Systematics of the Usnea fragilascens aggregate and its distribution in Scandinavia

Philippe Clerc


Systematics and taxonomy of Usnea cornuta, U. flamma and U. fragilascens are discussed. The morphology, chemistry and distribution of these species in Europe are described and a first attempt is made to provide a key for the erect-bushy to subpendant and sorediate species in Scandinavia. Compounds reported in this aggregate include lobaric acid (new to the genus). U. flamma is new for Scandinavia. U. strictula, U. inflata, U. intexta and U. subpectinata are reduced to synonymy with U. cornuta. U. dalmatica and U. rupestris to synonymy with U. flamma, U. glaucescens to synonymy with U. hirta and the new combination U. fragilascens var. mollis is proposed.

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Introduction

With fruticose lichens, it is well-known that under environmental pressure, the external morphology of the thallus shows a great deal of variation. As a result, there are too many described taxa in the literature. Usnea P. Browne ex adans is not an exception to the rule and its taxonomy is actually so confused that almost every specific name of this genus mentioned in lichenological papers must be questioned. This has been demonstrated recently for Usnea floridana (L.) Wigg. which is, after all, one of the best known Usnea species (Clerc 1984). Among macrolichens, Usnea is the genus which needs most urgently a thorough revision of its systematics and taxonomy.

During the study of some Scandinavian material of the Usnea fragilascens Havaas ex Lyne aggregate (erect-subpendant Usnea with soralia developing isidia (at least in young soralia), ± fusiform branches at the base, a rather thin cortex and mainly norstictic acid, stictic acid and/or salazinic acid in the medulla), I realized that U. flamma Stirrt. has not been cited to date in Scandinavia. Moreover U. cornuta Kuerb. has been reported only once for Scandinavia under the name U. intexta Stirrt. (Norway, Ins. Stord, 1927, Motyka) by Motyka (1936–1938) and since that time has never been mentioned again for this area. Nevertheless these two lichens are quite frequent, mainly on Pinus sylvestris in the southwestern part of Norway. The aim of this paper is to describe the species of the U. fragilascens agg. mainly on the basis of herbarium material from the whole distribution range in Europe. Furthermore the particular distribution in Scandinavia of the species concerned will be given. A provisional attempt will be made to provide a key for the sorediate, bushy to subpendulous Usnea occurring in Scandinavia.

Material and methods

The following account is based on herbarium specimens deposited in the following herbaria: BG, BERN, BM, BORD, COI, DUB, DUKE, GLAM, H, H-ACH, L, LISU, LWG, M, MURCIA, NTM, O, PC, PO, STU, TUR, W as well as in private herbaria of Dr J. C. Boisserie (Fontainebleau), Dr G. Degelius (Göteborg), Dr M. Seaward (Bradford), and the author (BERN).

Thin layer chromatography

Most of the material referred to in this paper was examined by thin layer chromatography (TLC) using the
techniques described by Culberson and Ammann (1979) and Culberson et al. (1981). Rf classes are given according to the solvent systems A/B/C/G, e.g.: 5/4/5/(5). Spot tests were performed with conventional reagents (Clerc 1984). Unless otherwise indicated, spot tests were performed on the medulla of a branch of the middle part of the thallus, longitudinally cut with a razor blade.

Estimation of soralianum and papilla density

Soralianum density was measured at ×50 using a stereomicroscope with a grid mounted in an eyepiece. For each specimen, three terminal or subterminal branches, where the soralia are the most abundant, were selected, the soralia were counted and the arithmetical mean of these three measurements was calculated. Young soralia (small white spots looking like pseudocyphellae) as well as mature ones were taken into account. The counting was done on 0.8 mm² and extrapolated for 1.0 mm².

Measurements of papilla density were done in the same way, on the main branches where the papillae are the most numerous. The counting was done on 0.16 mm² and extrapolated for 1.0 mm².

Analysis of internal structures

Anatomical measurements of the cortex (C), medulla (M) and central axis (A) were established according to the method given in Clerc (1984) (Fig. 1). They were made at ×50 with the stereomicroscope on the largest part of the largest branch and are given in percentage of the whole width of the branch, C = (c₁+c₂)/2, M = (m₁+m₂)/2, B = 2C+2M+A, %C = (C/B)×100, %M = (M/B)×100, %A = (A/B)×100, eg: %C/%M/%A: 6/30/28.

Field study

The author had the opportunity of undertaking field studies in France (Bretagne) during spring 1984 (annual excursion of the Botanical Institute of Berne).

Chemistry

There are few reports on the chemistry of this aggregate; see James (1978), Krog et al. (1980).

Some acids (salazinic acid in *U. cornuta*, when with norstictic acid and stictic acid, galbinic acid Fl in *U. flammee*) may occur in low concentration and therefore are difficult to detect. The method given in Culberson and Ammann (1979) is therefore recommended as it requires a pre-concentration of the lichen substances (the acids are extracted three times on a microscope slide before they are applied to the plates).

Usnic acid is usually present in large amounts in the cortex of all species. Atranorin has never been detected. The species of this aggregate produce depsidones as diagnostic medullary substances. The main lichen substances encountered in the present study are listed in Tab. 1. The appearances of the spots on the TLC plates are compared in Fig. 2.

The substance in Rf classes 3/5/5/(3-4) occurring in *U. flammee* mostly in low concentration has been identified as lobaric acid (co-chromatography with Stereocaulon evolutum Graewe). It turns pale yellowish green with diluted sulphuric acid after heating and is UV + blue (355 nm). It is the first time that lobaric acid is reported in the genus *Usnea*.

Quantitative variation in the production of norstictic acid was found to be of some taxonomical importance. In *U. cornuta*, norstictic acid occurs mostly in large quantities, while in *U. flammee* and *U. fragiliscens* it was mostly produced in small amounts to faint traces (*U. fragiliscens*). This chemical distinction is quite constant and was found to be of some help identifying poorly developed material. Krog (1980) emphasized such differences in the *Bryoria chalybeiformis* agg.

