Synopsis of the Genus *Usnea* (Lichenized Ascomycetes) in British Columbia, Canada

Pekka Halonen  
Botanical Museum, Department of Biology, University of Oulu, PO. Box 333, FIN-90571 Oulu, Finland

Philippe Clerc  
Conservatoire et Jardin botaniques, Case postale 60, CH-1292 Chambésy, Switzerland

Trevor Goward  
Herbarium, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 2B1, Canada  
(Mailing address: Edgewood Blue, Box 131, Clearwater, British Columbia V0E 1N0, Canada)

Irwin M. Brodo  
Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada

Katharina Wulff  
Freie Universitat Berlin, FB 23, WE 2, Altensteinstrasse 6, D-14195 Berlin, Germany

Abstract. Twenty-three *Usnea* species and species groups are reported from British Columbia, Canada. *Usnea chaetophora*, *U. diploptypes*, and *U. nidulans* s. lat. are new to North America, whereas *U. esperantiana* and *U. rigid* s. lat. are documented for the first time for Canada, and *U. ceratina* and *U. rubicunda* are new to British Columbia. New chemotypes are also reported, e.g., in *U. fragilesens* var. mollis and *U. subfloridana*. *Usnea stuppea* (a synonym of *U. substerilis*) is lectotypified. A key to the genus *Usnea* in British Columbia is provided.

The lichen genus *Usnea* in North America has received relatively little attention from modern taxonomists (Clerc 1991; Clerc & Herrera-Campos 1997; Dey 1978; Hale 1979; Tavares 1987), and is in urgent need of revision. Noble et al. (1987) listed 27 species from British Columbia, including many names now placed in synonymy. A few recent floristic studies on the lichens of British Columbia contain notes on *Usnea* species (e.g., Bird & Bird 1973; Brodo 1971, 1984; Goward & Ahti 1992; Thomson & Ahti 1994), though the most important studies have been performed primarily outside of North America (e.g., Clerc 1984a,b, 1987a, 1991, 1992, 1997; Halonen & Puolasmaa 1995; Mylly 1994; Swinscow & Krog 1979).

Motyka’s (1936, 1938, 1947) world monograph of the genus contains 451 species and numerous infraspecific entities, but we regard many of his taxa as environmentally induced modifications. More recently, Bystrek (1994) has continued the Motyka tradition, and has added many new species, most of which are doubtful.

The present study originated as a result of T. Goward’s ongoing work on the macrolichens of British Columbia and is based in large part on *Usnea* material collected by him, and housed mainly at UBC. Other important collections are those of T. Ahti (mainly in h), I. M. Brodo (mainly in CANL), and K. Wulff (UBC). Collecting activity has chiefly been concentrated on the Pacific coastal area, especially the Queen Charlotte Islands, where *Usnea* has its greatest diversity. Less field work has been performed in inland areas, especially in continental boreal lowland regions in the northeast of the province. This paper provides a synopsis and a key for the species of *Usnea* in British Columbia.

**Material and Methods**

Our study is based primarily on herbarium material deposited in CANL, H, OULU, TU, UBC, WIS, and in the personal herbarium of Bruce Ryan. In addition, several type specimens in H-ACH, LBL, TUR-V, and UPS were checked. The study also includes specimens collected during the field trip of the Fifth International Mycological Congress (IMC5) in August 1994, including those of P. Halonen (OULU). The field trip extended from the west coast of Vancouver Island to south-central British Columbia, especially Wells Gray Provincial Park and the Kamloops region. Specimens from other areas of North America were studied to evaluate distributions of some *Usnea* species.

Authors P. Clerc and P. Halonen are primarily responsible for the taxonomy, whereas all authors have contributed to the chemical studies and field observations. Chemistry was examined by means of standardized thin-layer chromatography (TLC), described by Culberson and Aumann (1979), Culberson et al. (1981), and White and James (1985).
MORPHOLOGY

Usnea consists of medium to large, fruticose lichens, easily recognized by their elongate, usually pale, yellowish green branches and especially by the presence of a cartilaginous central axis. The species are typically beard-like (hence the English name “beard lichens”), and may be either shrubby (the whole thallus divergent), subpendent (distinctly divergent from the basal parts and becoming pendent towards the apices) or long-pendent.

The thallus is connected to the substrate by an expanded holdfast which is able to penetrate into the substrate to some extent (illustration, Brodo 1974). Long, pendent species (e.g., U. cavernosa and U. longissima) may also grow without a holdfast. In the British Columbia species, the color of the basal part varies from distinctly jet black to brownish, yellowish-orangish, greenish, or even whitish. There usually is an undivided trunk at the base from which one or more main branches arise. These are normally then divided into few or several thinner secondary and terminal branches. The branching pattern is isometric-dichotomous when the dividing branches are somewhat equal in thickness, or anisometric-dichotomous (= sympodial) when they are not. Both branching patterns often occur in the same thallus.

The branches are circular in transverse section, or slightly angular, and may occasionally have foveoles that are round or oval pits in the cortex (Fig. 5). In longitudinal section, branches may either taper, or remain roughly the same thickness throughout, or may be irregularly shaped. Branches bear few to numerous inconspicuous to well demarcated annular cracks (Fig. 11, 13) which, when abundant and having inflated segments between them, may give a sausage-like appearance to the branches. The annular cracks may be lined by chalky white medullary rings probably consisting of calcium oxalate.

Usnea is characterized by the presence of a strong, cartilaginous central axis, which becomes visible when a branch is stretched. The central axis is usually white, but may also be grayish, pinkish, yellow, orange, or brown. The central axis is surrounded by the medulla, in which hyphae vary in arrangement from loosely arachnoid to compact. The outermost part of the medulla consists of a thin algal layer that contains coccolid green algae (Trebüxia). The algal layer normally lies directly under the cortex. The whole cortex or either the outer or inner part of it may be hard and glossy, and the surface is mat or shiny. Some pendent species (e.g., U. chaetophora and U. scabratula s. lat.) occasionally have elongate pseudocyphellae on the cortex. The color varies from pale straw-colored, to yellowish-green, gray-green, deep yellow, or rarely reddish. Specimens often change color with prolonged storage in the herbarium. For example, some species turn reddish-brown or deep brown (e.g., U. cornuta s. lat. and U. glabratula). 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) (see Clerc 1984a, 1987b).

All local Usnea species bear fibrils (e.g., Fig. 4). These are short, to (40–40) mm long, slender, unbranched or weakly branched cilia-like outgrowths which contain a central axis. Short, spinulose fibrils are often called spines. The fibrils may become abraded, leaving behind tuberculate or plane scars, on which soredia and/or isidia may develop. Clerc and Herrera-Campos (1997) call the tuberculate scars (resemble tubercules) “fibercles.”

Most British Columbia species also bear tiny wartlike papillae on the cortex. Papillae vary in shape from low and verrucose to tall and cylindrical. Tubercles are similar, but differ in their often larger size and in the presence of medulla. Tubercles may develop soredia and/or isidia.

Isidia (e.g., Fig. 9) are minute, corticate, finger-like or rarely sparsely branched outgrowths that lack a central axis. They occur singly or in clusters, and they readily break off and serve as vegetative diaspores. The second author regards true isidia to be absent in the species discussed in this paper, preferring to call the isidia-like propagules “isidiodromors” (see Clerc & Herrera-Campos 1997). In his opinion, they are morphologically and anatomically identical with the “isidiod spinules” in Bryoria furcellata (Brodo & Hawksworth 1977). Detailed anatomical and ontogenetic studies are needed to clarify this point. Preliminary observations made by the second author suggest, however, that these structures are not formed as an outgrowth of the cortex, but from medullary hyphae after the cortex becomes perforated, initiating the development of soralia once the isidiodroms break away. This would be in accordance with Hawksworth and Hill (1984) describing them as “soredia starting to grow into filaments while still in soralia . . . in some fruticose Bryoria and Usnea species.”

Soredia have a similar function to isidia, but are farinose to granulose and lack a cortex. Soredia arise from delimited soralia (e.g., Fig. 12), which are tuberculate, superficial or ± excavate. The soralia vary from minute and punctiform to large and expanded, when in some species soralia may even encircle the branches, and may also become confluent. Soralia develop on local breaks in the cortex or arise from scars. In most sorediate species soralia have isidia when young, in which case the isidia may partly or totally be replaced by soredia.
Table 1. Main secondary medullary metabolites in the genus *Usnea* in British Columbia. + = present in all specimens examined, = present in some specimens (chemoraces), a = accessory substance, not important for taxonomy and often present in small amount to faint traces, * = present only in soralia. ATR = atranorin, BAE = baemycetic acid, BAR = barbatic a., Cph-1 = conviresic a., Cph-2 = confumaprotoctearic a., CPSO = 2'-O-demethylpsoromic a., CRSTI = cryptostic a., CSTI = contestic a., DBAR = 4-O-demethylbarbatic a., DIF = diffractic a., EVE = evernic a., FAT = fatty acids (bourgeanic acid in *U. esperantiana* and the murolic acid complex in *U. hirta*), FUM = fumarprotoceric a., MEN = menegazzic a., NSTI = norsticic a., PRO = protoctearic a., PSO = psoromic a., SAL = salazinic a., SQU = squamatic a., STI = stiotic a., THA = thammolic a.

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Pycnidia are immersed to protuberant, pale or slightly darkened and lateral. Conidia are 1-celled, colorless, bacilliform, and often enlarged at one end. The ascocarp is an apothecium (Fig. 2), which is borne laterally or subterminally. Apothecia are at first concave, later ± plane, often very large, up to 2 cm or more, with fibrils and rarely soredia (e.g., *U. lapponica*) on the margins, sometimes fibrillate,
papillate and/or even with isidia on the lower surface. The disc is pinkish-orange, yellow-green, or rarely dark in color, and often ± pruinose. Spores are 1-celled, ellipsoid, colorless, and 8 per ascus. Apothecia are not common in *Usnea* species of British Columbia, nor do pycnidia occur in abundance. Only one species, *U. rigida s. lat.*, is characterized by the frequent occurrence of apothecia and pycnidia. In the material studied, apothecia were also rarely found in *U. cavernosa*, *U. chaetophora*, *U. fragiliscens var. mollis*, *U. glabrescens s. lat.*, *U. lapponica*, *U. longissima*, *U. scabralata s. lat.*, and *U. substerilis*.

**CHEMISTRY**

All *Usnea* species occurring in British Columbia contain usnic acid in the cortex. Usnic acid (C-9, CK+ yellow, K-, PD-) is a yellow pigment which in most species confers a characteristic yellowish or yellow-green color. *Usnea rubicunda* has a red pigment, which occurs extensively in the cortex, *U. wirthii* often has a red pigment scattered in small spots over the branches, *U. ceratina* contains a variable amount of rose pigment in the medulla, and *U. wirthii* contains a yellow pigment in the medulla and central axis. The nature of these pigments is not known.

The medulla has a much more complex chemistry (Table 1). Most chemical substances are closely related β-orincol depsidones (e.g., norstictic, stictic, psoromic, protocetraric, and salazinic acids) or β-orincol depsides (e.g., thamnolic, squamatic, barbicatic, baemysesic acids, and atranorin). Also present are various fatty acids (e.g., bourgeanie acid and the murolic acid complex), pigments and terpenoids (e.g., zeorin). In the material studied, salazinic acid constitutes the most common primary substance. Norstictic and stictic acids, that belong to the stictic acid group, are also relatively frequently present, whereas the other compounds of the group and protocetraric acid, for example, are less common and are often accessory. Furthermore, several unknown substances were found, but generally they are not mentioned in the section on “The Taxa,” because they are not taxonomically important.

**ECOLOGY AND DISTRIBUTION**

Most *Usnea* species are more or less hygrophilous and photophilous, and therefore occur primarily in moist, well-lit sites. All species present in British Columbia are primarily epiphytic, but may secondarily occur also on other substrates, especially decorticated wood (e.g., *Usnea hirta*) and rarely rocks. Most species are equally common on conifers and deciduous trees, but some display distinct phorphyte preferences.

