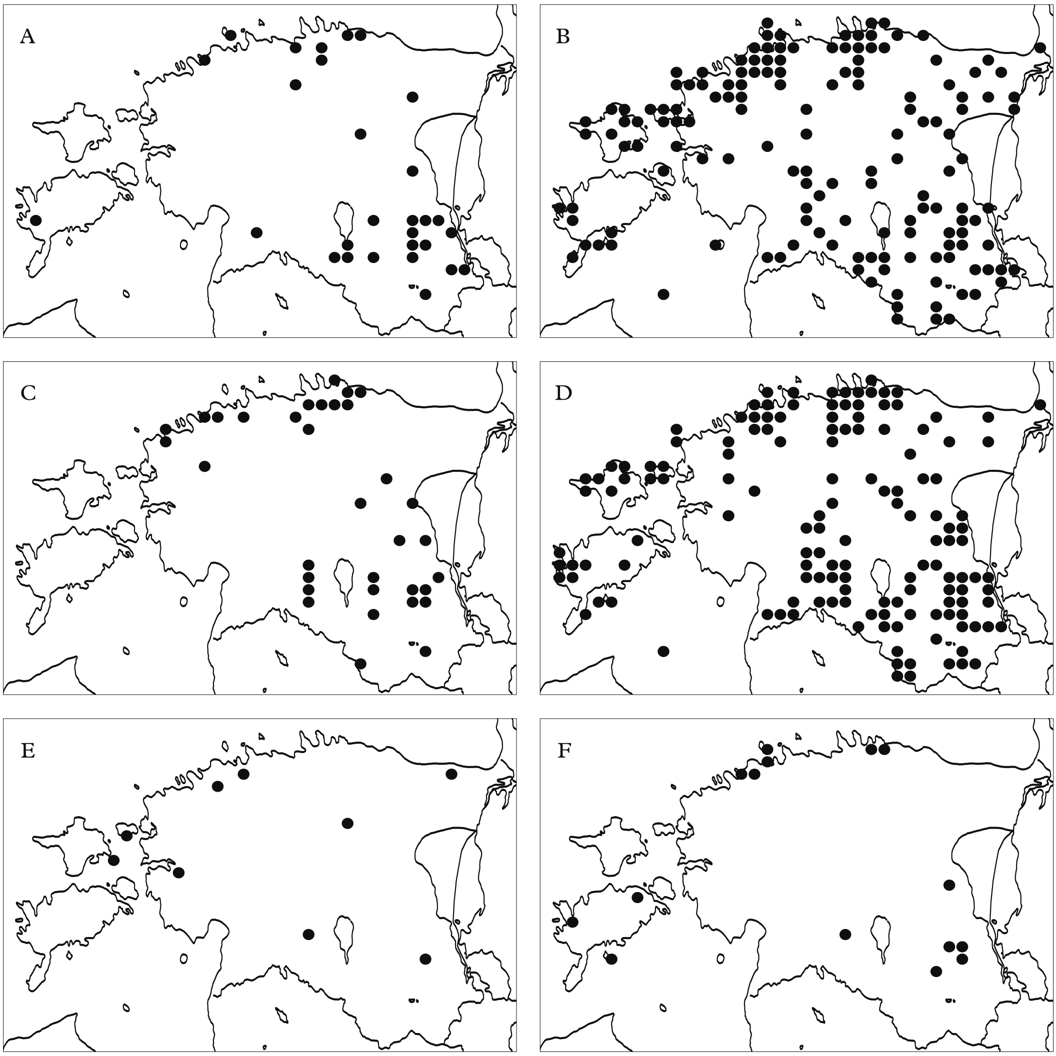

FIG. 5. Distribution of *Usnea* species in Estonia. A, *U. glabrescens*; B, *U. hirta*; C, *U. lapponica*; D, *U. subfloridana*; E, *U. substerilis*; F, *U. wasmuthii*.

nutrient-enriched bark. This is probably caused by alkaline emissions (Jüriado *et al.* 2003). *Usnea* species in the north-eastern forests may also be adversely affected by the distant pollution of sulphur dioxide as well as by the change in natural epiphytic communities.

Generally the local distribution patterns of *Usnea* species in Estonia (with the whole territory of only *c.* 45 000 km^2) are more a reflection of the distribution of vegetation types and habitats which are suitable for these species, than of general climatic or zonal factors. For example, *U. fulvoreagens*, with a general suboceanic distribution pattern (Halonen *et al.* 1999; Fos & Clerc 2000) is also recorded from the south-eastern region of Estonia which is locally the most continental area and *Usnea lapponica*, with a continental distribution (Clerc 1992) is known throughout Estonia, including northern coastal regions.