Tab. 1. Chemotypes (a, b, c) and main substances occurring in the *Usnea fragiliscens* aggregate. – 1, *U. flammee*, 2, *U. cornuta*, 3, *U. fragiliscens*. ± = not constant, + = faint or trace.

<table>
<thead>
<tr>
<th>Substances</th>
<th>1a</th>
<th>1b</th>
<th>2a</th>
<th>2b</th>
<th>2c</th>
<th>3a</th>
<th>3b</th>
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<tr>
<td>Usnic acid</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+s</td>
<td>+</td>
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<tr>
<td>Stictic acid</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
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<td>+</td>
<td>+</td>
<td>±</td>
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<td>±</td>
</tr>
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<td>Menegazziacid acid</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td>±</td>
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<td>±</td>
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<tr>
<td>Lobaric acid</td>
<td>+s</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Salazinic acid</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Protocetraric acid</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Unknown fatty acids</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
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<td>-</td>
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</table>
Pigmentation

In *U. cornuta* and *U. flammea* the thallus occasionally contains an ochraceous to orange-red pigment. In *U. cornuta* this pigment is restricted to the axis, whereas in *U. flammea* it lays in the medulla adjacent to the axis. However, pigments are lacking in all fresh specimens seen by the author while they are frequent in old herbarium material. This is an indication that these pigments could originate from some chemical transformation during storage in herbaria.

Morphology

The species of the *U. fragilesens* agg. have a thallus which is rarely longer than 10 cm (max. 15–20 cm). The thallus is fixed to the substrate by a holdfast. The trunk is defined as the part between the holdfast and the first main ramification point (not taking into account first minor branches). The main branches (br. I) are the thickest ones arising from the trunk at the main ramification point. Either two or more main branches of nearly the same width arise from the first main ramification point (Fig. 3), or there is only one main branch, the main ramification point thus being determined by the first branches of second order (br. II or secondaries) arising from the main branches (again not taking into account the first minor branches) (Fig. 4). Secondaries are the thickest branches arising from the main branches but distinctly thinner than the latter. They separate into branches of third order, etc.

Two main types of branching pattern (Hawkesworth 1972) (Figs 3–4) occur among the species treated here. In *U. flammea* and *U. cornuta* the branching is mostly isometric-dichotomous near the base, becoming anisotomic-dichotomous towards the apex. In *U. fragilesens* var. *fragilesens* it is mostly anisotomic-dichotomous over its full length.

The colour of the living thallus is of little use delimiting the species in *Usnea* (Clerc 1984). In a mixed population of *U. cornuta* and *U. flammea* collected by the author on *Salix* in a sheltered locality near St. Herbot (France-Finistère), all thalli were found to be of the same colour, i.e. pale green, which is contrasting with the greishy yellow to pastel yellow tint characterising mixed populations of the same species collected in a peat bog on *Calluna* (F-Finistère, Mts d’Arrée). After long storage in the herbarium, thalli of *U. cornuta* and *U. flammea* turn dark brown, whereas those of *U. frag-

Fig. 2. Chromatograms in solvent systems A (TDA), B (HEF) and C (TA) of the main lichen substances encountered in the *Usnea fragilesens* aggregate. – A. E.: References. – B. C: *U. cornuta*. – D: *U. flammea*. – 1, norstictic acid. 2, atranorin. 3, constictic acid. 4, salazinic acid. 5, usnic acid. 6, protocetraric acid. 7, menogazzianic acid. 8, cryptostictic acid. 9, stictic acid. 10, lobarianic acid.
The terminal branches are ± densely branched, sometimes crowded, with a “brush-like” appearance (axils about 60°, branchlets tenuous and acute) (Fig. 15C) or of spinulous appearance (axils about 90°, branchlets and fibrils thick and obtuse) (Fig. 15B) or not densely branched, loose, with a few fibrils, flexuose, slender (axils about 60°) (Fig. 15A).

Papillae constitute a very variable character which has been given too much emphasis in former works on Usnea. However, three types of papillae may be distinguished when they are well developed. The first is a low subhemispherical lump, broader than tall (Fig. 19). The second is a more prominent wart, truncate or not, as broad as tall or 1.5 times taller than broad (verrucous). The third is a cylinder, at least twice as tall as broad (cylindrical). The density of the papillae on the main branch was measured for each species (see Material and methods). These measurements (Fig. 21C, Tab. 2) indicate that the papillae are numerous in U. fragilissens (Fig. 19) and few in the two other species. This seems to be a reliable character by which to separate U. fragilissens var. fragilissens from the other three taxa.

Fibrils are lateral appendages, containing an axis as well as medulla, up to about 4–5 mm long. They can be tapered and slender with tenuous tips or thicker, ± obtuse, giving a spinulous appearance to the thallus (Fig. 15B). The abundance of fibrils seems to be environmentally controlled and has been found of no taxonomical value.