*Usnea* species are highly sensitive to atmospheric pollution (e.g., Hawksworth & Rose 1970) and have on this account become scarce or absent in urban areas and adjacent to heavy industry. By contrast, *U. hirta* exhibits a relatively high degree of tolerance to atmospheric pollution (Kauppi & Halonen 1992; Wirth 1980), and is able to persist to some extent even in urban areas. Intensive forestry operations are a further cause of decline in many species (e.g., *U. longissima* in Europe, see Esseen et al. 1981).

*Usnea* is a virtually cosmopolitan genus, occurring from the tropics to arctic andantarctic areas (there, only the subgenus *Neuropogon* (Nees & Flot.) Mot.). Species diversity, however, is distinctively lower in arid and arctic areas than in more humid regions of temperate latitudes. The Canadian *Usnea* flora consists mostly of species that are widely distributed in the Northern Hemisphere.

The climate of British Columbia varies markedly as one moves inland across successive mountain ranges running northwest by southwest. Following Goward et al. (1994a), four broad “life zones” may be recognized (Fig. 14), namely the hypermaritime (outer coastal), the maritime (inner coastal), the intermontane (east of the coast ranges and west of the Rocky Mountains), and the boreal (east of the Rocky Mountains). Taxa that occur in hypermaritime and/or maritime regions are referred to as “coastal,” where species present in intermontane and/or in boreal regions are described as “inland.”

The distribution of many *Usnea* species corresponds to the life zones to some extent (Table 2). The hypermaritime element is represented by *U. ceratina* (Fig. 16), *U. esperiantiana* (Fig. 17), *U. fragiliscens var. mollis*, *U. hesperina* (Fig. 20), *U. nidulans s. lat.* (Fig. 21), and *U. rubicunda* (Fig. 17). The northernmost known localities of *U. ceratina*, *U. esperiantiana*, *U. hesperina*, and *U. rubicunda* in Pacific North America are on the southwestern coast of Vancouver Island. *Usnea cornuta s. lat.*, *U. longissima* (Fig. 19), *U. madeirensis* (Fig. 18), and *U. wirthii* are distributed in both the hypermaritime and maritime zones, but are common only in hypermaritime regions. Other coastal species, or species with distinct coastal tendencies, include *U. chaetophora* (Fig. 15), *U. diploptys* (Fig. 17), *U. glabrescens s. lat.*, *U. rigida s. lat.* (Fig. 20), and *U. subfloridana*. The inland element is best represented by *U. hirta* (Fig. 20), *U. lapponica*, *U. scabra s. lat.*, *U. substerilis*, *U. trichoea* (Fig. 19), and less clearly by *U. glabrate*. *Usnea scabra s. lat.* and *U. substerilis*, however, are also rare to scattered in hypermaritime regions. *U. cavernosa* apparently occurs throughout the entire province.
(Fig. 16). *U. filipendula s. lat.* is widespread, but it is not found in the boreal zone.

**PROBLEMS IN TAXONOMY**

*Usnea* is universally regarded as one of the taxonomically most difficult of macrolichen genera, a majority of its species being highly variable in morphology. Many species also are very variable in chemistry and may include as many as three to five chemotypes. They are not accorded taxonomic rank since they are morphologically indistinguishable. Occasional specimens with an unusual chemistry are sometimes found, adding confusion, as in *Usnea fragilis* var. *mollis* for example, which may contain psoromic or squamatic acid—the latter compound otherwise found only in *U. subfloridana* in British Columbia. On the other hand, the taxonomically difficult *U. filipendula s. lat.* has a uniform chemistry, which thus provides little help in distinguishing the taxa.

According to Clerc (1987a,b), the most diagnostic morphological characters in this genus are 1) the color and frequency of segmentation of the basal portions, 2) the shape of the secondary branches, 3) the dominant branching patterns, 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 modified to a considerable extent by environmental conditions. The color of the living thallus has only minimal diagnostic value (Clerc 1984a), except when other pigments in addition to usnic acid are present.

Most local *Usnea* species have wide ranging or essentially circumpolar distribution. Even so, certain morphological and chemical differences are noted between the British Columbia material and their counterparts in Europe. Because a continuum of variation can often be seen in these species, however, it is not easy to evaluate the role of genetic vs. environmental factors.

Intermediate morphs of some closely related taxa, e.g., *U. fulvoreagens* and *U. glabrescens*, have been noted in British Columbia. Some of these intermediate specimens may represent vegetative “hybrids” (see Brodo 1978; Clerc 1984a; Fahselt 1991; Henssen & Jahns 1974), though hybridization in lichens is still incompletely understood.

**KEY TO THE GENUS USNEA IN BRITISH COLUMBIA**

When using the following key, it is important to appreciate that most *Usnea* species are variable in morphology and chemistry. Descriptions given in the key mainly refer to the variation present in the British Columbia material. Juvenile or poorly developed specimens are often difficult to identify, especially when soralia are lacking in species which are normally sorediate. Color reactions should in most cases be checked in the medulla. Norstictic and salazinic acids give a K+ yellow reaction (with low concentrations of the substances) or turn slowly to orange or red (with higher concentrations of the substances).

1. Main branches soon decorticate; thallus very long, up to several meters, sparsely branched; central axis I+ blue; evernic acid often present
   14. *U. longissima*
   2. Cortex containing a red pigment
   2. Cortex lacking a red pigment or pigment restricted to scattered spots
   3. Medulla and axis C+ yellow and CK+ deep yellow-orange, with a rose pigment, this sometimes faint; cortex bearing conspicuous, raised tubercles
   2. *U. ceratina*
   3. Medulla and axis C-, CK- or CK+ yellow-orange (when salazinic acid present), without a rose pigment; conspicuous, raised tubercles present or more often absent
   4. Thallus with a yellow pigment in the medulla and axis, this sometimes faint, rarely absent; cortex usually red-spotted; thallus shubby, small, normally less than 4 cm
   23. *U. wirithii*
   4. Thallus lacking a yellow pigment in the medulla and axis, also lacking red spots over the cortex (yellowish or orangish tint sometimes present in some other species, red spots may be present in the *U. fragilis* agg.); thallus usually larger at maturity
   5. Central axis brown; papillae, soralia, and isidia absent; annular cracks conspicuous
   5. Central axis not brown; papillae, soralia, and isidia present in most species; annular cracks various

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Table 2. Known distribution of the British Columbia *Usnea* species in the life zones and elevations. + = rare, ++ = scattered, + (+) = locally scattered, +++ = common, +++ (+) = locally common; L = lower (under 500 m); M = middle (500 m to under 1000 m); U = upper (1000 m or more).

<table>
<thead>
<tr>
<th>Life zones</th>
<th>Hypermaritime</th>
<th>Maritime</th>
<th>Intermontane</th>
<th>Boreal</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Usnea cavernosa</em></td>
<td>+</td>
<td>+ (+)</td>
<td>(+)</td>
<td>(+)</td>
<td>L-M</td>
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<tr>
<td><em>Usnea ceratina</em></td>
<td>+</td>
<td>+ (+)</td>
<td></td>
<td></td>
<td>L</td>
</tr>
<tr>
<td><em>Usnea chaetophora</em></td>
<td>+++</td>
<td>+ (+)</td>
<td></td>
<td></td>
<td>L-M</td>
</tr>
<tr>
<td><em>Usnea cornuta s. lat.</em></td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
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<tr>
<td><em>Usnea diplopyrus</em></td>
<td>+</td>
<td>+</td>
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<td>L</td>
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<tr>
<td><em>Usnea esperantiana</em></td>
<td>+</td>
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<tr>
<td><em>Usnea filipendula s. lat.</em></td>
<td>(+)</td>
<td>+ (+)</td>
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<td>L-M</td>
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<tr>
<td><em>Usnea fragiliscens var. mollis</em></td>
<td>+++</td>
<td>-</td>
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<td>L-M</td>
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<tr>
<td><em>Usnea glabrata</em></td>
<td>-</td>
<td>+ (+)</td>
<td></td>
<td></td>
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<tr>
<td><em>Usnea glabriscens s. lat.</em></td>
<td>++</td>
<td>+ (+)</td>
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<td>L-M</td>
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<tr>
<td><em>Usnea hesperina</em></td>
<td>+</td>
<td>-</td>
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<tr>
<td><em>Usnea hirta</em></td>
<td>-</td>
<td>+ (+)</td>
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<td>L-M</td>
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<tr>
<td><em>Usnea lapponica</em></td>
<td>-</td>
<td>+ (+)</td>
<td></td>
<td></td>
<td>L-M</td>
</tr>
<tr>
<td><em>Usnea longissima</em></td>
<td>++ (+)</td>
<td>+ (+)</td>
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<td></td>
<td>L-M</td>
</tr>
<tr>
<td><em>Usnea madeirensis</em></td>
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<td>+</td>
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<tr>
<td><em>Usnea nidulans s. lat.</em></td>
<td>+ (+)</td>
<td>-</td>
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<td>L</td>
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<tr>
<td><em>Usnea rigida s. lat.</em></td>
<td>-</td>
<td>+</td>
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<tr>
<td><em>Usnea rubicunda</em></td>
<td>+</td>
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<td>L</td>
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<tr>
<td><em>Usnea scabratula s. lat.</em></td>
<td>++</td>
<td>++ (+)</td>
<td>++ (+)</td>
<td>++ (+)</td>
<td>L-U</td>
</tr>
<tr>
<td><em>Usnea subfloridana</em></td>
<td>+++</td>
<td>++ (+)</td>
<td></td>
<td>++</td>
<td>L-U</td>
</tr>
<tr>
<td><em>Usnea substerilis</em></td>
<td>+</td>
<td>+ (+)</td>
<td></td>
<td>++</td>
<td>L</td>
</tr>
<tr>
<td><em>Usnea trichodea</em></td>
<td>-</td>
<td></td>
<td></td>
<td>++</td>
<td>L</td>
</tr>
<tr>
<td><em>Usnea wirthii</em></td>
<td>+++</td>
<td>+</td>
<td></td>
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<td>L</td>
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</tbody>
</table>

6. Base conspicuously blackened, rarely for only a short distance; cortex bearing numerous an- nular cracks, especially at base; cortex thick (10–20%); medulla compact, thin (7–15%); soralia larger than half branch diameter, isidiate at least when young. 15. *U. madeirensis* 6. Base variously colored, with only a few an- nular cracks when conspicuously blackened; medulla, cortex, and soralia various. 7

7. Thallus shrubby to subpendent when mature, rarely pendent; branches mostly divergent along the entire length of the thallus. 8

7. Thallus pendent when mature; branches parallel for most of the length of thallus. 20

8. Apothecia numerous; soralia and isidiate absent; protocetraric acid present in high quantities in British Columbia, K–, PD+ orange. 17. *U. rigida s. lat.*

8. Apothecia absent or sparse; soralia and/or isidia usually present; protocetraric acid absent or in low quantities (note protocetraric acid strain of *U. cornuta s. lat.*). 9

9. Branches fusiform (i.e., tapering) or constricted at their point of attachment; cortex shiny, usually thin; medulla lax, thick; axis thin. 10

9. Branches not fusiform or constricted at their point of attachment; cortex, medulla, and axis various. 13

10. Soralia numerous, minute, smaller than half branch diameter, but often coalescing and then forming larger soralia-like patches. 4. *U. cornuta s. lat.*

10. Soralia at maturity larger than half branch diameter, discrete. 11

11. Base generally distinctly blackened; soralia scattered over secondary branches and apices, rarely fully excavate, isidiate at least when young; low papillae present on main branches (×50). 8. *U. fragiliscens var. mollis*.