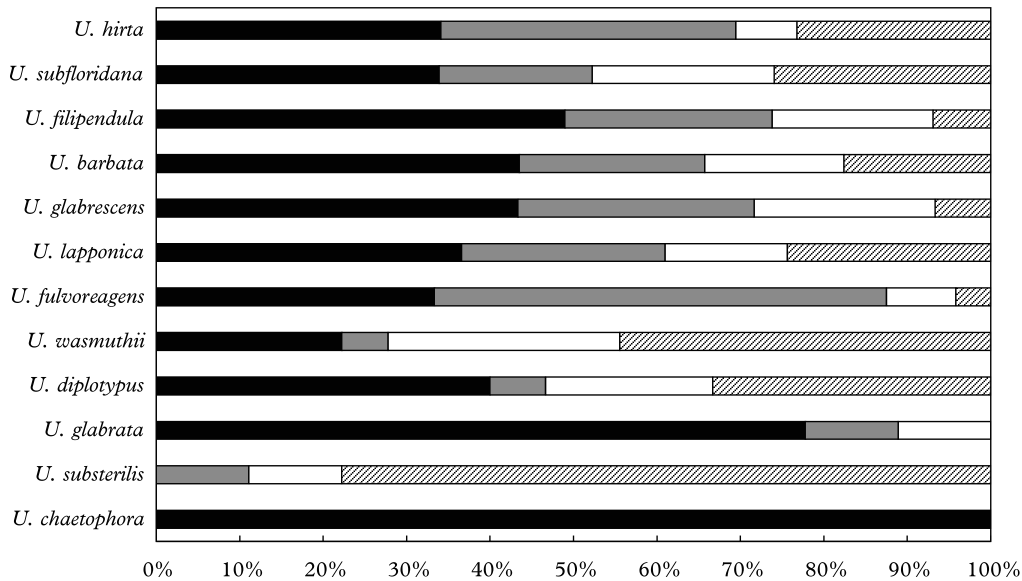

FIG. 6. Proportions of different substrata (■ *Picea*, ▒ *Pinus*, □ *Betula* and ▨ other substrata) for *Usnea* species in Estonia. Other substrata include other coniferous trees except *Picea* and *Pinus*, other deciduous trees except *Betula*, wood and rock.

Substrata

Usnea species recorded in Estonia are primarily epiphytes on conifers, but occasionally also occur on deciduous trees, wood, and exceptionally on rock. Species such as *U. chaetophora* and *U. glabrat*a grow mainly on *Picea* (100% and 78% of specimens collected, respectively) while most species, for example *U. filipendula* (50%), *U. barbata* and *U. diplotypus* (both 44%), prefer *Picea* to other phorophytes as a substratum (Fig. 6). Only two taxa differ in their substratum preferences: *U. fulvoreagens* grows preferably on *Pinus* (50%) and *U. substerilis* on deciduous trees such as *Alnus*, *Betula*, *Salix*, or *Sorbus* (50%). The remaining species have a wider substratum amplitude having been collected in similar proportions from *Picea* and *Pinus* (*U. glabrescens*, *U. hirta*, *U. lapponica*) or from *Picea*, *Pinus* and *Betula* (*U. subfloridana*). Other deciduous trees, such as *Alnus glutinosa*, *Quercus robur* and *Salix caprea*, are inhabited by *Usnea* species (e.g. *U. substerilis* and *U. diplotypus*) though infrequently. Wood is another substratum which is colonized by a few individuals of *U. hirta* (9%), *U. diplotypus* and *U. lapponica* (both 7% of samples collected). *Usnea subfloridana* is the only species in Estonia which has also been recorded on rocks (0·3% of specimens collected).

Substratum preferences of *Usnea* species are probably local in character as similar information reported for East Fennoscandia (Halonen *et al.* 1999) does not correspond to our data. For example, *U. glabrata* clearly prefers *Picea* in Estonia and deciduous trees in East Fennoscandia (78% of specimens collected in both cases); *U. fulvoreagens* often grows on *Pinus* in Estonia (50%) but only rarely in Finland and north-eastern Russia. In Estonia *Picea* is definitely the phorophyte most favourable for both pendent and shrubby *Usnea* species, but in East Fennoscandia *Betula, Alnus* and *Picea* are colonized with similar frequency by shrubby species (data for pendulous species are not available).

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