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Saxicolous Species of *Usnea* Subgenus *Usnea* (Lichenized Ascomycetes) in North America

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Abstract. *Four primarily saxicolous species and eight corticolous, secondarily saxicolous species of Usnea are known in North America. Morphology, chemistry, anatomy, ecology, and distribution of the mainly saxicolous Usnea amblyocladula (Müll. Arg.) Zahlbr. (Syn. nov. U. globularis Motyka). U. ammannii P. Clerc & Herrera-Campos sp. nov., U. halei P. Clerc sp. nov., and U. nashii P. Clerc & Herrera-Campos sp. nov., are described. Usnea ceratina Ach., U. cornuta Koerb., U. dasaea Stirt., U. hesperina Motyka, U. mutabilis Stirt., U. rubicunda Stirt., U. subscabrosa Motyka, and U. wirthei P. Clerc are found only occasionally on rocks, and are briefly described. Usnea dasaea, (syn. nov. U. dolosa Motyka, U. galbinifera Asah., U. spinigera Asah., U. spinulifera (Vain.) Motyka, U. undulata Stirt.) is described in detail. Usnea amblyocladula is new for North America. Usnea dasaea is new for North America, South America, Africa, and Asia. A key for species occurring on rocks in North America is provided. A new term, fibericles, is proposed for more or less protuberant scars left on branches after fibrils have broken.*

In North America as in many regions of the world, the genus *Usnea* is still insufficiently known. Hale (1979) published a key for this area but only the United States, and southern Canada were considered, and not all species occurring in this area were included. The saxicolous species are especially in need of a revision and Hale (1979) stated when discussing *U. herrei*: "It is the commonest saxicolous Usnea . . . , you will collect other species on rock which do not fit here, and which cannot be identified in our present state of knowledge." Since that time our state of knowledge has not improved, and most of the collected saxicolous specimens in North America have remained unidentified or labeled as *U. diplotypus* Vain. (Thomson 1956), *U. subfuscus* Stirt. (Hale 1956, 1958), or *U. herrei* Hale nom. illeg. (Hale 1979). For reasons discussed in this article, these three names should not be used at all when considering saxicolous North American species. The aim of this paper is to clarify the taxonomy of the species of *Usnea* subgenus *Usnea* growing primarily on rocks in North America and to provide detailed descriptions of their morphology, anatomy, and chemistry. In North America, *Usnea* subgenus *Usnea* species growing mainly on rocks occur only in the southern part of the United States, and in Mexico. Many corticolous taxa might however grow incidentally on rocks in the whole studied area. Most of them are included in the key to the saxicolous species, and a short description is given for each. It is, however, possible that some more, mainly corticolous, *Usnea* species occur on rocks, rarely though. *Usnea dasaea* Stirt., mainly a corticolous taxon, is treated in detail here because it is closely related to *U. amblyocladula* (Müll. Arg.) Zahlbr. and because it has not been well understood.

**MATERIAL AND METHODS**

This study is based on material collected during several field trips made by the senior author in Arizona, California, Georgia, North Carolina (USA), and Baja California.
(Mexico) during 1988 and 1989, and by the second author in Mexico and Arizona between 1990 and 1995. Specimens from the following herbaria have been studied: ASU, BM, BRLU, CUW, DUKE, FG, H, H-ACH, H-NYL, LBL, LE, M, MIN, S, TNS, TUR, TUR-V, UPS, US, W, and the private herbarium of B. Ryan (Tempe). All material has been studied with thin-layer chromatography (Culberson & Ammann 1979), with the solvent B modified (Culberson & Johnson 1982).

Thickening of the cortex (C), medulla (M), and central axis (A) were established according to the method given in Clerc (1984a). Thickness of the structure measured is given in percentage of the whole width of the branch on which the measurement was done: %C = thickness of the cortex, %M = thickness of the medulla, %A = thickness of the central axis. In the descriptions, n refers to the number of individuals analyzed.

Soralium 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 arithmetic mean of these three measurements was calculated. Young soralia (small white spots appearing as pseudocyphellae), as well as mature ones were taken into account. The counting was done on 0.23 mm² and extrapolated for 0.5 mm².

In addition to the types of the European species, the original material of most of the some 140 Usnea species reported by Motyka (1936–1938) to occur in North and South America has been seen and studied by us. Types of selected eastern Asiatic species described by Asahina (1956) have been studied as well.