11. Base pale, occasionally slightly blackened; soralia mostly restricted to vicinity of branch apices, numerous, excavate to tuberculate, never isidiate but occasionally with isidia-like spines; papillae absent to numerous. 12

12. Soralia excavate to tuberculate; papillae absent or scattered; thallus usually less than 4 cm; usnic acid alone, K–, PD–, or protocetraric ± furmarprotocetraric ± barbatic acids, K– or K+ brownish, PD+ red-orange; not found in hypermaritime regions. 9. *U. glabrata*

12. Soralia plane to slightly tuberculate; papillae abundant; thallus often more than 4 cm; salazinic, bourgeanic, ± constitic acids, K+ red, PD+ yellow; hypermaritime. 6. *U. esperantiana*

13. Mature soralia strongly excavate, when well de- veloped often revealing the central axis, never isidiate, but short spines may be present on soralia. 14

13. Mature soralia tuberculate to slightly excavate but never strongly excavate, with or without isidia. 15

14. Branching mostly anisotomic-dichotomous; branches often ± deformed and/or foveolate, sometimes irregularly swollen; base pale or blackened; medulla usually ± thick (12–30%); never with stictic acid group. 13. *U. lapponica*

14. Branching mostly isometric-dichotomous; branches cylindric, never swollen; base conspicuously blackened; medulla thin to moderately thick (8–22%); normally with stictic acid group. 10. *U. glabriscens s. lat.*
15. Isidia tall, scattered to crowded; soralia indistinct when present; base pale; main branches ± deformed, angular and foveolate; papillae absent; fatty acids often present 

12. U. hirta

15. Isidia absent or usually short and in clusters when present; soralia punctiform to enlarged; base pale or blackened; main branches cylindrical or ± deformed and foveolate; papillae generally present; fatty acids only rarely present 

16. Cortex distinctly glossy and translucent; fibrils often fasciculate; papillae low, nearly indistinct to absent; soralia distinctly tuberculate when present 

16. U. nidulans s. lat.

16. Cortex mat to slightly glossy, never translucent; fibrils single, rarely fasciculate; papillae always present, usually distinct; soralia tuberculate to excavate 

17. Mature soralia punctiform to slightly enlarged, often ± tuberculate, with numerous isidia 

17. Mature soralia enlarged, plane to slightly excavate, not tuberculate, isidia absent to numerous 

19. Terminal branches mostly anisotomic-dichotomous, not tapered but similar in diameter over their entire length, often sinuose, not all of the same length; base pale or blackened; salazinic ± barbatic acids, K+ yellow to red, PD+ yellow or orange 

5. U. diploptus

18. Terminal branches mostly isotomc-dichotomous, tapered, usually not sinuose, all of the ± same length; base conspicuously blackened; squamatic ± baecomycese ± barbatic acids, or rarely thamnoic acid, K−, PD−, or K+ yellow, PD+ yellow 

20. U. subfloridana

19. Branching mostly anisotomic-dichotomous; branches often ± deformed and/or foveolate, sometimes irregularly swollen; base pale or blackened; mature soralia slightly excavate, but remaining superficial, irregular, usually isidiate at least when young, soredia usually granulose; nev er with stitic acid group 

21. U. substelis

19. Branching mostly isotomc-dichotomous; branches cylindrical, not swollen; base conspicuously blackened; mature soralia slightly to distinctly excavate, often rounded, rarely isidiate when young, soredia usually farinose; normally with stitic acid group 

10. U. glabrescens s. lat.

20. Papillae absent; base pale 

21. Papillae present; base usually blackened 

22. Isidia and soralia absent; fibrils absent or sparse; primary branches ± angular and foveolate; cortex thin (3–6%), glossy; medulla usually lax; salazinic acid, K+ yellow to red, PD+ orange, or usnic acid alone, K−, PD−; widespread 

1. U. cavernosa

21. Isidia and soralia present; fibrils sparse to relatively abundant; primary branches circular, at most slightly foveolate; cortex relatively thick (8–14%), mat; medulla compact, protocetraric acid as main substance, K+ yellow, PD+ orange; hypermaritime 

11. U. hesperina

22. Most branches (usually up to terminal parts) distinctly divided into segments by numerous annular cracks (6–15/cm), often with gaps between segments and visible medullary tissues; papillae sparse (mainly on thickest branches) and low; soralia absent to scattered and generally minute 

3. U. chaetophora

23. Annular cracks absent or few (0–8/cm) and present only on largest branches close to base, other branches only with thin and inconspicuous cracks, not distinctly segmented; usually with numerous verrucous to cylindric papillae; usually with numerous tuberculate soralia 

23. Branches uneven in thickness, ± swollen, often sinuose; base pale or slightly blackened; fibrils irregularly arranged; cortex thin (2–8%); medulla usually lax 

19. U. scabretla s. lat.

23. Branches even in thickness, not swollen, rarely sinuose; base distinctly blackened; fibrils nearly absent to frequent and then ± regularly arranged in a "fishbone" pattern; cortex thick (8–14%); medulla lax to dense 

24. Fibrils normally frequent, especially near the basal parts, mostly in "fishbone" pattern; papillae usually tall, cylindric; soralia tuberculate, arising mostly from scars left when fibrils become abraded; salazinic acid, K+ yellow to red, PD+ yellow or orange 

7. U. filipendula s. lat.

24. Fibrils absent to sparse, never in "fishbone" pattern; papillae short, verrucous; soralia plane to tuberculate, arising from small tubercles; squamatic ± baecomycese ± barbatic acids, K−, PD− or PD+ yellow 

20. U. subfloridana (pendent morphotype)

THE TAXA

USNEA Adans., Fam. Pl. 2: 7. 1763.

1. USNEA Cavernosa Tuck., Lake Superior 171. 1850. (FIG. 5)

Usnea cavernosa is usually easily distinguished by the pendant habit, and the ± angular, foveolate branches. Primary branches, whose abundance varies remarkably, normally are slender, but occasionally reach to 1.5 mm in diameter. Terminal branches are sinuose and capillary. The branching pattern is mainly isotomc-dichotomous. The base is pale, but is often lacking. Annular cracks may be numerous, but they usually are inconspicuous. Usnea cavernosa characteristically has a thin cortex (3–6%) and normally a lax medulla. Furthermore, soralia, isidia, and papillae are absent, and fibrils are absent or very sparse (resembling Alectoria sarmentosa).

Specimens with thin branches may resemble Usnea chaetophora, which also contains salazinic acid. Papillae, soralia, and isidia are, however, usually present in Usnea chaetophora, at least to some extent. This species also has a thicker cortex and at most only sparse foveoles, and is more distinctly segmented as a result of annular cracks. Papillae, soralia, and isidia are also absent in Usnea trichoea, but it characteristically has a brown central axis.

Distribution and ecology.—Widespread in North America from northern boreal regions to Mexico (Motyka 1936; Thomson 1984), although absent in temperate eastern areas of the United States. Especially well developed under conditions with high atmospheric humidity (Thomson 1984). Also found
in Asia and some montane areas in Europe (Motyka 1936). In British Columbia (Fig. 16), rare to scattered in the whole region at lower (under 500 m) to middle, forested elevations (under 1,000 m). Mainly on conifers, especially on Picea.

Chemistry.—Usnic and salazinic acids (K+ yellow to red, PD+ orange); this strain was recognized by Motyka (1936) as subsp. sibirica (Räsänen) Mot. but was reported from Asia and Europe only. Very rarely usnic acid alone (K–, PD–) in British Columbia.

Representative specimens examined.—Mt. Robson Provincial Park, Kinney Lake, on Tsuga heterophylla, 915 m, 53°06'N, 119°10'W, 1985, Marsh 1135 (CANL), fertile, usnic and salazinic acids; Vancouver Island, Goldstream, Mt. Wells, on Pseudotsuga menziesii, 1958, Ahti 14944 (h), usnic and salazinic acids; W shore of Williams Lake, on Picea glauca, 500 m, ca. 52°10'N, 122°10'W, 1983, Goward 83–961 (UBC), usnic acid.

2. Usnea ceratina Ach., Lich. Univ. 610. 1810. (Figs. 1, 6)

Usnea ceratina is readily identified by the presence of a rose pigment in the medulla. The pigment, however, may sometimes be very faint. Furthermore, the medulla is typically compact and the cortex is thick and glossy. The species tends to reach several dm in length, probably due to the favorable climate on the Pacific coast of British Columbia. Branches are gray-green, robust, to ca 1.5–2.0 mm in diam., and more or less uneven in thickness. Both anisotomic and isotomic-dichotomous branching are frequently present. The base is pale or more rarely (secondarily) blackened. Annular cracks may be rather abundant and conspicuous. Numerous tubercles, which soon become whitish, commonly bear isidia and occasionally coarse soridia. Tubercles often are large and evenly elongated and may become confluent, forming ridges. Fibers and low papillae are sparse to abundant.

Usnea ceratina may superficially resemble some morphs of other species e.g., U. chaetophora and U. subfloridana, but it is easily determined by the rose medullary pigment (C+ yellow and CK+ deep yellow-orange color reactions may be due to the pigment), the thick and glossy cortex, and the chemistry with diffractaic acid. In the material from British Columbia, we have also found diffractiac acid in U. longissima (slender, long thallus with abundant fibrils and ± decorticate main branches), in U. trichodea (a brown central axis and slender branches without tubercles), and very rarely in U. hirta (usually small, shrubby thallus, ± thin cortex, and lax medulla), but those species clearly differ morphologically from U. ceratina.

Distribution and ecology.—Widely distributed with oceanic tendencies. In North America, it is also recorded from eastern parts of Canada, the United States, and Mexico (Herrera-Campos & Clerc in press; Motyka 1938). Very rare in British Columbia, since it is found from only three localities, all on Vancouver Island (Fig. 16). All the herbarium specimens previously identified as Usnea ceratina, except for the specimens listed here, represent other species, mainly U. chaetophora. In open but sheltered hypermaritime sea shore forests over conifers and shrubs.

Chemistry.—Usnic, diffractaic, barbatic, 4-O-de-methylbarbatic acids, and several accessory substances (C+ yellow, CK+ deep yellow-orange, K–, PD–) found in all specimens in British Columbia. This chemotype is widespread and commonly known in the species.

Specimens Examined.—Vancouver Island, Ucluelet, on W side of Hyphococ Island, on Tsuga heterophylla, ca sea level, 48°56’N, 125°32’W, 1984, Ahti 42923 & Noble (h); Vancouver Island, Barnfield Inlet, on Picea sitchensis, ca sea level, ca 48°47’N, 125°10’W, 1991, Goward 91–619a (UBC); Vancouver Island, Clayoquot Sound, Sloman Island, N side, on Vaccinium, 2 m, 49°12’N, 125°54’W, 1993, Wulff 93–153 (UBC). New to British Columbia.


Usnea chaetophora is a pendent species, occasionally reaching several dm in length. It is distinguished by the smooth branches (often resembling Alectoria sarmentosa) without papillae, or with papillae that are irregularly distributed (mainly on the thickest branches) and irregularly distributed fibrils. Branches are normally abundant, slender, usually less than 1 mm in diameter—very rarely to 1.5 mm. Both anisotomic and isotomic-dichotomous branching are common. The base is slightly to distinctly blackened. Most branches, normally up to the terminal parts, are divided into segments by the presence of abundant annular cracks (6–15/cm), with the gaps between the segments revealing the medullary tissues. Annular cracks often are slightly constricted or even have white rings, which give a bamboo-like appearance to the branches. Poveoles are absent to sparse, and terminal branches may rarely be sinuose. Soralia are mostly borne on small tubercles and are sparse to scattered or rarely abundant. The size of the soralia is normally minute, occasionally somewhat enlarged and protruding. Isidia are usually absent on the tubercles, but are rarely fairly abundant, and then short. The cortex is moderately thick and usually glossy on secondary branches, and the medulla is dense, only rarely lax.

Morphotypes of U. chaetophora with relatively abundant papillae are close to U. filipendula s. lat., which, however, has more isidia on soralia, and sor-
alia (usually borne on scars of detached fibrils) are abundant when fibrils are few. Usnea chaetophora never has abundant fibrils and soralia are usually few. Both these species normally have distinctly darkened main branches mainly caused by fungal parasites—a character having only minor diagnostic value since many other species may also have darkened main branches. Usnea chaetophora may also resemble other pendent species, for example U. cavernosa, U. hesperina, U. scabrata s. lat., and U. trichodea. Usnea cavernosa has a thinner cortex and angular branches with frequent foveoles on main branches; U. hesperina does not contain salazinic acid and has a different morphology (see text under that species); U. scabrata s. lat. has a thinner cortex, normally a lax medulla, uneven branches, often a pale base, and usually more abundant soralia, which more frequently contain isidia; U. trichodea is epipallate, has a brown central axis, and does not contain salazinic acid.