Concerning Usnea, some terms used in the literature such as primary or secondary soralia (Swinscow & Krog 1975) are misleading because they are not defined on the base of anatomical or ontogenetical studies. There are, in fact, few studies on the ontogeny of vegetative structures in Usnea. Beltman (1978) paid little attention to this genus, emphasizing the necessity of further detailed studies. According to Beltman, soralia in Usnea originate from pseudocypella, except in U. flammaea where they seem to develop before a local breakdown of the cortex occurs. My own observations show that every soralia develops from a pseudocypella (local breakdown of the cortex). Two types of development can be observed. In the first one, isidia arise (see above) from the pseudocypella. In a later stage the pseudocypella may widen and lose all or part of the isidia and begin to produce soredia (U. cornuta, U. diploptopus Vain., U. flammaea, U. fragilissens and U. subfloridiana Stirt.). In the second one, the pseudocypella widens without producing isidia but soredia (U. glabra Achn., U. glabrescens Vain. and U. lapponica Vain.). Soralia may originate on various structures: a) directly on the surface of the cortex; b) on the top of eroded papillae; c) in annular cracks between the segments; d) on the warts left after fibrils have broken down. All four types occur in all species studied here. They can be very small and confluent, thus looking like a single expanded soralium (Fig. 11) or they can be large and widely spaced (Figs 13, 14). Shape and size of soralia as well as their
Figs 5–13. Usnea. – Figs 5–7 Basal part of the thallus. – Fig. 5. *U. cornuta*, N-Hordaland, 1979, Blom (BG), trunk quiet indistinct. – Fig. 6. *U. flavissima*, N-Rogaland, 1939, Krog (0), “pseudo roots” (a), annular cracks (b) and pale trunk. – Fig. 7. *U. fragilis* var. *fragilis*, F-Vire, 1838, Delise? (PC), trunk very distinct. – Rule = 1.2 mm. – Figs 8–10. Br. II and III. – Fig. 8. *U. cornuta*, N-Rogaland, 1980, Holtan-Hartwig & Tindal (0), br. II constricted at the very base. – Fig. 9. *U. flavissima*, N-Hordaland, 1978, Krog & Østhagen (0), br. II not constricted nor fusiform. – Fig. 10. *U. fragilis* var. *fragilis*, N-Ragefjord, 1905, Havaas (BG), br. II fusiform. – Rule = 1.7 mm. – Figs 11–13. Soralia. – Fig. 11. *U. cornuta*, N-Rogaland, 1967, Ryvarden (0), soralia minute, crowded and confluent. – Fig. 12. *U. flavissima*, N-Hordaland, 1984, Jørgensen (BERN), soralia with numerous isidiomorphs. – Fig. 13. *U. fragilis* var. *fragilis*, F-Mortain (PC), soralia broad, scattered, not confluent, with a distinct cortical rim. – Rule = 1 mm.
Figs 14–20. Usnea. – Fig. 14. Soralia of *U. fragilesens* var. *fragilesens*, F-Mortain (PC). – Rule = 1 mm. – Fig. 15. Terminal parts of the thallus. – A: *U. fragilesens* var. *fragilesens*. B: *U. cornuta*. C: *U. flammeea*. – Rule = 2 cm. – Figs 16–18. Sections of the thickest part of br. I. – Fig. 16. *U. fragilesens* var. *fragilesens*, F-Vire, 1838 (PC), medulla loose. – Fig. 17. *U. flammeea*, N-Hordaland, 1984, Jørgensen (BERN), medulla dense. – Fig. 18. *U. flammeea*, N-Hordaland, 1946, Dahl (0), medulla compact. – Fig. 19. Subhemispherical papillae in *U. fragilesens* var. *fragilesens*, F-Mortain (PC). – Rule = 0.5 mm. – Fig. 20. A: *U. wirthii* Clerc. B: Lectotype of *U. inflata* (Duby) Mot. C: *U. cornuta* Körb. – Rule = 5 cm.
density on branches are of primary importance delimiting the taxa of this aggregate. The density of soralia was measured for each species of the *U. fragiliscens* agg. (see Material and methods). The measurements, (Fig. 21A, Tab. 2) reveal two groups, one comprising *U. cornuta* with a high density of soralia, the other comprising *U. flammee* and *V. fragiliscens* with a low density of soralia. This character is very reliable for the separation of *U. cornuta* from *U. fragiliscens*.

Isidia have been found in all three species at least in young soralia (Fig. 12). However, they are sometimes absent as for instance in *U. fragiliscens*. The variation in the production of isidia (size, quantity) seems to be environmentally controlled.

As described by Dahl and Krog (1973), pseudoisidia are soredia having the outwards appearance of isidia but lacking a proper cortex. They often occur in *U. glabrescens* and in *U. lapponica*.

### Anatomy

There is a profusion of data in the literature concerning the thickness of the cortex, medulla and central axis. Unfortunately they have no statistical value as they are based on too few specimens. Furthermore, owing to the way these data are presented, they are difficult to interpret and to compare among themselves (CMA of Ashina (1956) or adjectives like “thin”, “large”, etc.). The method used here (see Material and methods) was applied on more than 300 specimens. The results are shown in Fig. 22 and summarised in Tab. 2.

The variability found in the thickness of the different structures is striking. However some trends are manifest:

1. *U. flammee* has a thicker axis and a thinner medulla than the three other taxa, with very little overlapping of the mean values.
2. *U. fragiliscens* has a very thin cortex, thinner than 6.5%, with few exceptions.

### Tab. 2. Summary of anatomical and morphological data on the *Usnea fragiliscens* aggregate. For n = number of specimens analysed, see Figs 21 and 22.

|                | *U. cornuta* | *U. flammee* | *U. fragiliscens* var. *fragiliscens* | *U. fragiliscens* var. *mollis*
<table>
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<tr>
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</thead>
<tbody>
<tr>
<td>Annular cracks/0.5 cm</td>
<td>(0)–0.8–2.6–4.4–(10)</td>
<td>(1)–4.6–5.9–(12)</td>
<td>(0.5)–1.3–2.3–(5)</td>
<td>(0.5)–0.5–1.6–2.7–(3.5)</td>
</tr>
<tr>
<td>Number of papillae/mm²</td>
<td>0–21–43–(75)</td>
<td>0–7–19–(38)</td>
<td>(38)–59–84–109–(150)</td>
<td>(0)–5.5–107–(200)</td>
</tr>
<tr>
<td>Number of soralia/mm²</td>
<td>(15)–28–41–54–(71)</td>
<td>(15)–20–27–34–(73)</td>
<td>(10)–12–16–20–(26)</td>
<td>(14)–17–21–25–(30)</td>
</tr>
<tr>
<td>Thickness of the cortex (%)</td>
<td>(3.5)–4.4–5.8–7.2–(9.5)</td>
<td>(3)–5.8–7.5–9.2–(12.5)</td>
<td>(3)–3.4–4.6–5.8–(9)</td>
<td>(3.5)–4.3–5.4–6.5–(8.5)</td>
</tr>
<tr>
<td>Thickness of the medulla (%)</td>
<td>(5.5)–27.1–31.6–36.5–(40.5)</td>
<td>(8.5)–17.5–22.7–27.9–(32.5)</td>
<td>(23.5)–31.6–34.7–37.8–(40)</td>
<td>(25.5)–28–31.8–35.6–(39)</td>
</tr>
<tr>
<td>Thickness of the central axis (%)</td>
<td>(12)–17.6–25–32.4–(44)</td>
<td>(23)–30.2–39.6–49–(67)</td>
<td>(13)–16.6–21.4–26.2–(35)</td>
<td>(14)–17.9–25.4–32.9–(40)</td>
</tr>
</tbody>
</table>
3. The anatomy of *U. fragilesceclus* var. *fragileseclus* and var. *mollis* shows some differences which are statistically significant, i.e. the medulla is thicker (Student *t*, *p* = 0.001) and the cortex is thinner (*p* = 0.05) in the var. *fragileseclus*.