Distribution maps are mainly based on material seen from ASU, DUKE, MIN, and US, and represent, for each species, the general overall distribution in North America.

MORPHOLOGY

Studying morphology in the genus Usnea, one has to be especially careful when sorting characters used for taxonomy. Several characters which are usually rather variable within Usnea species, and therefore of little value for taxonomy at the species level, have been identified (Clerc 1991). Only characters which are more or less constant within species are therefore considered in the following discussion.

Habit.—Usnea is a genus of fruticose species with radially symmetrical branches. The thallus is shrubby (Figs. 1c, 2a) i.e., short thallus with strongly divergent branches; subependant (Fig. 1b) i.e., middle-sized thallus with strongly divergent main branches and more or less parallel terminal branches; or pendent i.e., long thallus with all branches running more or less parallel. Most species studied in this paper are shrubby to subpendent.

Branching.—We follow here the terminology adopted by Hawksworth (1972): a) isotomic-dichotomous with dichotomies of approximately the same thickness, b) anisotomic-dichotomous with dichotomies of different thickness, and c) filamentous-dichotomous where type a occurs in the basal part of the thallus, and type b predominates in the apical parts. Branching types a or b are often best seen at the thinnest branches of the extremities of the thallus, however, this character is sometimes quite variable and difficult to analyze.

Trunk (Figs. 6b, 8d).—An important character in many species, requiring a correct sampling of specimens. It is defined here as the part between the holdfast (point of fixation of the thallus to the substrate) and the first main ramification point (not taking into account first minor branches). The color in the first few millimeters from the base is diagnostic for most species. It can be of the same color or paler than the main branches or have a yellowish to reddish hue or be jet black.

Branches.—Branches are tapered when their diameter decreases regularly towards the terminal part of the thallus; cylindrical when they have the same diameter for most of their length and become thinner only close to the tips; or irregular when their diameter varies irregularly throughout their length.

Segments.—Branches in Usnea are more or less distinctly segmented, and frequency of segmentation can be an important character. The shape of main branch segments (the thickest ones) in transverse, and longitudinal sections is an important character as well. In transverse section, segments may be terete (Fig. 6b) or ridged (Fig. 2f). In longitudinal section, segments may be cylindrical or sausage-like. Furthermore, segments can be deformed by the presence of depressions in the cortex such as foveolae (circular depressions at the surface of the cortex, Fig. 2g) or transversal furrows (transversal depressions).

Papillae versus tubercles.—We follow Swinscow and Krog (1979) and differentiate papillae (Fig. 4c) that are hemispheric, conic or cylindrical protuberances composed mainly of cortex, from tubercles that are the same type of cortical outgrowth but larger, with medulla inside. Medulla is usually bursting at the top of the latter, which therefore appears whitish punctuate. At a later stage, tubercles may start to produce soredia, as in U. catennis.

Fibercles (Figs. 2e, 8c).—We propose to introduce this term for structures that appear much the same as tubercles with bursting medulla at their summit, but which have a different origin: a more or less protuberant scar or gap left after the breaking away of fibrils. On young fibercles, the hole left by the central axis of the fibril can still be observed. As tubercles do, fibercles also can produce soredia at their summit at a later stage, as for instance in U. amblyocladia (Fig. 2e). In Usnea nashii (Fig. 8c) they produce up to three short thin fibrils at their apex. It is important to differentiate tubercles from fibercles as some species produce only tubercles (U. catennis) while others species produce only fibercles (U. amblyocladia and U. nashii).
**Fibrils** (Fig. 4c).—Fibrils are short, branch-like appendages with a central axis. The central chord, however, is not attached to the central axis of the branches on which they occur. Short fibrils (1–3 mm) are *spinulose* (Fig. 10b). In many species they are usually longer and slender. They are probably, especially in the group treated here, efficient short range propagules. When fibrils break off the branches, fibericles are produced.

**Pseudocyphellae.**—This term is here used only for small, whitish, usually thin and elongate, more or less fusiform breaks in the cortex that never produce soredia at a later stage of their ontogeny. As defined here, pseudocyphellae are absent in the species treated in this paper. They can be found, for instance, in *U. articulata* Hoffm.