**Distribution and ecology.**—We have also seen specimens from the Pacific coast of the United States (e.g., Washington, Ahti & Rhodes 51009 H), but the total North American distribution is poorly known. The species is rare in Europe. Locally common in coastal areas of the province (Fig. 15) especially on the Queen Charlotte Islands. Mainly on conifers in humid forests at lower to middle elevations.

**Chemistry.**—Usnic and salazinic acids (K+ yellow to red, PD+ yellow or orange). Only one specimen with usnic acid alone (K-, PD-) found in the studied material.

**Specimens examined.**—Queen Charlotte Islands, Moresby Island, S entrance to Louise Narrows, on conifer, ca sea level, 52°57'N, 131°54'W, 1971, Brodo 17921 (*can.); Vancouver Island, Barnfield Inlet, ca sea level, 48°48'N, 125°09'W, 1994, Ahti 52374b (H); 25 km SE of Hazelton, near Boulder Creek, on Pinus contorta, 490 m, 55°06'N, 127°28'W, 1981, Goward 81–1845b (UBC). Usnic and salazinic acids in all specimens. New to North America.

4. **Usnea cornuta** Körber, Parerga Lichenol. 2. 1859, s. lat. (Syn.: *U. inflata* (Duby) Mot.)

Usnea cornuta s. lat. belongs to the *U. fragiles
cens* agg. with *U. esperantiana*, *U. fragiles
cens* var. *mollis*, *U. glabrata*, and *U. wirthii*. The aggregate is characterized by the glossy and ± thin (ca 3–9%) cortex, generally lax and thick (ca 25–40%) medulla, and usually thin (ca 12–44%) central axis (Clerc 1987a). Distinct annular cracks are present and branches are more or less constricted or fusiform at the bases. Branches and fibrils often are more or less inflated.

The thallus of *U. cornuta* s. lat. is usually divergent, erect and bushy, rarely to subpendent. The branching pattern is mainly anisotomic-dichotomous. Branches vary from relatively slender and tapering to thick and inflated, and secondary branches are distinctly constricted. Foveoles may be sparse to rather numerous. The basal part is pale or blackened and usually not constricted. Soralia are minute, numerous, and often confluent forming large soralia patches. They are borne on low tubercles and over the scars of detached isidia, and are located mainly on terminal branches, being absent or sparse on secondary branches. Isidia are minute to tall. Papillae are absent (especially near the terminal parts) to verrucous and numerous. Fibrils are sparse to abundant. *U. cornuta* s. lat. often has a divergent and spinulous habit given by isidia, fibrils, and side branches with axes of ca 90°. Although the color of the central axis is usually white, it can be orangish in *U. cornuta* s. str. when salazinic acid is present (see Clerc 1987a).

Usnea cornuta s. lat. is close to *U. fragiles
cens* var. *mollis*, however, it typically has a subpendent habit; a more distinctly blackened base; and larger, more scattered soralia that are commonly present both over the terminal branches and the secondary branches. These two species are not always easily distinguished when the soralia are not fully developed. *Usnea wirthii* has a smaller thallus with red spots on the surface (rarely present in the other species of the aggregate), a yellow pigment in the inner medulla and axis (sometimes faintly), and soralia that are more rarely isidiate. *Usnea esperantiana* and *U. glabrata* often have a smaller thallus and different soralia types, which lack isidia. Furthermore, these species have different chemistry, and *U. glabrata* has a more continental distribution. Small, juvenile thalli of *U. cornuta* s. lat. may be difficult to separate from the other species of the aggregate.

**Distribution and ecology.**—Found in oceanic regions of North and South America and Europe (Clerc 1987a; Jørgensen 1996). Locally common in hypermaritime regions of British Columbia, but very rare in maritime areas. In open forests at lower elevations, less common in shady sites. Collected more frequently over conifers than over deciduous trees, also on shrubs.

**Chemistry.**—Variable chemistry. Usnic and salazinic acids ± compounds of the stictic acid group, or usnic acid with various combinations of compounds of the stictic acid group (K+ yellow to red, PD+ yellow or orange). An unknown fatty acid is found in one specimen (Rf values A4–5/B5/C5). *Usnea occidentalis* Mot., which produces psoromic, ± 2′-O-demethylpsoromic and/or protocetraric acids (K– or K+ yellow, PD+ yellow or orange), was described from Washington State (*U. cornuta* s. str. may also rarely contain psoromic and 2′-O-
demethylpsoromic acids). Here *U. occidentalis* is included in *U. cornuta s. lat.* A strain with thamnolic and protocetraric acids is found in California in the United States (Clerc & Herrera-Campos 1997).

Representative specimens examined.—Queen Charlotte Islands, Graham Island, Seal Inlet in Rennell’s Sound, on *Picea stichensis*, ca sea level, 53°29’N, 132°47’W, 1967, Brodo 10301b et al. (CANL), usnic and salazinic acids; Vancouver Island, Keeha Beach, on *Picea*, ca sea level, 48°47’N, 125°10’11”W, 1994, Vitikainen 13069 (H), usnic, salazinic and constictic acids in one thallus, and usnic, psoromic and protocetraric acids in another; Vancouver Island, Clayoquot Sound, Sloman Island, N side, on *Vaccinium*, 2 m, 49°12’N, 125°53’W, 1993, Wulff 93–152 (UBC), usnic, norstictic acids and unknown fatty acid.


*Usnea diploptys* has a shrubby to occasionally pendent thallus with ± irregularly swollen, slender branches which may have foveoles and depressions. Terminal branches are often sinuose and not tapering, but ± similar in diameter over their entire length, and not all the same length. The branching pattern is mainly anisotomic-dichotomous. The base is pale or blackened. Soralia that mainly develop on a plain cortex, typically are minute and usually contain numerous, tall isidia. Papillae are short to cylindric, and the abundance of papillae and fibrils is variable. The cortex is thin, and the medulla is lax to dense and very variable in thickness.

A closely related species, *U. substerilis*, differs by its large and superficial soralia, and isidia that are short and often lacking on mature soralia. *Usnea diploptys* may be sometimes difficult to separate from *U. subfloridana*, but the latter species has tapering branches that are about equal in length, with a mainly isotomic-dichotomous branching pattern. It also has a different chemistry (i.e., lacking salazinic acid). Pendent morphs of *U. diploptys* resemble *U. scabrata s. lat.*, but can be distinguished by the different soralia. In *U. scabrata s. lat.* these mainly arise from tubercles, and isidia are usually short or are often lacking. Furthermore, barbatic acid is occasionally produced in *U. diploptys*.

Distribution and ecology.—The previous North American records, all of which are saxicolous specimens, are misidentifications of other species (Clerc & Herrera-Campos 1997). The species is primarily epiphytic as it is in Europe (Clerc 1987a), where it is found mainly in the Alps, and scattered in Fennoscandia and western parts. In British Columbia (Fig. 17), only three specimens are identified as *U. diploptys* with certainty, and a few other collections may also belong to the species. These are collected from coastal regions at lower elevations. Gooward and Ahti (1992) reported *U. diploptys* as new to the province from an inland area, but the specimen cited actually represents *U. substerilis*.

Chemistry.—Usnic, salazinic, ± barbatic, and ± 4-O-demethylbarbatic acids (K+ yellow to red, PD+ yellow or orange). In Europe, a strain with usnic and alectorolaric acids is also found.

Specimens examined.—Queen Charlotte Islands, Moresby Island, Davey Islet, on *Thuja*, ca sea level, 53°03’N, 131°59’W, 1971, Brodo 17181 & Wong (CANL), usnic and salazinic acids; Vancouver Island, Sidney, on trees, 1913?, Macoun (CANL), usnic, salazinic, barbatic (trace) and 4-O-demethylbarbatic (trace) acids; Vancouver, on *Populus*, 1994, Halonen 94/506 (OULU), usnic, salazinic, barbatic, and 4-O-demethylbarbatic acids. New to North America.


The species has a shrubby, or more rarely a subpendent thallus, to ca 8 cm. The branching pattern is mainly anisotomic-dichotomous. The basal part is pale and not constricted. Main branches, which divide from a short trunk, are relatively thick, to ca 2 mm in diam., ± foveolate, and swollen. Branches often are constricted at the base. The apices are characteristically recurved, with plane to slightly excavate and ± confluent soralia. Isidia are absent. Papillae are distinct and numerous and fibrils are abundant. The cortex is glossy and usually thin, the medulla is lax to dense, and the central axis is normally thin. The specimens found on Vancouver Island have a very thin cortex; a thick and lax medulla; and a thin, orangish central axis.

*Usnea esperantiana* may resemble *U. glabrata*, which also lacks isidia. *Usnea glabrata* differs, for example, by the different soralia and the epapillate or sparsely papillate main branches. In addition, *U. glabrata* has a different chemistry, containing the protocetraric acid group and/or barbatic acid or usnic acid alone. *Usnea glabrata* also has a more continental distribution pattern. For points of distinction in the *U. fragilesens* agg., see comments under *U. cornuta s. lat.*

Distribution and ecology.—Southern and western in Europe (Clerc 1992), and recently found from California and South America (Clerc pers. com.). Very rare in British Columbia, with only one locality found so far (Fig. 17).

Chemistry.—Usnic, salazinic, bourgeoisian, and ± constictic acids (K+ red, PD+ yellow). This chemotype is also found in Europe (Clerc 1992) and the United States.

Specimens examined.—Vancouver Island, Barnfield Inlet, on conifers, ca sea level, 48°48’N, 125°09’W, 1994, Ahti 52390, 52393 (H). New to Canada.

*Usnea filipendula* s. lat. has several morphotypes that vary both in branching pattern and in the abundance of branches and fibrils. Typical *U. filipendula* s. str. has a pendent thallus, to ca 20(–50) cm; ± abundant, slender branches, usually less than 1 mm, often ca 0.2–0.5 mm; and a mainly anisotomic-dichotomous branching pattern. Branches may occasionally be weakly sinuose near the apices. The base is distinctly blackened. Soralia, which are usually borne on scars left behind when fibrils (including spinules) become abraded, are scattered to abundant, but absent near apices, and become rarely enlarged. The soredia are fainose. Abundant isidia are present, and are usually tall. Scars are often esorediate but covered by isidia. Papillae are ± cylindrical and abundant. Fibrils are normally abundant, especially near the base, and are arranged in a more or less “fishbone” pattern. This species has a moderately thick cortex (8–14%) and usually a dense medulla.

Some morphs of *U. chaetophora* come close to *U. filipendula* s. lat. (see the points of separation under *U. chaetophora*). Young thalli of *U. filipendula* s. lat. may especially resemble several other species e.g., *U. diploptus*, *U. madeirensis*, and *U. subfloridana*. *Usnea diploptus*, which may also become pendent, has ± swollen and foveolate branches and occasionally produces barbatic acid together with salazinic acid. *Usnea madeirensis*, which is also has salazinic acid, is distinguished by numerous angular cracks especially at the base, as well as by very thick cortex and central axis, thin medulla, and large soralia. Furthermore, this species basically has a shrubby and divergent branching, later often becoming subpendent or pendant. *Usnea subfloridana* is rarely pendent, has short papillae, often enlarged soralia, the branching pattern is mainly isometric-dichotomous, and fibrils are not in a “fishbone” pattern. It is also easily separated by the chemistry with squamatic, ± baemomyces, ± barbatic acids, or thammolic acid instead of salazinic acid.

**Distribution and ecology.**—Circumpolar in boreal and temperate (mainly montane) zones. In North America, the species is apparently most common in eastern parts of Canada and northeastern regions of the United States. Scattered to locally common from hypermaritime to intermontane regions of British Columbia, but not collected in boreal areas. Mainly on conifers, especially on *Picea* in forests at lower to middle elevations.