As these data are very variable, they should be carefully interpreted and used only with caution in the separation of taxa.

The surface of the cortex can be mat to slightly shiny or distinctively glossy like broken glass. This feature is fairly constant and is one of the best criteria for separating badly or not typically developed morphotypes of *U. cornuta* and *U. flameea*. This brilliancy can be observed at the surface of the cortex at 10×, but should be checked under a dissecting microscope at 50× on a longitudinal section of br.II.

The medulla can be homogeneous, consisting of one uniform layer (Fig. 16, 18) or heterogeneous, composed of two distinct layers: a thin, compact external one and a thicker, dense to loose internal one (Fig. 17).

Examining the medulla at a 10× magnification it is possible to distinguish roughly three types:

a) loose: few hyphae very loose and conspicuous (Fig. 16).

b) dense: hyphae closer, more numerous, but always clearly visible (Fig. 17).

c) compact: hyphae agglutinated, not visible (Fig. 18).

Depending on the part of the thallus where the observation is made, the variation is considerable, the three types sometimes being seen in the same specimen. However, some trends are obvious (see under the species treated) if the observations are always made on the largest part of the largest branches (not on the trunk).

**Ecology**

The label data compiled in Tab. 3 show that all three species are corticolous as well as saxicolous. However, both *U. cornuta* and *U. flameea* are more frequently corticolous. *U. fragileseclus* var. *fragileseclus* is mostly saxicolous while the var. *mollis* seems to be mainly corticolous. They grow in well-lit open localities, on boles and branches of trees, as well as on shrubs in peat bogs, on *Calluna* for example (*U. cornuta* and *U. flameea*). The most frequent phorophytes are *Pinus* and *Quercus*, followed by *Fagus*, *Betula*, *Castanea*, *Corylus*, * Sorbus*, *Salix*, *Ulmus*, *Erica*, *Alnus* and *Calluna*.

The saxicolous thalli grow on exposed coastal rocks and boulders as well as inland on vertical rock outcrops or on sheltered vertical cliffs, always in localities with high atmospheric humidity. They were collected mainly on siliceous rock, very rarely on calcareous substrate (A. Vézda, Lich. Select. Exs. 1173).

**Distribution**

*U. cornuta*, *U. flameea* and *U. fragileseclus* belong to the eu-oceanic element in the sense of Degelius (1935), i.e. these species are limited to extremely oceanic parts of W Europe, with some rare mediterranean localities.

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**Tab. 3.** Relative abundance (%) of the *Usnea fragileseclus* aggregate on bark and rock in Europe. *N* = number of specimens considered, (*) = percentage for Norway only, (**) = only one specimen.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Corticolous (%)</th>
<th>Saxicolous (%)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>U. cornuta</em></td>
<td>81</td>
<td>19</td>
<td>156</td>
</tr>
<tr>
<td><em>U. flameea</em></td>
<td>67 (85)</td>
<td>33 (15)</td>
<td>117</td>
</tr>
<tr>
<td><em>U. fragileseclus</em> var. <em>fragileseclus</em></td>
<td>4 (**)</td>
<td>96</td>
<td>25</td>
</tr>
<tr>
<td><em>U. fragileseclus</em> var. <em>mollis</em></td>
<td>90</td>
<td>10</td>
<td>21</td>
</tr>
</tbody>
</table>
With a few exceptions, they do not occur beyond 10° east of Greenwich.

*U. cornuta* and *U. flammaea* belong to the “omnivage euoeozasische Element” (Degelius 1935), i.e. species ranging from SW Norway to Portugal. *U. fragilascens* seems to occur only in northern Europe and belongs therefore, according to Degelius (1935), to the “nördliche euoeozasische Element”.

In Scandinavia the distribution of *U. cornuta*, *U. flammaea* and *U. fragilascens* is restricted to the coast of SW Norway where the annual precipitation exceeds 1000 mm. Though the hydric factors (precipitations, atmospheric humidity, moisture) are considered by Degelius (1935) as being the most significant factors determining the distribution of the oceanic species, the thermic factors seem here to play an important role and are probably responsible for the absence of these three species in the interior of Norway. As a matter of fact these *Usnea* occur only in coastal areas with a low number of days with a temperature below 0° (not more than 100 days) and with high temperatures in January (+1°, +2°), maximum for Scandinavia: +2° (Almborn 1948, Krog et al. 1980). See distribution maps for each species (Figs 27–29).

### Systematics

**Usnea cornuta** Koerb.


**Usnea inflata** Delise ex Duby, Botanicon Gallicum, pars secunda, p. 615, 1830, nom. nudum (Code, Art. 34).


**Usnea intexta** Stirton, Scottish Natural. 6: 102, 1881. – Lectotype (selected here): Scotland, Crinan Canal, leg. (? BM!). (%C%M%M%A: 5.5/30/30. Chemistry: norstictic, stictic, constictic, menegazziae, salazinic (trace in plate A and C) acids).


### Nomenclatural note

Duby (1830) published *U. ceratina* var. *inflata* on the basis of material collected by Delise and deposited in the herbarium of the latter under the name *U. inflata* Delise. In his publication, Duby mentioned *U. inflata* Delise only as herbarium name under the epithet “*U. ceratina var. inflata*” which is the one he accepted. The combination *U. inflata* was therefore not validly published (Code, Art. 34). Motyka (1936–1938) seems to be the first to have published correctly this combination. *U. cornuta* therefore has priority.