**Soralia** (Figs. 4b, 6c, d, 10c, d).—The main types of soralia in *Usnea* have been described by Clerc (1987b). Furthermore, it is essential to observe on which structures soralia begin their development: on the plain cortex, at the top of a tubercle, on fibericles, at the edge of an eroded segment, or on an eroded ridge. Although many of these structures might be involved in the ontogeny of the soralia in the same species, one of them is usually specifically preponderant. Morphology and ontogeny of soralia are indeed two of the most important characters in the taxonomy of sorediate species. However, like other characters, they show some variation due to environmental parameters. For instance, punctiform soralia may enlarge, or soralia which are usually level with the cortex may sometimes become more or less concave. The exact causes for such modifications in *Usnea* are not known, however extreme habitats which are dry and especially exposed to strong illumination (saxicolous habitats), or which are inversely very humid, are often correlated with such modifications.

**Isidiomorphs.**—Short (100–200 μm) and thin ‘isidia-like’ structures that rarely occur singly are common in bundles on soralia of *Usnea* species. Soredia are usually produced in the gaps left after the breaking of isidiomorphs. However, isidio- morphs can arise secondarily on well-developed, often more or less capitate soralia (Fig. 6d). All species treated here produce isidiomorphs. Isidiomorphs of *U. amblyoclada* are often typically black pigmented at their tips (Fig. 2d).

**Cortex.**—Superficially the cortex is smooth as in *U. dasaea* to more or less cracked (Figs. 6b, 8d), especially close to the basal part. Cracks may be annular, giving the branches a conspicuously segmented appearance as in *U. halei* (Fig. 6b); or oblique to irregularly longitudinal as in *U. ambly- oclada* and *U. nashii* (Fig. 8d). White tissues of everted medulla or deposits of calcium oxalate can occur at the edge of the cracks, giving a typical appearance to the branches as in *U. nashii* (Fig. 8d). In longitudinal section, the cortex may appear glossy (*U. dasaea, U. amblyoclada*) or mat (*U. halei*). Although this character is sometimes difficult to check, especially on old herbarium material, it is an important feature in *Usnea* that provides clues for phylogeny.

**Medulla.**—The medulla of the species studied here is white or sometimes slightly orange pigmented, especially around the central axis (decomposition of norstictic acid?). We differentiate three types of medulla: *lax* (Fig. 6f) with bundles of hyphe more or less loosely arranged with large empty spaces between them; *dense* (Fig. 6e) with more or less densely disposed hyphe, without space between them but still visible individually; and *compact* with hyphe arranged so densely that they form a compact mycelial mass. Sometimes, the medulla is heterogenous i.e., with a thin layer of compact tissue close to the cortex and a larger, and more loose layer around the central axis.

**Central axis.**—A cartilaginous and more or less elastic strand that runs throughout the innermost part of the thallus, and is composed of solid, thick-walled, conglutinate, longitudinally arranged hyphe that are white or sometimes pinkish or yellowish.

**Chemistry**

The main and taxonomically important secondary compounds (Table 1) produced in the medulla by the species discussed in this article are β-oricinol depsidones, including stictic acid, norstictic, galbinic, and protocetraric acids, β-oricinol parapadesides including barbate and diffractaia acids, a β-oricinol metadepside, thannolic acid, and diverse fatty acids e.g., fatty acids of the murolic acid group in *U. mutabilis*. With the exception of *U. cornuta s. l.*, each species has a constant chemistry and chemical variation is so far absent or rare. For instance, in *U. dasaea*, among 43 specimens analyzed, only one thallus has been found without galbinic acid, the diagnostic medullary substance; this seems to be the same elsewhere in the world for this species. In *U. amblyoclada*, among 81 specimens analyzed, only three have been found without galbinic acid whereas *U. halei* (n = 62), *Usnea nashii* (n = 14), and *U. ammannii* (n = 18) display a constant chemistry.

**Ecology**

There are only a few primarily saxicolous *Usnea* species in the world. In Europe, individuals occurring on rock are rare; only *U. fragiliscens var. fragiliscens* is found exclusively on stone, but it is rather uncommon (Clerc 1987a). However, obser-
TABLE 1. Main secondary metabolites in North American saxicolous Usnea. Ch., chemotype; +, present in all specimens examined; ±, not always present (accessory); −, not present. Bar, barbatic acid; Dif, diffraetaic acid; Tha, thanolic acid; Pro, protocetraric acid; Nor, norstetic acid; Gal, galbinic acid; Sti, stictic acid; Sal, salazinic acid; Pso, psoromic acid; Fat, fatty acid(s).