**Chemistry.**—Usnic, salazinic, and ± protocetraric (trace) acids (K+ yellow to red, PD+ yellow or orange). In Europe, a strain with usnic acid alone is also found.

**Representative specimens examined.**—Queen Charlotte Islands, Moresby Island, Kwuna Point, on *Picea sitchensis*, ca sea level, 53°13′N, 131°59′W, 1967, Brodo 11226 & Shchepanek (CANL); 35 km SW of Prince George, near Mt. Baldy Hughes, on *Picea*, 700 m, ca 53°25′N, 123°00′W, 1981, Goward 81–1549 (UBC); Vancouver Island, Lake Cowichan, on *Thuja* and *Tsuga*, 1931, Kujala (H).


The species has an anisotomic-dichotomous, subpendent thallus, to ca 20 cm, or more rarely a shrubby habit. The thallus is sparsely branched especially towards the apices. Foveoles may be sparsely present on branches. The base is usually distinctly blackened, rarely pale, and not constricted, but it is often fusiform. Branches are narrowed to distinctly constricted at the base. *Usnea fragiliscens* var. *mollis* may be distinguished by its large, discrete, plane to moderately excavate, soralia and presence of isidia. The soralia in this species are present both over the secondary branches and over the terminal portions, and arise mainly from low tubercles. Papillae are low and numerous, but sometimes are barely visible and may be absent in juvenile thalli. Fibrils are sparse to relatively abundant. The cortex is thin and glossy, the medulla is thick and lax, and the central axis is thin and normally white but may be orangish when salazinic acid is present.

**Usnea fragiliscens** var. *mollis* may resemble other related species, especially when soralia are not well developed. For the points of distinction with other species in the *U. fragiliscens* agg., see comments under *U. cornuta* s. lat.

**Distribution and ecology.**—Distributed in oceanic areas, being rare in western Europe (Clerc 1987a; Jørgensen 1996) and disjunct on the eastern and western coasts of North America. This is one of the most common species of *Usnea* in the hypermaritime zone of British Columbia. Frequent both on conifers and deciduous trees in open forests at lower elevations, occasionally also on shrubs. *Usnea fragiliscens* var. *fragiliscens*, which is found mainly over rocks in Europe (Clerc 1987a), is not recorded from British Columbia. The taxonomic status of the varieties of *U. fragiliscens*, however, needs further investigation.

**Chemistry.**—Variable chemistry with more chemotypes in British Columbia than in Europe. The most common chemotypes have usnic acid and various combinations of compounds of the stictic acid group (K+ yellow to red, PD+ yellow or orange). Chemotypes producing usnic and salazinic
acids (incl. Lich. Can. Exs. 215) ± compounds of the stictic acid group or atranorin (one specimen) (K+ orange or red, PD+ orange) were also found in British Columbia. Specimens with only usnic acid (K−, PD−), or usnic acid with psoromic ± 2'-O-demethylpsoromic acids (K− or K+ yellow, PD+ yellow), or squamatic acid (K−, PD−, UV+ whitish blue) were occasionally found in the studied material. Psoromic, 2'-O-demethylpsoromic, squamatic acids, and atranorin were not previously known to occur in this species.


Representative specimens examined.—Queen Charlotte Islands, Moresby Island, between Sandspit and Copper Bay, on Malus, ca sea level, 53°13'N, 131°47'W, 1967, Brodo 12875 et al. (CAND), usnic, norstictic, stictic, and constrictic acids; Vancouver Island, Ucluelet, on Tsuga heterophylla at height of ca 20–30 m, ca 48°55'N, 125°32'W, 1982, Goward 82-1829 (UBC), usnic, psoromic, and 2'-O-demethylpsoromic acids; Vancouver Island, Clayquot Sound, Sloman Island, on Thuja plicata, 2 m, 49°12'N, 125°54'W, 1993, Wullf 93-132 (UBC), usnic and squamatic acids.


This species is characterized by the small thallus, usually less than 4 cm; with abundant, inflated, ± foveolate branches that are constricted or fusiform at the base. The branching pattern is mainly anisotomic-dichotomous. The base of the thallus is pale to slightly blackened. The apices are straight to distinctly recurved. Soralia are located mostly near the apices, are usually large and tuberculate, sometimes excavate (when eroded), often become confluent, and contain ± granulose soredia. Isidia are absent, but spinules may be present around soralia. Papillae are absent or more rarely scattered. Fibrils are usually abundant. As in other members of the U. fragilisens agg., the cortex is thin and shiny, the medulla is thick and lax, and the central axis is thin.

Another inland species, U. hirta, may have a similar chemistry with usnic acid alone and may resemble U. glabratia in habit. Usnea hirta is distinguishable by the numerous, tall isidia and by the ± angular branches that are not constricted at the base. For points of distinction with other species in the U. fragilisens agg., see the comments under U. cornuta s. lat.

As pointed out by Goward and Ahti (1992) and Myllys (1994), Usnea kujalae, which was described from Hazelton, British Columbia (Rääsänen 1933), is a synonym of U. glabratia.

Distribution and ecology.—Circumpolar in boreal and temperate regions with continental tendencies (Myllys 1994). Widely distributed in North America from Canada to Mexico (Motyka 1938; Thomson 1984). Scattered in maritime localities of British Columbia and locally common in intermontane areas. Not found in hypermaritime regions, unlike the other members of the aggregate (see Usnea cornuta s. lat.). Mostly over deciduous trees in open, humid forests at lower to middle elevations.

Chemistry.—Usnic, protocetraric, ± fumarprotocetraric, ± barbatic, ± 4-O-demethylbarbatic acids, ± Cph-1 (convivresic acid), and ± Cph-2 (con-fumarprotocetraric acid) (K− or K+ brownish, PD+ red-orange). Less commonly usnic acid alone, or usnic and barbatic acids (K−, PD−). Usnea florid var. pilina Vain. from Siberia also contains norstictic, ± salazinic, and ± fatty acids (Myllys 1994), and is a synonym of U. glabratia.

Representative specimens examined.—Clearwater River Basin, near entrance of Wells Gray Provincial Park, Hemp Creek, Helset’s Farm, on Pseudotsuga menziesii, 600 m, 1961, Ahti 6516a (h), usnic and protocetraric acids; Clearwater River Basin, Wells Gray Provincial Park, Ray Farm, on Malus, 640 m, 52°05'N, 120°08'W, 1994, Halonen 94/509 (OULU), usnic acid; S of Vancouver, Burns Bog, on Pinus contorta, 640 m, 49°10'N, 123°20'W, 1982, Goward 82-319 et al. (UBC), usnic, protocetraric, fumarprotocetraric acids, Cph-1 and Cph-2.


Usnea glabrecens s. lat. is identified by the shrubby to subpentad thallus; the relatively long, tapering terminal branches; the distinctly blackened base; and by the absence of isidia on mature soralia. Soralia are borne on a plane cortex, especially near apices, and on tubercles. The cortex is moderately thick (8–15%); the medulla is dense, rarely somewhat lax, and thin (8–22%); and the central axis is thick (32–56%). Distinct papillae occur only on the main branches where they are numerous. The branching pattern is mainly isotomic-dichotomous, but anisotomic branching is also common especially near the extremities. Usnea fulvovearegens (Rääsänen) Rääsänen (basionym: U. glabrecens var. fulvovearegens Rääsänen) is often incorrectly regarded as a synonym of U. lapponica (Clerc 1992). Here U. fulvovearegens is included in U. glabrecens s. lat. Usnea glabrecens s. str. is distinguished from U. fulvovearegens by the former’s larger, more often subpentad thallus; fewer fibrils; usually lower papillae; and soralia that are ± discrete, rounded and plane to only slightly excavate. Young soralia may rarely have sparse isidia. U. fulvovearegens never has isidia and the soralia are irregularly shaped, ± confluent, and deeply excavate often reaching the central axis. White medullary rings along annular
cracks are common in both taxa, but they usually are thicker in *U. fulvoreaens*. The species also have some differences in chemistry. These two species are not always easily separated since *U. glabrescens s. str.* is variable in morphology and sometimes may have deeply excavate soralia. Some of the specimens collected from British Columbia appear to represent more or less intermediate morphs of *U. fulvoreaens* and *U. glabrescens* (e.g., Goward 94–950, 1994, UBC). Further studies are needed before the status of *U. fulvoreaens* can be clarified.

*Usnea glabrescens s. lat.* may resemble *U. subfloriana* in habit, although species may be distinguished by its soralia with isidia and by the presence of squamatic or thamnolic acid. Morphs with deeply excavate soralia may resemble *U. lapponica* (see the discussion under that species).

**Distribution and ecology.**—Wide range from boreal to temperate regions. The total distribution in North America is poorly known, but we have also seen specimens from eastern parts of Canada and Pacific areas of the United States. In British Columbia, scattered on the coast and rare in intermontane areas but not found in boreal regions. Over conifers and deciduous trees in humid forests at lower to middle elevations.

**Chemistry.**—Usnic acid with various combinations of norstictic, salazinic acids, and compounds of the stictic acid group (K+ yellow to red, PD+ yellow or orange). Salazinic acid is common in *Usnea glabrescens s. str.*, but is also occasionally present in *U. fulvoreaens*. In Europe, *U. glabrescens s. str.* may have psoromic acid (Clerc 1992) or usnic acid alone, and *U. fulvoreaens* sometimes contains diffractaic acid (Clerc 1992).

Representative specimens examined (**U. glabrescens s. str.**).—Queen Charlotte Islands, Maude Island, S shore, on *Malus*, ca sea level, 53°12’N, 132°05’W, 1967, Brodo 11288 & Schepanek (CANL, GULU), usnic, norstictic, stictic, and constrictic acids; Clearwater River Basin, Wells Gray Provincial Park, Ray Farm, on *Picea engelmannii × glauca*, 640 m, 52°05’N, 120°08’W, 1988, Goward 88–246 & Brodo (UBC), usnic and norstictic (trace) acids in one thallus, and usnic and salazinic acids in another.

**11. USNEA HESPERINA** Mot., Lich. Gen. *Usnea* Stud. Monogr. 2: 383. 1938. (Fig. 8)

The species is characterized by its pendent thallus and annular cracks that are abundant especially at the base that is pale. Branches are slender, circular, epapillate and at most slightly foveolate. *Usnea hesperina* has few to abundant minute soralia, which develop on low tubercles or when isidia become detached. The isidia are short, sparse to scattered, and often soon becoming abraded. Fibrils are long, curved, and sparse to relatively abundant. The cortex is mat and moderately thick (8–14%), the medulla is thin (6–16%) and compact, and the central axis is thick (43–64%).

*Usnea hesperina* may resemble some other pendant species, especially *U. chaetophora*, which differs, for instance, by the blackened base, the usually papillate main branches, and the different anatomy (C/M/A) and chemistry. Another epapillate species, *U. trichodea*, is readily separated by its brown central axis. *Usnea hesperina* is easily determined by the chemistry with protocetraric acid as the main substance. Most of the other species in British Columbia have protocetraric acid, at most, only in minor quantities. Protocetraric acid may be, however, the main substance in *U. cornuta s. lat.* (often), *U. glabrata* (often), and *U. rigida s. lat.*, but these species differ distinctly in morphology from *U. hesperina*. *Usnea cornuta s. lat.* and *U. glabrata* have shrubby thalli with distinct soralia, constricted branches, and lax medulla. *Usnea rigida s. lat.* has a fertile thallus without isidia and soredia.

**Distribution and ecology.**—Southwestern in Europe and also in the tropics. Disjunct in North America and also found on the east coast (Clerc 1992). Collected over conifers (*Picea* and *Tsuga*) along the hypermaritime sea shore on Vancouver Island (Fig. 20).

**Chemistry.**—Usnic and protocetraric acids, with Cph-2 and traces of unknown substances (may contain compounds of the stictic acid group) (K+ yellow, PD+ orange). A strain with usnic acid and compounds of the stictic acid group ("*Usnea schadenbergiana*") is found in the Philippines (Clerc 1997).