The lectotype here selected belongs to the Delise herbarium in PC. It consists of two specimens (B and C) glued on the same plate, together with *U. wirhieii* Clerc (specimen A), the whole being annotated *U. inflata* D. D. (Fig. 20). The material indicated as type by Motyka (1936–1938) is located at W and there is no evidence that it belongs to the specimens seen by Duby. It represents the chemotype 2a (see Tab. 1) of *U. cornuta* and looks very similar to the lectotype in PC.

**Description:** Fig. 24. Thallus erect, 3–7 cm long, forming shrubby tufts, ± compact, anisotomic-dichotomous near the base, becoming ± isotomic towards the extremities, rarely subpendant, 9–10 (15) cm long, the whole thallus being anisotomic-dichotomous. *Trunk* brownish black or concolourous with the main branches (Fig 5). Annullars cracks sparse (Tab. 2). *Br. I* terete, typical irregularly swollen when well developed (Fig. 24), ± articulated. *Br. II* clearly constricted at their base when well developed (Fig. 8), usually with swollen segments. *Terminal branches* ± thick, axils nearly 90°, with numerous soralia; sometimes strongly curved in extreme morphotypes. *Papillae* sparsely and unevenly distributed, verrucous, with ± a rounded apex when well developed, sometimes eroded, giving rise to a soralium. *Fibrils* short (2–3 mm), spinnous, often distorted, thick, curved, ± fusiform, unevenly distributed on the whole thallus, often numerous on the tips, giving a spinous aspect to the terminal part of the thallus (Fig. 15B). *Soralia* even, typically minute (58–200 μm), often becoming confluent, thus looking like a single large soralium (Fig. 11); without a sharply delimited margin and a cortical rim, plane to slightly concave, very numerous (Tab. 2) on the terminal branches and fibrils; isidia numerous at the beginning but often absent on mature soralia. *Cortex* shiny like broken glass, usually thin (Tab. 2). *Medulla* mostly heterogeneous, internal part mostly loose, seldom dense (Tab. 2). Axis usually thin (Tab. 2), sometimes orange pigmented. *Chemistry:* 1. K+ yellow turning reddish orange, *Pd*+ yellow turning orangish yellow (stictic acid, norstictic acid, ± salazinic acid). 2. K+ yellow turning blood red, *Pd*+ yellow turning orangish red (salazinic acid, ± proteocetraric acid). (see Tab. 1). *Substrate:* corticolous and saxicolous (Tab 3.)

**Variation:** *U. cornuta* is a highly variable taxon, its numerous morphotypes being connected by a series of transitional forms. These morphotypes are probably only phenotypical modifications. The most variable characters are the size of the thallus, the degree of swelling of the branches, the frequency of fibrils and papillae, the degree of crowding of the soralia, the density of isidia and the aspect of terminal branches (curved or not, thick or not). *U. cornuta* occurs as three chemical strains in Europe (Tab. 1). The three strains can be found side by side in the same herbarium packet and are

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morphologically indistinguishable. Salazinic acid occurs in 86% of the 142 specimens analysed with TLC. The strain with norstictic acid and stictic acid only, occurs in 14% of the specimens analysed whereas the strain with only salazinic acid and the one with norstictic acid, stictic acid and salazinic acid are the most frequent, each one with 43% of the specimens analysed. The type collection of *U. cornuta* consists of ± compact specimens with distorted, ± fusiform, curved fibrils and terminal branches, with crowded soralia. All specimens studied produce salazinic acid as main substance in the medulla. These specimens correspond to extreme morphotypes occurring at the limit of the species distribution area (beyond 10° east of Greenwich).

The type specimens of *U. intexta* and *U. subsectinata* are similar to that of *U. cornuta*, although a little more slender and more branched with thinner fibrils, thinner terminal branches and soralia which are not crowded. The type of *U. constrictula* represents a form in which primary and secondary branches are more robust and less branched. Specimens optimally developed, with a 10 to 13 cm long thallus, subpendant, branches I and II.
strongly constricted at their base, with swollen segments and thin uncurved apices, are well in agreement with the lectotype of *U. inflata*.

**Distinction:** *U. cornuta* can usually be reliably recognized on the basis of its minute, numerous and confluent soralia, its secondary branches distinctively constricted at their base, its glossy cortex and its spinulose habit. This species often grows mixed with *U. flammaea*, the latter being readily separable by the larger soralia, the pale basal part with numerous annulations, the cortex which is mat and the absence of salazinic acid and frequent occurrence of lobaric acid in the medulla. For the separation from *U. fragilis*, see this taxon.

**Taxonomic remarks:** *U. subcornuta* Stirr. and *U. dasea* Stirr. have been considered by Hawksworth et al. (1980) to be conspecific with *U. cornuta*. My investigations show that *U. subcornuta* Stirr. (Lectotype [here selected]): Portugal, Madeira, near Funchal, leg. Payne (BM). Chemistry: unknown 3/1–2/2 light yellow, unknown 6/2/5 yellow, unknown 6/2/5 light yellow, unknown 6/2–3/5–6 light yellow (colouration after developing with 10% H$_2$SO$_4$ and heat) is a distinct species with a pink-red pigment under the cortex in the medulla, and *U. dasea* (Lectotype [here selected]): Portugal, Madeira, Funchal, leg. Payne (BM). Chemistry: galbinic acid, norstictic acid, salazinic acid, constrictic acid) is a south European species characterised by a distinct morphology and chemistry. These two species will be discussed in a further paper.

**Distribution:** Specimens examined were from France, Germany, Great Britain, Italy, Luxembourg, Norway, Portugal, Spain and Switzerland. Distribution in Norway (Fig. 27).


*Usnea flammaea* Stirr.

Stirton, Scottish Natural 6: 102, 1881. – Lectotype: Madeira, Funchal, Payne (BM), (%C% M%A: 8/26/32. Chemistry: norstictic (trace), stictic, constrictic, menegaazzic acids); isotypelectotypes in BM!(1). (Chemistry: norstictic, cryptostictic (only in one specimen), stictic, constrictic, menegaazzic, lobaric (only trace in one specimen) acids).