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<td>U. subscabrosa</td>
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vations on the influence of the saxicolous habitat on the morphology of Usnea species made in this study could make us reconsider the separation of U. fragilesens into two different taxa as proposed by Clerc (1987a). A few other species grow occasionally on rocks, as for instance U. cornuta Koerb., U. flammea Stirt., U. subscabrosa Motyka, U. diploptus, and U. filipendula Stirt. Other species occur only exceptionally on rock. In North America, the situation is quite different, and saxicolous Usnea can be quite frequently collected, especially in the southern regions, in dry habitats where the most frequent species growing on rocks is U. amblyoclada, which has been found only rarely growing on trees. Usnea halei is mainly saxicolous, but can be found quite often on trees. Usnea nashii and U. ammannii are rare species that have been found to date only on rocks. A few other species that are mainly corticolous can be found exceptionally on rocks e.g., Usnea ceratina, U. cornuta s. l., U. dasaea, U. hesperina, U. mutabilis, and U. wirthii. All species seem to grow indifferently on acidic or calcareous rocks.

**DISTRIBUTION**

Usnea species which are primarily saxicolous have restricted distribution patterns compared to corticolous species (Herrera-Campos & Clerc in press). In Mexico, the aridity increases from the southeast to the northwest (Rzedowski 1986). Most of the saxicolous Usnea were collected towards the most arid part of this gradient, mainly in the north part of the Sierra Madre Occidental (Rzedowski 1986). Coniferous forest with Pinus and associated Quercus is the main type of vegetation occurring in the collecting sites between 1,650 and 2,800 m. In general, the climate is essentially temperate with rains during the warm season, differing locally in temperature and humidity. Only one species (U. amblyoclada) was collected in the xerophytic shrubland vegetation type (matorral xerofilo) on rock outcrops (mainly rhyolite). This area is subject to high insolation and low humidity, with mean annual precipitation lower than 700 mm (ca 100 mm in Baja California) (Rzedowski 1986).

In the United States, saxicolous Usnea occur especially in the south, rarely north of 40° latitude (however see Taylor 1968), in the warmest part of the country with July mean temperature around 25°C (Vankat 1979). In the southeastern part of the country, saxicolous Usnea colonize exposed rock surfaces that are mainly scattered throughout the Ozark Mountain-southern Appalachian region, and more rarely in the Piedmont (Dey 1979). In these areas, rock surfaces (mostly schist boulders and sandstone) are found on the summit of mountains, on roadsides, on vertical cliffs or in such vegetation as shrub bals, heath bals, fire cherry communities, or spruce-fir forests (see Dey, 1978 for details on these community types), between 300 and 2,000 m. In the south-central and the southwest, which are the driest parts of the country, saxicolous Usnea occur on exposed and xeric, igneous rocks in Pinus cembroides, Juniperus, Quercus forests between
1,800 and 2,400 m, as for instance in Big Bend National Park, Texas (Wetmore 1976), or on rhyolite, volcanic rocks, and limestone in Pinus and Pinus-Quercus forests between 1,800 and 2,200 m in southern Arizona.

**Key to Species**

Note.—Species 5 to 12 occur secondarily on rocks and are thus found only rarely on this substrate. Usnea ammannii and U. nashii are known, so far, only from Mexico.

1. Cortex with red pigment, especially conspicuous close to the basal part; lateral branches not narrowed at attachment point 10. **U. RUBICUNDA**

2. Medulla C+ yellow, CK+ deep yellow orange, with pink pigment in the medulla; diffractic acid present 5. **U. CERATINA**

3. Medulla with wine red pigment; soralia punctiform, with numerous isidiomorphs; papillae absent; fatty acids of the mucilaginous group present; medulla K–, PD+ 9. **U. MUTABILIS**

4. Medulla with yellow pigment; lateral branches distinctly narrowed at point of attachment; cortex glossy; either norstictic or psoromic acids in soralia 12. **U. WIRTHI**

5. Medulla K– and PD+ red orange; protocetraric acid as main substance 6

6. Large fibers with white summits present (Fig. 8c); short isidiomorphic-like fibrils occurring on fibers; soralia absent ... 4. **U. NASHII**

7. Medulla with red pigment; soralia punctiform like fibrils absent; soralia mostly present 7

8. Lateral branches distinctly narrowed at point of attachment; thallus erect-shrubby with divergent branches 6. **U. CORNUTA** (chemotype 6)

9. Lateral branches not narrowed at point of attachment; thallus subpendant to pendant with more or less parallel branches 8