Representative specimens examined.—Vancouver Island, Ucluelet, on trees, 1909, *Macoun* (CANL); Vancouver Island, Bamfield Inlet, ca sea level, 48°48’N, 125°09’W, 1994, Ahti 52374 (t); Vancouver Island, Ucluelet, on *Tsuga*, ca sea level, ca 48°55’N, 125°32’W, 1982, Goward 82–1735 (UBC).

12. USNEA HIRTA (L.) F. H. Wigg., Prim. Fl. Hols. 91. 1780. (Syn.: *U. variolosa* Mot.; Clerc 1997) (Fig. 9)

*Usnea hirta* generally has a small and shrubby thallus, usually less than 6 cm, but may also be sparsely branched and pendent. The branching pattern is mostly anisotomic-dichotomous, becoming isometric near the apices. The species is characterized by its pale base, ± deformed and foveolate branches, absence of papillae (found very rarely in Europe), and abundant isidia. The isidia frequently become tall, spinule-like, and occur both singly and in clusters. They occur also near apices and often along low ridges. Indistinct, minute soralia containing farinosin soredia may rarely develop when isidia become detached. The abundance of fibrils varies
markedly, but they usually are abundant near the basal part. The cortex is usually thin (5–10%), the medulla is thick (20–32%) and lax, more rarely moderately dense, and the central axis is thin to relatively thick (20–40%).

This species might be confused with *U. glabrata*, which may also contain usnic acid alone. *Usnea glabrata*, however, does not have abundant, tall isidia, has distinct soralia, and branches that are constricted or fusiform at the base.

**Distribution and ecology.**—*Usnea hirta* has a wide world distribution (Clerc 1997) with continental tendencies. Its North American range extends from the boreal zone to Mexico by way of the western mountains (Thomson 1984). In British Columbia, however, *U. hirta* is found only in the southern parts of intermontane regions (Fig. 20) where it is locally common. In the Wells Gray Park area, it is most common in semi-arid forests (Goward & Ahti 1992) and is indeed the most xerophytic of the local *Usnea* species. Mainly on acid bark and lignum in sites at lower to middle forested elevations.

**Chemistry.**—Usnic acid alone, or more rarely usnic acid with fatty acids in the murolic acid complex (K−, PD−). We have also found one specimen with usnic and diffiractic acids (K−, PD−). This strain was not previously known in *Usnea hirta*. In Europe, the strain with fatty acids is clearly the most common chemotype, and the species also occasionally produces norstic acid (e.g., Halonen & Puolasmaa 1995).

Representative specimens examined.—Clearwater River Basin, near Hemp Creek Ranger Station, Blake's Farm, on fence rails, 1961, Hølmer-Ahti & Ahti 13834b (nt), usnic and fatty acids; Clearwater River Basin, Phillip Creek, on wooden fence, 700 m, 51°52'N, 120°01'W, 1994, Ryan 31842 (herb. Ryan), usnic and diffiractic acids; Chilcotin River Basin, 25 km SW of Williams Lake, on *Pseudotsuga menziesii*, 650–700 m, 51°55'N, 122°07'W, 1981, Goward 81–2159 (UBC), usnic acid.


(Fig. 10)

*Usnea lapponica* is shrubby or more rarely subpendent, and normally has ± deformed, swollen, and foveolate branches. The branching pattern is mainly anisotomitic-dichotomous but an isotomitic pattern is also common near the basal parts. The base is pale to distinctly blackened. The species typically has deeply excavate soralia when mature, which often reach the central axis and never bear isidia (sometimes with spinules: see Goward and Ahti (1992); as *Usnea stippea*). Soralia are borne mainly on a plane cortex, especially near apices and on tubercles. Soredia are farinose and the cortex around soralia is often torn. Papillae are low to cylindrical and usually numerous. Fibrils are often abundant and present also near apices. The cortex is usually thin (4–11%), the medulla is lax to dense and very variable in thickness, but usually ± thick (12–30%), and the central axis is ± thick (27–60%).

The species may resemble *U. glabrescens s. lat.*, which often also has distinctly excavate soralia (especially in *U. fulvoreagens*). *U. glabrescens s. lat.* differs by having more isotomitic-dichotomous branching pattern, more distinctly blackened base, tapering and not swollen or depressed branches, and different anatomy (C/M/A). It also has a different chemistry, usually with various combinations of norstic, salazinic acids, and compounds of the stictic acid group. There are confusing statements in the literature on the taxonomy and nomenclature of *U. lapponica* and the closely related species *U. substerilis* (see the discussion under *U. substerilis*).

The main difference between *U. lapponica* and *U. substerilis* is the latter's superficial, slightly excavate soralia that normally have granulose soredia and often develop isidia. There are some differences in chemistry between *U. lapponica* and *U. substerilis*. In *U. substerilis*, psoromic acid is not found, and barbatic acid is much more common, and the strain with usnic acid alone is less frequent than in *U. lapponica*. Modifications of these two species may be difficult to distinguish if the soralia are not developed to the point of being deeply concave (may even be convex) and/or are spinulose in *U. lapponica*, and if the isidia are sparse or abraded in *U. substerilis*.

**Distribution and ecology.**—Circumpolar and continental. Distributed in montane and boreal areas of North America. One of the most common *Usnea* species in British Columbia in the intermontane and the boreal zones, but rare in suboceanic coastal forests and not found in hypermaritime regions. Open to somewhat sheltered localities at lower to upper forested elevations. Collected most frequently over conifers, especially *Picea* and *Pseudotsuga*, but also common on deciduous trees and shrubs.

**Chemistry.**—Usnic acid alone (K−, PD−), or usnic and salazinic acids (K+ yellow or orange, PD+ yellow or orange). The two chemotypes are about equally common. We have also found one specimen with usnic, salazinic, barbatic, and 4-O-demethylbarbatic acids (K+ yellow or orange, PD+ yellow or orange), and one specimen with usnic, psoromic, and 2'-O-demethylpsoromic acids (K−, PD+ yellow). Terpenoids are commonly present and a trace of protocetraric acid has been detected in one specimen containing salazinic acid. Protocetraric acid may easily be overlooked, and it is present only as an accessory substance. In ad-
dition, a strain with usnic and caperatic acids has been reported from Europe (Clerc 1992).

**Representative specimens examined.**—Liard River Basin, Fairy Lake, on *Picea*, 57°20′N, 123°56′W, 1977, *Brodo* 21879 & *Hamilton* (CANL, h), usnic and salazinic acids; Clearwater River Basin, Edgewood Blue, on *Picea*, ca 700 m, 51°52′N, 120°01′W, 1994, Halonen 94/520 (OULU), usnic acid; Osoyoos area, mountain S of Richter Pass, on *Pseudotsuga menziesii*, 1260 m, 49°05′N, 119°35′W, 1990, Goward 90-622x (UBC), usnic, psoromic and 2′-O-demethylpsoromic acids.

**14. USNEA LONGISSIMA** Ach., Lich. Univ. 626. 1810. (Fig. 4)

*Usnea longissima* is a conspicuous species that is easily recognized by the relatively sparsely branched, long thallus, which may rarely reach several meters in length. Branches are slender and have abundant, perpendicular fibrils (or fibril-like side branches), up to ca 40 mm long. The fibrils are sometimes isotonometrically branched and occasionally have tubercles which may bear isidia and coarse soredia. Spinules also are present on the main branches. The base is black, but it is rarely present. The main branches generally soon become more or less decorticate, exposing the thin, compact, white medulla, and giving the main stem a somewhat rough and angular appearance. Prior to losing the cortex, the branches develop abundant annular cracks. The central axis is very thick, flat, or ± angular on the main branches and characteristically has an I+ blue color reaction. The color of the axis is white in corticate branches, becoming at first pinkish, and later turning to a deep reddish-brown in decorticate branches.

*Usnea longissima* is the only *Usnea* species in British Columbia in which evertnic acid is present. Furthermore, diffractaic acid is not a common substance in the local Usneas. Juvenile thalli that still have corticate branches and may be confused with other species, can therefore usually be identified at least by the chemistry and by the thick, I+ blue central axis.

One of the many described varieties of the species (Motyka 1938), *Usnea longissima* var. *perci liata* Mot. was collected from Vancouver Island (Trelease, 1894, us?, n.v.). However, the taxon appears to be a synonym of *U. longissima*.

**Distribution and ecology.**—Wide distribution in both hemispheres from low boreal to (montane) tropical regions, but the species is endangered throughout most of its European range (Sérsiaux 1989). Southern boreal to suboceanic in North America occurring along the Pacific coast from the northern California to Alaska, and in eastern parts of Canada and northeastern regions of the United States (Hale 1979). In British Columbia, present along the coast at numerous localities, but locally common only in hypermaritime regions (Fig. 19). On conifers, deciduous trees and shrubs in open, humid forests at lower to middle elevations. Collected especially on *Picea sitchensis*, *Tsuga heterophylla*, and *Malus fusca*.

**Chemistry.**—Usnic acid with various combinations of depsides: evertnic, diffractaic, barbatic, and 4′-O-demethylbarbatic acids, or more rarely only usnic acid (probably also other substances are present in very low amounts) (all strains K−, PD−). Evertnic acid seems to be the most common substance together with usnic acid. Diffractaic acid, which is the main substance in Fennoscandia (Halonen 1997; Thøgersen & Høiland 1976), is less common than barbatic acid in British Columbia. We have also found one specimen with usnic, salazinic, barbatic, 4′-O-demethylbarbatic acids, and atorarin (depside) (K+ yellow, PD+ orange), and one specimen with usnic and fumarprotocetraric (trace) acids (K+ brownish, PD−). The strains with fumarprotocetraric or salazinic acid, and atorarin are also found in Japan (Asahina 1967), where salazinic and barbatic acids are the most common substances in *Usnea longissima*. Asahina (1956) divided morphologically identical but chemically different material into many taxa, but as pointed out by Brodo (1984), there are no consistent morphological and geographic criteria to separate them. Brough (1992) reported six chemotypes in British Columbia and related them to the wide range of wool dye colors obtained.


**Representative specimens examined.**—Queen Charlotte Islands, Louise Island, Vertical Point, on fallen *Picea*, ca sea level, 52°54′N, 131°37′W, 1967, *Brodo* 12039 & *Shepapanek* (CANL), usnic and evertnic acids; Vancouver Island, Tofino area, Ocean Village, 3 km S of town, on *Picea sitchensis*, 3 m, 49°07′N, 125°52′W, 1991, Goward et al. 91–95 (UBC), usnic, salazinic, barbatic, 4′-O-demethylbarbatic acids, and atorarin; Vancouver Island, Clayoquot Lake, SW side, on *Tsuga heterophylla* at height of 32–38 m, 49°13′N, 125°30′W, 1994, *Wulff* 94–19, 94–33, 94–70 (UBC), usnic and diffractaic acids.

**15. USNEA MADEIRENSIS** Mot., Revista de Biologia 4: 131. 1964. (Fig. 11)

*Usnea madeirensis* is usually easily identified by the abundant annular cracks, especially near the base that is distinctly blackened at point of attachment, and by the large, slightly tuberculate to slightly concave soralia with isidia. Soralia are often numerous and confluent. The cortex is thick (10–20%), the medulla is thin (7–15%), and the central axis is thick (45–80%). This is an externally quite polymorphic species, although it is less vari-
able in British Columbia than in Europe. Most variable characters are the size, growth form, and the abundance of fibrils and papillae (Clerc 1991). In British Columbia, *U. madeirensis* usually grows subpentad to pendent (basically shrubby and divergent), to 25 cm, and has abundant fibrils and papillae. The branching pattern is mainly isotomodichotomous becoming anisotomodichotomous near the extremities.

Soralia are occasionally absent or sparse, in which case the species may resemble poorly developed *U. filipendula s. lat.*, which also contains salazinic acid. *Usnea madeirensis*, however, has more abundant annular cracks near the base, a thicker cortex, and a thinner medulla. *Usnea subfloridana*, which is very variable in morphology, is most reliably separated by its chemistry, since it lacks salazinic acid.