**Nomenclatural note:** Østhagen and Krog (1976) questioned the validity of this name because of the omission of “sp. nov.” after it. I think this name has been validly published (Code, art. 32), the “sp. nov.” not being a condition for an epithet to be valid. Furthermore Stirton never indicated that he didn’t fully accept names he published without “sp. nov.”.

**Description:** Fig. 23. Thallus erect to subpendant, 3–7 cm long, slender, rarely compact, branching often iso-tomic-dichotomous near the base, becoming anisotomic towards the extremities. Trunk never blackened, concolourous with the main branches, frequently whitish (Fig. 6), usually densely divided into segments by annular cracks (Tab. 2), sometimes with everted medullary tissues. Br. I terete, tapered, rarely fusiform, sometimes of uneven outline but never swollen or inflated. Br. II terete, typically tapered (Fig. 9), rarely constricted at the base. Terminal branches slender, axils nearly 60°, showing a typical brush-like habit (Fig. 15C) when densely branched. Papillae often absent on the whole thallus, when present verrucous, not abundant (Tab. 2), unevenly distributed, sometimes eroded, giving rise to a soralium. Fibris slender, not spinulos, 2–4 mm long, unevenly distributed. Soralia even to slightly tuberculated, plane to slightly concave, efflorescent (Fig. 12), ± rounded, sometimes with a thin irregular cortical rim, moderately dense (Tab. 2), mostly densely covered with isidia. Cortex mat to slightly shiny, thin to moderately thick (Tab. 2). Medulla cottony, moderately thin (Tab. 2), homogeneous to heterogeneous, dense (Fig. 17) to compact (Fig. 18), sometimes orange pigmented adjacent to the axis. Axis moderately thick (Tab. 2), sometimes orange pigmented. Chemistry: K+ yellow turning reddish orange, PD+ yellow turning orange to yellow (see Tab. 1). Substrate: corticolous and saxicolous (see Tab. 3).

**Variation:** When all typical features are well developed, *U. flammaea* is an easy species to recognize. The most variable characters of these species are the frequency of fibrils and papillae as well as the ramification type. Lobaric acid occurs in about 80% of the specimens analysed (nearly 100). It can be considered a diagnostic substance for *U. flammaea* as it has not been found in other species.

**Taxonomic remarks:** The type collections of *U. flammaea* represent, as a whole, quite well the typical features of this taxon. Unfortunately the lectotype chosen by Motyka consists of two fragments without basal part, lacking lobaric acid. The secondaries of the type specimen of *U. dalmatica* are slightly but distinctly constricted at their base, ± fusiform, sometimes unevenly swollen. The branches of first order are provided with some lateral depressions in the cortex. With this exception, the morphology and the chemistry (lobaric acid present!) agree well with *U. flammaea*. I saw a similar specimen.
Fig. 25. Usnea fragilesens var. fragilesens, F-Vire, 1838, (?) Delise (PC), showing typical habitus with anisotomic dichotomous thallus and fusiform branches. – Rule = 2 cm. – Fig. 26. U. fragilesens var. mollis, GB-North Devon, 1971, Krog (0), showing typical habitus with thallus richly and divergently branched at the base. – Rule = 2 cm.

collected in Greece (Thessalia, 9.8.1938, Regel (G)) with the same chemistry. I think that U. dalmatica is an extreme morphotype of U. flammea, occurring at the limit of the distribution area of this species (beyond 15° east of Greenwich). It is noteworthy that Motyka first determined the type specimen of U. dalmatica as U. fragilesens ssp. dalmatica before he made it a distinct species.

P. James (London) annotated (20.4.1975) the holotype of U. rupestris with the following text: “appears to be an extreme variant of U. flammea”. There is no doubt that the specimens collected by M. C. Knowles in Clare Island are concordant with U. flammea even if lobaric acid could not be detected in these specimens.

**Distinction:** U. flammea is normally a well-marked species which can be separated from other sorediate members of the genus by its pale basal part with numerous annulations, its efflorescent, ± protuberant soralia with numerous isidia and its chemical properties (norstictic, stictic ± lobaric acids).

**Distribution:** Specimens examined were from Great Britain, Greece, Norway, Portugal, Spain and Yugosla-
via. Distribution in Norway (Fig. 28).


**Usnea fragiles Havaas ex Lyng**


Nomenclatural note: See var. mollis.

**Description:** Fig. 25. Thallus subpendant, 3–6 cm long, seldom shrubby, sparsely branched, branching anisotomic-dichotomous. Trunk typically long (2–5 mm), thinner at the base (Fig. 7), always jet black over 1–2 mm, annular cracks sparse (Tab. 2), thin, without everted medullary tissue. Br. I terete, branching anisotomic-dichotomous, very long and distinct, much thicker than the other branches, typically fusiform, sparsely branched, axils 90° angle. Br. II distinctly narrowed at the base, mostly fusiform (Fig. 10), much thinner than the br. I, sparsely branched. Terminal branches sparsely branched, slender, long, ± filamentous, with few fibrils, axils 60°–90° angles (Fig. 15A). Papillae usually numerous on the br. I and II where they are ± evenly and densely distributed (Tab. 2), they are low hemispherical lumps broader than tall, ± flattened near the base and sometimes difficult to see (Fig. 19). Fibrils rather long (3–5 mm), slender, unevenly distributed, sparse to absent. Soralia even, plane to slightly concave, large when mature (190–300(600)μm), not confluent, typically rounded, usually with a sharply delimited margin and a distinct cortical rim (Figs 13, 14), sparse (Tab. 2); isidia rarely present on mature soralia. Cortex shiny like broken glass, usually thin (Tab. 2). Medulla thick (Tab. 2), loose, mostly homogeneous to heterogeneous (then external part very thin), never pigmented (Fig. 16). Axis thin (Tab. 2), never pigmented. Chemistry: K– or K+ faint yellowish, Pd– or Pd+ light orangish yellow near the central axis (see Tab. 1). Substrate: mostly saxicolous (Tab. 3).

**Variation:** The most variable features are the frequency of fibrils, the size of the thallus, the degree of branching at the extremities and the distribution of papillae towards the distal parts of the thallus.