**Distribution and ecology.**—Oceanic areas of North America (disjunct distribution) and Europe, including Macaronesia (Clerc 1991). *Usnea madeirensis* is threatened in Europe (Clerc 1991), whereas it is one of the most common Usnæ in hypermaritime regions of British Columbia (see Fig. 18), but it is found only rarely in the maritime zone there. On conifers, deciduous trees, and shrubs in open, humid forests at lower elevations.

**Chemistry.**—Relatively uniform chemistry. The main compound is salazinic acid, with protocetraric and conystic acids often present as accessory substances (K+ yellow to red, PD+ yellow or orange). We have found one specimen that has barbatic and 4-O-demethylbarbatic acids in addition to salazinic acid (K+ orange, PD+ orange). This chemotype was not previously been reported in *Usnea madeirensis*.


**Representative specimens examined.**—Queen Charlotte Islands, Graham Island, Kumdis Bay 3.2 km NE of Port Clements, on *Malus fusca*, ca sea level, 53°42′N, 132°08′ W, 1971, Brodo 18159 & Wong (CANL), usnic and salazinic acids; Vancouver Island, Kuyuquot Sound, Spring Island, on *Picea sitchensis*, ca sea level, 1958, Taylor & Szczawinski (h), usnic and salazinic acids; Vancouver Island, Ucluelet, on *Tsuga heterophylla*, ca sea level, ca 48°55′N, 125°32′W, 1982, Goward 82–1807 (UBC), usnic, salazinic, barbaric, 4-O-demethylbarbatic (trace), conystic, and protocetraric (trace) acids.


*Usnea nidulans* s. lat. is characterized by its shrubby habit, and by its inflated, ± spinulose fibrils that often are fasciculate in bundles of two to four. The thallus is shrubby or more rarely subpendent, and the branching pattern is mainly anisotomodichotomous. The base is pale to strongly blackened. The branches are usually sparse to scattered and axils are mostly ca 90°. The branches are segmented by annular cracks, which often have thin, white medullary rings, and segments are sometimes slightly swollen, although the ramification points are not constricted. Depressions and foveoles are only occasionally sparsely present in British Columbia. The cortex is relatively thin (6–12%), distinctly glossy and translucent, and the medulla is lax to dense. Soralia are tuberculate, and bear isidia or fibrils when young. Papillae are low and verrucose, nearly indistinct to absent. The type material of *U. nidulans* (contains usnic and psoromic acids) differs from the North American specimens in the presence of numerous and deeper depressions, and by the more regularly fasciculate fibrils. Bundles of spinulose fibrils are occasionally found also in other species but *U. nidulans* s. lat. has, in any case, a distinct suite of morphological and chemical characters. Juvenile, poorly developed specimens may still be difficult to identify.

According to Motyka (1938), *U. nidulans* has been collected twice in South America, specimens representing the only known material of the species. The type material ("terricolous," perhaps fallen from a tree) is from Argentina, Tierra del Fuego, Río Grande, (*Dusén, 1896, upsl*). The present material from British Columbia is close to the type material of *U. nidulans*, but may represent an undescribed taxon. Therefore the taxon is treated here as *U. nidulans* s. lat. We have also seen one specimen from the United States (OREGON, Carl G. Washburne Memorial State Park, Goward 90–306, 1990, UBC). Specimens from British Columbia and Oregon represent the first records of *U. nidulans* s. lat. for North America.

**Distribution and ecology.**—Apparently western North American–South American. Rare to scattered in humid, hypermaritime forests of British Columbia (Fig. 21) at lower elevations. On conifers and deciduous trees.

**Chemistry.**—Usnic, norstictic, ± salazinic, ± protocetraric (trace) acids, and ± stictic acid group (K+ yellow to red, PD+ orange), or usnic, psoromic and ± 2′-O-demethylpsoromic acids (K−, PD+ yellow).

**Specimens examined.**—Queen Charlotte Islands, Kunghit Island, Howe Bay, on *Picea sitchensis*, ca sea level, 52°01′N, 131°03′ W, 1971, Brodo 17654 & Wong (CANL), usnic, norstictic, stictic, cryptostictic, and conystic acids; Vancouver Island, Ucluelet, on *Tsuga heterophylla*, ca sea level, ca 48°55′N, 125°32′W, 1982, Goward 82–1808 (UBC), usnic, salazinic, norstictic (trace), and protocetraric (trace) acids; Vancouver Island, Clayoquot Lake, W side, on dead deciduous tree, 15 m, 49°13′N, 125°30′W, 1993, Wulf 94–227 (UBC), usnic, psoromic and 2′-O-demethylpsoromic acids. **New to North America.**
17. *Usnea rigida* (Ach.) Mot., Lich. Gen. *Usnea* Stud. Monogr. 1: 177. 1936, *s. lat.* (Fig. 2)

The taxonomy of *Usnea rigida s. lat.* is difficult and species are still poorly known (Clerc 1984a). The species group is distinctive and is characterized by the presence of numerous apothecia and pycnidia, abundant papillae and fibrils, and by the absence of isidia and soralia. The apothecia, however, may occasionally be sparse and/or poorly developed. The thallus is first erect, later becoming subpendent or pendant. Branches are ± irregularly swollen, not tapering, and may have foveoles or depressions in the cortex. The branching pattern is mainly anisomeric-dichotomous. The British Columbia specimens have a pale or brownish-black base. The cortex is thin, the medulla is thin and lax, and the central axis is thick. In fact, most of these characters are also present in *U. diplopterus, U. lapponica, U. scabrata s. lat.*, and *U. substerilis*. They could be regarded as sterile species of the *U. rigida* agg. in which *U. rigida s. lat.* is the primary and fertile counterpart.

Some other species in British Columbia may sometimes have apothecia, but only *U. rigida s. lat.* bears apothecia and produces protocetraric acid as the main medullary substance.

*Distribution and ecology.*—*Usnea rigida s. lat.* occurs in some montane areas in Europe with continental tendencies (Clerc 1984a). In North America, the aggregate is known from the southwestern parts of the United States, in addition to British Columbia. There it is found in two maritime areas (Fig. 20) in sheltered deciduous forests at lower elevations. The species (as *Usnea c fr. florida*) is included in a preliminary list of endangered species (status “Critically imperilled”) in British Columbia (Goward 1996).

*Chemistry.*—In British Columbia, protocetraric acid (K−, PD+ orange) is the main substance in all specimens, with traces of unknown compounds as accessories. This chemotype was not previously known in *Usnea rigida s. lat.* Strains producing usnic acid alone or with salazinic acid are found in Europe. Salazinic acid is also known in *Usnea arizonica* Mot., that is another representative of the group in North America (Clerc pers. com.).


*Usnea rubicunda* is easy to recognize even in the field by the reddish color of its cortex, varying from rose to dark reddish-brown. The thallus becomes pendent with tapering branches and an anisomorphic to isomorphic-dichotomous branching pattern. Specimens with a faint red color may resemble other, especially pendent species. It is also characterized, however, by its pale base, abundant soralia with granular soredia usually intermixed with isidia, and by thin, compact medulla. Fibrils and papillae are sparse to frequent.

*Distribution and ecology.*—Widespread from temperate to tropical regions. Widely distributed in eastern Canada (probably rare there), in the United States (southeastern parts and along the Pacific coast), and in Mexico (Motyka 1938). In spite of the characteristic appearance, *Usnea rubicunda* has not previously been documented for British Columbia, so it is apparently rare in the province. It was collected in a perhumid *Thuja plicata-Tsuga heterophylla* forest near the sea shore (Fig. 17).

*Chemistry.*—The collection from Vancouver Island contains usnic, salazinic, norstictic, and traces of protocetraric, stictic, and constrictic acids (K+ orange, PD+ orange). Besides the chemotype with salazinic, norstictic acids, and other compounds of the stictic acid group, a chemotype without salazinic acid has also been reported (James 1979).

Specimens examined.—Vancouver Island, Ucluelet, on W side of Hyphocbus Island, on *Vaccinium ovatum*, ca sea level, 48°36′N, 123°32′W, 1984, Ahti 42924 & Noble (h). New to British Columbia.


*Usnea scabrata s. lat.* is a highly polymorphic species in which many intergrading morphotypes occur. These polymorphic characters, which are seemingly controlled mostly by environmental parameters, include the morphology of the papillae, the occurrence of foveoles, the density of branching and fibrils, and the thickness of the branches. Being so broadly defined, this species has been described under several names. It may represent a group of somewhat intergrading species. We are provisionally using the name *U. scabrata s. lat.* rather than *Usnea barbata* (L.) F. H. Wigg., recently typified to this group by Jørgensen et al. (1994), pending further studies on its species composition. *Usnea scabiosa* Mot., which was described from New
Mexico, has a rugose, abundantly foveolate thallus and it probably represents U. scabrata s. str., although Brodo (1984) regarded it as distinct.

Usnea scabrata s. lat. is distinguished by the thin, often "paper-like" cortex (2–8%); normally lax medulla; pale or slightly blackened base; and pendent, irregularly shaped, non-tapering branches. The central axis varies markedly in thickness, but it is often thin. The main branches are usually relatively thick, to ca 2 mm and are mainly isotomically divided, but other branches are often anisotomic-dichotomous. Annular cracks are sparse to abundant, and are often ± constricted and sometimes separated by inflated segments. Foveoles are absent to numerous and branches may be rugose. Terminal branches may be strongly sinuose, especially in specimens from inland areas. Papillae are inconspicuous to cylindric and usually frequent at least on the thickest branches, but may sometimes be almost absent. Fibrils are sparse to abundant and spinules often are present along the branches, sometimes frequently. Fibrils, especially spinules, easily break off and leave numerous tuberculate scars. Scars and tubercles may develop into soralia, which are sparse to abundant, often minute, but may also be distinctly raised and enlarged, without isidia or may bear usually short isidia and contain farinose soredia.

Weakly sinuose and foveolate specimens may resemble U. filipendula s. lat. and U. chaetophora, but the two latter species always have a blackened base, tapering branches, a thicker cortex, usually a denser medulla, and they more often produce salazinic acid. Pendent morphs of U. diploptus come close to U. scabrata s. lat. (see the discussion under U. diploptus).

Distribution and ecology.—Western North American–western Eurasian according to Thomson (1984), but more likely incompletely circumpolar in boreal regions and also ranging to southern temperate (mainly montane) areas. The species has continental tendencies and is indeed one of the most common Usneas in inland boreal forests, together with Usnea lapponica and U. substerilis. In British Columbia, however, its range extends to the coast. Mainly on conifers, especially on Picea in open forests at lower to upper forested elevations, rarely to over 2,000 m.

Chemistry.—The strain with usnic acid alone (K–, PD–), the "subsp. nylanderiana" of Motyka (1936) is the main chemotype in inland regions, while the strain with usnic and salazinic acids (K yellow to red, PD yellow or orange) is the only chemotype found along the coast. Unknown terpenoids and fatty acids are also rarely found together with usnic acid.

Usnea subfloridana.—Brodo, Lich. Can. Exs. 218 (h). Representative specimens examined.—Peace River Basin, Robb Lake, on Picea engelmannii, 56°54'N, 123°48'W, 1977, Brodo 22063 & Hamilton (CANL), usnic acid; 50 km NW of Fort St. John, Mile 81 Alaska Highway, on Picea glauca, 850 m, 57°34'N, 121°24'W, 1967, Ahit 23175 (h), usnic acid; Mt. Robson Provincial Park, Berg Lake trail, on Picea glauca, ca 1,000 m, 1978, Go ward 78–919b (UBC), usnic and salazinic acids.


Usnea subfloridana is characterized by distinctly blackened base, generally verrucose to rarely ± cylindric papillae, and typically isidia-bearing soralia. The soralia, which are borne on tubercles, vary from minute to enlarged, and the shape is tuberculate to slightly excavate, when isidia may be abraded. Soralia are usually present also near the apices. Fibrils are often abundant near the base, but become sparse towards the apices. Branches may have sparse to scattered foveoles, especially in specimens collected from hypermaritime areas. The cortex is moderately thick (10–15%), the medulla is thin (7–20%), and the central axis is thick (32–66%). The terminal branches are typically relatively long and tapering. The species is normally shrubby or subependent with a mainly isotomitic-dichotomous branching pattern, but some exceptionally long (to ca 25 cm) specimens are found on the Queen Charlotte Islands and Vancouver Island. It is possible that the British Columbia material here attributed to U. subfloridana actually represents more than one taxon.