**Distinction:** _U. fragiles_ is a characteristic lichen which cannot be confused with any other _Usnea_ when optimally developed. It is distinct from _U. cornuta_ mainly in the size and density of the soralia, in the ramification pattern which is clearly anisotomic-dichotomic,
in the secondary branches which are typically fusiform and in its chemistry. However, some transitional forms between the two species seem to exist. It often concerns morphotypes in which the soralia are badly developed or absent. It is then necessary to check the chemistry with TLC, looking at the presence of salazinic acid (U. cornuta) or of norstictic acid as main substance (indication of U. cornuta) or as trace (indication of U. fragiliscens, see chemistry above). Concerning the separation from the var. mollis, see under this taxon.

**Taxonomic remarks:** U. leucina Mot. (Holotype: Portugal, Madeira, Paul da Serra, below Rabaçal and Bica da Cana, 15.5.1952, leg. Persson (LISU). Chemistry: stictic, menegazziaic, norstictic (trace), fatty acids) is very similar to U. fragiliscens var. fragiliscens. However, more material from the macaronesian area should be studied before its status can be determined.

**Distribution:** Specimens examined were from France, Great Britain and Norway. Distribution in Norway (Fig. 29).

*Usnea fragiliscens var. mollis* (Vain.) Clerc comb. nov.


**Nomenclatural note:** Zahlbruckner (1930) published a nom. nov. (*U. malacea* Zahlbr.) for *U. mollis* Stirton, nom. illeg. but he proposed at the same time the new combination *U. malacea* (Stirt.) Zahlbr. for *Chlorea malacea* Stirr. As *U. malacea* (Stirt.) Zahlbr. is currently accepted as validly published (Motyka 1936–1938, Krog 1976), *U. malacea* Zahlbr. has to be considered as nom. illeg. (Code, Art. 64.4).

**Description:** Diffsers from var. fragiliscens in the following characters (Fig. 26): *Thallus* subdichotomously and richly branched, at least close to the base. *Trunk* slightly or not thinner at its base, but rather ± broadened. *Br. I* short, not fusiform. *Br. II*. The ones close to the basal part not distictively fusiform. *Soralia* often ± densely covered with isidia when mature, sparse (Tab. 2). *Cortex*, *medulla* and *axis* (see Tab. 2). *Substrate*: mostly corticolous (Tab. 3).

**Variation:** See under var. fragiliscens.

**Taxonomic remarks:** Studying *U. fragiliscens* s.str. I found that the small morphological and anatomical differences were quite well correlated with the substrate preference. The type specimen of *U. mollis* represents the corticolous specimens and the corresponding mor-

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**Provisional key for the sorediate, bushy to subpendulous Usnea occurring in Scandinavia**

**Important note**

Young, necrotic or abnormal specimens with badly developed characters or growing in extreme localities are difficult to recognize. Thus, the chemistry should be in...
vestigated with TLC and possibly specialists be consulted. Even in well developed specimens, some typical features may be lacking. In fact, as stated by Swinscow and Krog (1975), discrimination between Usnea species depends more on the combination than on the presence or absence of characters, the latter being themselves often more relative than absolute. Therefore it is often necessary to study the whole set of characters or permutations which makes the use of a dichotomous key problematic. In doubtful cases, the use of this key in conjunction with pictures and comments made in the next may be of some help.

Key
1. Secondary or tertiary branches clearly constricted at the base or fusiform
   2
2. Soralia without isidia, large when mature, excavate, extending to the full width of the branches and sometimes encircling them, the whole circumference being thus sorediate. Papillae absent or rarely sparsely present in the basal part of the thallus. K−, Pd− orange-red (protopetric acid) or K−, Pd− (usnic acid only) ... U. glabrata Aech.
3. Soralia, at least the young ones, ± densely covered with isidia, minute or large, never excavate and never encircling the branches. Papillae mostly present. Protopetric acid never as main substance
   3
3. Cortex mat to slightly shiny but never glossy; medulla dense to compact, cottonous, moderately thick (18%–23%–28%); axis moderately thick (31%–40%–49%), basal part with numerous (5–90.5 cm) and conspicuous annulations. Trunk whitish to brownish ... U. flammaea
4. Cortex glossy; medulla loose to moderately dense, thick (28%–33%–38%); axis rather thin (16%–24%–33%); basal part with few (2–4/0.5 cm) and thin annulations. Trunk brownish to jet black
   4
4. Soralia crowded mostly on terminal branches and on frbrils, minute but often becoming confluent and thus looking like a single large soralium (be sure to look at single sorals). Medulla K+ yellow (salazinic acid only) or K+ yellowish-red (stictic, norstictic, ± salazinic acids) ... U. cornuta
5. Soralia never crowded but widely spaced, rarely becoming confluent, large when mature, rounded. Medulla K+ pale yellowish or K− (stictic ± norstictic (trace) acids) ... 5
5. Trunk thinner at its base. Thallus subsupymodial and mostly sparsely branched over its whole length. Br. I long, conspicuous, fusiform. Mostly saxicolous
   5
   6
6. Soralia usually densely covered with isidia (but sometimes easily dislodged and dropping off in herbarium, some young isidiate soralia being however always present), even to ± tuberculose, minute to moderately large ... 7
7. Soralia never developing isidia (not to be confused with pseudoisidia!), even to excavate, large and conspicuous when mature
   10
8. Basal part concolorous with the br. I or paler, never with conspicuous blackening, with numerous and conspicuous annulations. Papillae absent except towards the apices. Papillae sparse or absent, verrucose, never cylindrical. Stictic, norstictic, ± lobaric acids ... U. flammaea
9. Basal part jet black at least for 1 mm (here some very rare morphotypes of U. flammaea with brownish black base, see morphology and chemistry under 9(2)) with few annulations. Fibris distributed on the whole thallus. Papillae usually numerous, verrucous or cylindrical
   9
10. Terminal branches with mostly anisometric dichotomities, elongated, not tapered but of the same width throughout most of their length, twisted, some of them growing beyond the others, the whole giving a filamentous, contorted aspect to the tips of the thallus. Papillae verrucous or cylindrical. K+, Pd+ (salazinic acid) U. diploptus agg.
11. Terminal branches with mostly isotomich dichotomities, tape-red, not twisted, all ending ± at the same height, apices not filamentous nor contorted. Papillae verrucous, neyer cylindrical. K+, Pd+ (thamnolic acid) or K−, Pd−, UV + (soralial) (squamic acid) ... U. subfloridana
12. Soralia excavate when mature, concave, often becoming confluent and then revealing the central axis of the small branches. Fibris usually present on the apices
   12
13. Soralia even, plane or slightly concave, distictively rounded, widely spaced, rarely revealing the central axis. Fibris absent on the apices ... U. glabrescens agg.