Usnea subfloridana may be confused with several species (see under U. ceratina, U. diploptus, U. filipendula s. lat., U. glabrescens s. lat., U. madirensis, and U. substerilis). In such cases, U. subfloridana is most easily identified by chemistry, with squamatic or thamnolic acid as its main substance.

Distribution and ecology.—Widespread from the northern boreal to temperate regions. In North America, from Alaska and eastern parts of Canada to Mexico (Motyka 1936). Locally quite common in coastal areas of British Columbia and rare in intermontane regions, but not found in the boreal zone. On conifers, deciduous trees, and very rarely on rocks in open, humid sites at lower to middle elevations.

Chemistry.—The most common chemotypes produce usnic, squamatic (UV+ whitish blue), ± baemyceric, ± barbatic (usually trace), and ± 4-O-de-methylbarbic (trace) acids (K–, PD–, or PD+ yellow, when baemyceric acid is present). Both baemyceric and barbatic acids are common. Only two specimens with thamnolic acid (K+ yellow, PD+ yellow-orange, UV–) were found, although
the compound is common in *Usnea subfloridana* in Europe (e.g., Krog et al. 1994). Furthermore, in Europe, a chemotype with alcteralid acid is found, but chemotypes with baemoycesic and barabatic acids are not known from there.

**Representative specimens examined.**—Queen Charlotte Islands, Kunghit Island, Rose Harbour, on shrub at shore, 52°09’N, 131°05’W, 1971, Brodo 17717a & Wong (CANL), usnic, squamat, baemoycesic and barabatic (trac) acids; Brandywine Falls Provincial Park, on *Pseudotsuga menziesii*, 500 m, 50°02’N, 123°05’W, 1994, Halonen 94/527 (OUL), usnic, squamat, baemoycesic, and barabatic (trac) acids; S Hazelton area, Seeley Provincial Park, on *Picea glauca*, 400 m, 55°12’N, 127°42’W, 1991, Goward 91–1609 (UBC), usnic and thannolides.


*Usnea subterellas* is a shrubby or more rarely subpentent species that normally has ± deformed, swollen, and foveolate branches. The branching pattern is mainly anisotomic—dichotomous, but an isometric pattern is also common. The base is pale to distinctly blackened. Soralia are borne mainly on tubercules and low pustules. Mature soralia are slightly tuberculate to slightly excrulate, but remain superficial and are normally irregular in shape and often bear isidia at least when young. The soredia are usually ± granulose. Papillae are low to cylindric and usually numerous. Fibrils are often abundant and are present even near the apices. As in *U. lapponica*, the cortex is ± thin, and the medulla is lax to dense and variable in thickness, but usually thick, and the central axis is also ± thick.

The closely related species, *U. lapponica*, is separated by its deeply excrulate soralia that typically lack isidia and bear farrinoid soredia. See further points of distinction under *U. lapponica*. *Usnea diploptypus* differs from *U. subterellas* by the former’s often subpentent or even pendent thallus, minute soralia, and tall isidia that are abundantly present even on mature soralia. *Usnea subterellas* may also resemble *U. subfloridana* that usually has a more distinctly blackened base, shorter papillae, less fibrillose terminal branches, and contains squamat or thannolic acid. Furthermore, *U. subfloridana* has a mainly isotomic—dichotomous branching pattern and somewhat terete, not deformed, branches.

*Usnea subterellas* was recorded by Goward and Ahti (1992) as *Usnea stuppea*, which is a synonym of *U. subterellas*. The type material of *U. stuppea* was collected from Hazelton in British Columbia. Thomson (1984) adopted the name *U. subterellas* for a group of shrubby species without isidia, including *U. glabrescens s. lat.* (sometimes, however, with isidia on young soralia) and *U. lapponica*.

**Distribution and ecology.**—Probably circumpolar from boreal to southern temperate regions. Wide ranging in British Columbia, but rare in hypermaritime areas. One of the most common *Usnea* species, often occurring together with *U. lapponica*. Open inland forests and steppe margins at lower to upper forested elevations, rarely to over 2,000 m. Collected most frequently on conifers, especially *Picea* and *Pseudotsuga*, but also common on deciduous trees and shrubs.

**Chemistry.**—The most common chemotype contains usnic and salazinic acids (K+ yellow or orange, PD+ yellow or orange). The chemotype with usnic, salazinic, barabatic, and ±4-O-demethylbarabatic acids (K+ yellow or orange, PD+ yellow or orange) is also common. We have found three specimens with only usnic acid, and two specimens with usnic, barabatic, and 4-O-demethylbarabatic acids (K−, PD−). Terpenoids are also found in the studied material.

**Representative specimens examined.**—Queen Charlotte Islands, Graham Island, Port Lewis, on deciduous shrubs, ca sea level, 53°41’N, 132°55’W, 1967, Brodo 10502 et al. (CANL), usnic, salazinic, and barabatic acids; Hazelton, on *Pinus contorta*, 1931, Kajala, (H. Gyelnik, Lichenotheca 17, lectotype of *Usnea stuppea*, here selected), usnic and salazinic (trac) acids; Clearwater area, Vavenby, on *Pseudotsuga*, 350 m, 51°35’N, 119°45’W, 1983, Goward 83–773e (UBC), usnic, salazinic, barabatic, and 4-O-demethylbarabatic acids.


*Usnea trichodea* is a pendent species which has grayish-green, cylindric, and slender branches. The branching pattern is mainly anisotomic—dichotomous. The base is pale. The species is readily identified by the brown central axis. Furthermore, the medulla is characteristically compact and the cortex is mat. Soralia, isidia, and papillae are absent. Fibrils are sparse to scattered, and they vary from spinulose to long and curved. Annular cracks are ± abundant, conspicuous, and often revealing the medulla. The British Columbia specimen does not contain apothecia, but fertile material is often found in other areas.

*Usnea trichodea* is often confused especially with *U. chaetophora*, but the latter species is separated morphologically by its generally papillate thallus and white central axis, and chemically by the production of salazinic acid. *Usnea trichodea* may resemble *U. cavernosa*, which also lacks papillae, isidia, and soralia. The latter is distinguished by ± angular, foveolate branches; thinner cortex; usually lax medulla; white central axis; and it usually contains salazinic acid. The superficially quite similar *U. hesperina* differs in having soralia, white
central axis, and protocetraric acid as the main secondary substance.

**Distribution and ecology.**—*Usnea trichodea* is a North American species that occurs mainly in the eastern and southern parts of the continent from Canada to Mexico (Motyka 1936). Only one specimen from British Columbia was found in this study. The locality (Fig. 19), which has been flooded by Williston Lake basin, was located at lower elevations in northern parts of the intermontane zone near boreal regions. The substrate of the specimen is not known. All the other British Columbia collections determined as *U. trichodea* represent other species, mainly *U. chaetophora*.

**Chemistry.**—The specimen from British Columbia has usnic, constictic, salazinic (trace), and diffractic (trace) acids (K+ orange, PD+ orange). Chemotypes producing usnic, constictic, and/or diffractic acids, or usnic acid alone (Brodo 1984) are found in other areas.

**Representative specimen examined.**—Rocky Mountain Trench, Finlay Forks, ca 56°01’N, 123°50’W, 1965, Revel 6 (UBC).

**23. USNEA WIRTHII** Clerc, Saussurea 15: 34. 1984. (Fig. 13)

*Usnea wirthii* has a small thallus, usually 1–4 cm, rarely to 6 cm, and is abundantly branched. The branching pattern is mainly anisotomic-dichotomous. The base is pale or slightly blackened and often constricted. Branches are distinctly segmental as a result of annular cracks that often are lined by white medullary rings. Soralia are frequent, especially near the apices, plane or slightly excavate, and sometimes bear minute isidia. Papillae are usually distinct and abundant on the main branches. Fibrils are absent or sparse. The cortex is thin, ± foveolate, shiny, and normally is covered by scattered red spots. The medulla is thick and lax, and the central axis is thin. *Usnea wirthii* typically has a yellow inner medulla and central axis (best seen on the axis), but the yellow tint may be faint or rarely lacking.

Other related species e.g., *U. cornuta* s. lat. and *U. fragilissens* var. mollis, may also rarely have red spots on the cortex and faintly yellowish to orangish (when salazinic acid is present) central axis, in which case the species must be separated using other characters (see texts under the species).

**Distribution and ecology.**—Macaronesia and oceanic-western regions of Europe and North America (Clerc & Diederich 1991). Also found from Chile in the Southern Hemisphere (Clerc 1997). Reported recently as new to Canada from British Columbia (Goward et al. 1994b). This is a coastal species, locally common in hypermaritime regions, but rare in maritime areas. Usually near the sea shore on conifers, deciduous trees, and shrubs. At lower elevations in open, humid forests and less common in shady sites.

**Chemistry.**—Norstictic acid (often faint) occurs in the soralia, usually with other compounds of the stictic acid group (K+ yellow, PD+ yellow or orange). Occasionally only usnic and stictic acids are present. An unknown fatty acid (Rf values A3/B3) was found in one specimen. Psoromic acid (K+ yellow, PD+ yellow), which is common in Europe (Clerc 1984b), and also recorded from the state of Washington (Clerc & Diederich 1991), was found only once in the British Columbia specimens.

**Representative specimens examined.**—Queen Charlotte Islands, Moresby Island, Jedway, on *Picea*, ca sea level, 52°18’N, 131°13’W, 1967, *Brodo* 12550 et al. (CANL), usnic, norstictic and stictic (trace) acids; Vancouver Island, Keena Beach, on *Picea*, ca sea level, 48°47’N, 125°10’11’’W, 1994, *Vitikainen* 13027 (h), usnic, norstictic and stictic (trace) acids; Vancouver Island, Clayoquot Sound, Soman Island, SW side, on *Picea sitchensis*, 2 m, 49°12’N, 125°54’W, 1993, *Wulff* 93–222 (UBC), usnic and psoromic acids.

**EXCLUDED SPECIES**

*Usnea angulata* Ach. and *U. capitata* Mot. (probably a herbarium name) were reported as new to British Columbia by Thomson and Ahti (1994), but their records are based on misidentifications of *U. lapponica*, *U. scabrata* s. lat., and *U. substerilis*. *Usnea articulata* (L.) Hoffm. was reported from British Columbia by Howe (1910). We have not seen the specimens, but they probably represent another species since *U. articulata* is not known from North America. The fertile species *U. florida* (L.) F. H. Wigg. (contains squamatic or thomannolic ± alectorialic acids) was first reported for British Columbia (as *U. barbata* (L.) F. H. Wigg. var. *florida* Fr) by Müller (1889), and has often been mentioned since then. In fact, this species is distributed in oceanic regions of Europe (Clerc 1984a) and may be present also in the United States (Fiscus 1972), although it is not expected to occur in British Columbia. John Macoun’s collections of “*U. barbata var. florida*” from Mayne Island (Macoun 1902) were not found, but we have seen *U. rigida* s. lat. specimens collected from the same locality. *Usnea merrillii* Mot., which is closely related to *U. trichodea*, is regarded as a North American species that occurs in the eastern and southern parts of the continent (Motyka 1938) but its occurrence in the province is doubtful. In this study, all the specimens previously determined as *U. merrillii* were found to be other species, mainly *U. chaetophora*. The name *Usnea plicata* (L.) F. H. Weber has been used for many taxa (*Lichen plicatus* L. actually rep-
resents *U. ceratina* and it has been proposed for rejection by Jørgensen et al. (1994). *U. wasmuthii* Räsänen, which is close to *U. subfloridana* and is found from Eurasia (Motyka 1936), was reported as new to North America by Goward and Ahti (1992). The cited specimens, however, represent *U. substerilis*. The specimen from Alaska reported as *U. wasmuthii* by Thomson and Ahti (1994) actually belongs to *U. lapponica*.

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**LITERATURE CITED**


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