Discussion of some species treated in the key
This key is a preliminary attempt and the following species not discussed in detail in this paper have to be studied more thoroughly before a definite conclusion can be reached.

U. diploptus aggare


This species has been considered a long time as exclusively saxicolous. In central Europe I found it to be mainly corticolous. In herbaria, most of the specimens are found under U. subfloridana. U. diploptus produces salazinic acid as main substance in the medulla but preliminary studies seem to indicate that the chemistry of this species is very variable (alectorialic, barbatic acids).


U. glabrescens aggare

This aggregate is morphologically close to U. subfloridana Stir., the soralia of the latter producing numerous isidia.
U. extensa Vain. Holotype: Siberia, Levusch ad flumen Konda, 1880, leg. Vainio (TUR!). (Chemistry: norstictic and salazinic acids). This taxon differs from all other species of this aggregate, having thin terminal branches conspicuously foveolated. Further material needs to be studied before the status of this Siberian taxon can be asserted.

U. glabrescens (Vain.) Type ?: Finlandia, Tavastia australis, Korplahiti, Tienan, Kuusen oksala, 1873, leg. Lang (TUR!). (Chemistry: norstictic, salazinic acids.). Syn. (?): U. compacta Mot. (Type ?: Polonia merid. Montes Tatry, vallis Koscieliska, ca. 1100 s.m. ad truncum Laricis europeae/culcels. 20.7.1924, leg. Motyka (LUB, specimen seen in 0!). (Chemistry: norstictic, salazinic acids)). Some species treated in the key (U. glabrescens, U. hirta, U. lapponica and U. subfloridana) show to some extent such morphotypes characterised by a compact thallus with numerous short main branches, thick densely ramificated apices, and a very thick central axis, especially near the basis. I regard such specimens as being extreme morphotypes environmentally induced. Their determination is often difficult as the characters are badly developed. This can be sometimes solved with the help of TLC for species with distinctive compounds.


(Type not seen) (Syn. U. glaucescens Vain.). A very characteristic species, its chemistry including a series of fatty acids (murolie acid complex) ± norstictic acid (Krog et al. 1980, White & James 1985). The type of U. glaucescens Vain (Lectotype (here selected): Karelia australis, Viipuri, Hovi, Kuusi, 11.5.1919, leg. Pulkkinen (TUR!) (Chemistry: murolie acid complex)) is an extremely depauperized morphotype with a few fibrillae (most of them having fallen off as the presence of scars shows) and completely eroded soralia without any isidia. However, the basal part (which is not blackened), the lack of true papillae, the main branches (± foveolate, ± angulate), as well as the chemistry correspond very well to U. hirta.

U. lapponica aggregate

This aggregate seems to be very close to U. diplotypus, differing by its excravate soralia which do not develop isidia.


U. lapponica Vain. Lectotype (here selected): Russia, Lapponia, Imandrae, Lowosersk, ad ramulos Piceae, 25.5.1887, leg. A. Osw. Kihlman (HI!). (Chemistry: salazinic acid or usnic acid only).


U. perplexans Stirton. Holotype: India, Himalaya, Pangi, leg. Watt (GLAN!). (Chemistry: salazinic acid). Carlin and Swahn (1977) reduced the whole lapponica aggregate to synonymy with U. perplexans. However, the axis of the type material of U. perplexans is slightly orange pigmented. I had the opportunity to see two more specimens of U. perplexans collected in the western Himalayas (Jammu & Kashmir State, Gilmarg, 77.476 Dange (LWG)). They are morphologically and chemically identical with the type material. Owing to the fact that, in the species of the U. lapponica aggregate, the axis is never pigmented, U. perplexans is here considered as an extra-European species which is not conspecific with any species belonging to the U. lapponica aggregate in Europe.

U. subfloridana aggregate

U. subfloridana Stirton. Type ?: Scotland, Killin, 19 July 1881, leg. ? (BM!). (Chemistry: thamnolic acid) (Syn. U. comosa (Ach.) Vain. Lectotype: Suecia, 1857C (H-ACH). (Chemistry: thamnolic, hypothamnolic acids)). This taxon must be considered as the secondary species of U. florida (L.) Wigg. em. Clerc (Clerc 1984). The medulla of this species produces thamnolic or squamatic acids or both. All the specimens containing salazinic acid can be referred either to U. diplotypus, to U. glabrescens, to U. madeirensis Mot. (Holotype: Portugal, Madeira, Paula de Serra, below Rabaçal and Bica da Cana, 15.5.1952, leg. Persson (LSU!). (Chemistry: salazinic acid, unknown 2/42 orangish brown) or to U. wasmuthii Räs. (Holotype: U.S.S.R., Estonia, Tallinna, Kakumäe, on Picea excelsa, 13.7.1908, leg. Wasmuth (HI!). (Chemistry: barbatic acid)). U. syriaca Mot. Holotype: Syria, ad pedes Akma Dagh, copiose in sylva Abietinum, alt. 6000', 19.6.1862, Th. Kotschy, Pl. Syriae bor. ex. Amano prope Beilan, 40 (W!). (Chemistry: norstictic, salazinic acids) is very close to U. subfloridana. However, more material from the eastern part of the mediterranean area must be studied before any conclusions can be reached.

As the type specimens of Usnea arnoldii Mot., U. distincta Mot., U. silesiaca Mot. and U. sorediifera (auct.) Mot. nom. illeg. non (Arn.) Lyng, all in LBL, were not available, their status could not be determined.

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**References**