10. Cortex distinctly glossy to vitreous, main branches not conspicuously annulated 11. **U. SUBSCABROSA**

11. Cortex mat, main branches distinctly annulated, especially close to basal part 8. **U. HESPERINA**

9. Base jet black; soralia large, ± circular, reaching the whole branch diameter when mature (Fig. 4b) and often encircling the branch, slightly concave, with few isidiomorphs; lateral branches not narrowed at point of attachment (Fig. 4c); salazinic acid alone 2. **U. AMMANNII**

9. Basal part of trunk pale or brownish to reddish pigmented; soralia rarely reaching the whole branch diameter when mature, never encircling the branch, of irregular shape, level to cortex to slightly tuberculous, with few or numerous isidiomorphs; lateral branches usually slightly to distinctly narrowed at point of attachment (Fig. 2d); salazinic acid not alone (see, however, chemotype 1 of **U. cornuta**) 10

10. Cortex glossy to vitreous; soralia ± tuberculous and convex when mature, usually reaching ½ branch diameter or more (Figs. 6c, d), with numerous, and clustered isidiomorphs (Fig. 6d); fibers usually absent 3. **U. HALEI**

11. Isidiomorphs thick, usually not clustered but often sitting alone on sorallium, black-tipped (Fig. 2d), always present; soralia punctiform, never enlarged, ± tuberculous, numerous, densely disposed (Figs. 2b, e), occurring on fibers; 11

12. Fibrils short and spinulose, densely but ± irregularly covering restricted parts (rarely the entire length) of branches (Figs. 9a, 10a, b); soralia enlarged to ½ branch diameter or more when mature, often slightly fusiform, not coalescing (Figs. 10c, d); galbinic acid present, 7. **U. DASAEA**

12. Fibrils usually longer and slender, scattered on whole thallus; soralia punctiform, often coalescing and forming extensive larger soralia-like areas; galbinic acid absent, 6. **U. CORNUTA** s. lat.

**Primarily Saxicolous Species**

1. **USNEA AMBLYOCLADA** Müll. Arg.) Zahlbr., Cat. Lich. Univ. 6: 534. 1930. (Figs. 1, 2, 3)


Note.—The type specimen of *U. globularis* as designated by Motyka (1936–38) was housed in the herbarium of B. de Lesdain in Dunkerque, which has been destroyed during the second World War. Most fortunately J. Motyka when studying this material kept a piece of the thallus in his herbarium which is now the only original material that exists.
Thallus shrubby, compact (Figs. 1a, c, 2a), rarely subpentdent (Fig. 1b), 2–10 cm long, grayish green; branching isometric-dichotomous at least close to apices; trunk short, up to 3 mm long, distinctly paler than branches or of same color, with numerous and conspicuous annular cracks; branches usually ± irregular, inconspicuously segmented, lateral branches not narrowed or slightly to distinctly narrowed at point of attachment; segments terete to distinctly ridged (Fig. 2f), cylindrical to weakly sausage-like; foveoles absent or present (Fig. 2g); transversal furrows absent or present; apices short, thick, usually sparsely branched (Fig. 2b); papillae absent; tubercles absent; fibers low, numerous, mostly sorediate; fibrils short (1–3 mm), often spinulose (Fig. 2c), mostly present in oldest part of thallus, breaking away early in younger branches leaving conspicuous scars (fibercles); soralia punctiform, smaller than half the diameter of branches (Fig. 2e), densely disposed (16–) 29–40–51(–70) soralia/0.5 mm² (n = 22), slightly tuberculate, arising on fibers; isidiomorphs on soralia or isolated on plain cortex (very young fibrils?), sometimes on ridges, frequently black pigmented at tips (Fig. 2d); apothecia rare; cortex thin [(2.5–) 4.5–6.5%–9(–13.5), n = 110], shiny, distinctly transversely, and longitudinally cracked at the base of main branches, the edges of cracks slightly upturned; medulla moderately large [(8.5–) 17.5–23%–28.5(–36.5), n = 110], compact to dense close to the axis, often orange to pink-pigmented close to the axis; axis thick [(19–) 32–41%–50(–60), n = 110], often pale pink pigmented.

Chemistry.—1. Usnic, norstictic, galbinic, and salazinic acids, sometimes with traces of protocolaric acid (n = 78). 2. Usnic acid, norstictic, and salazinic acids (n = 3).

Variation.—Usnea amblyocladula is quite a variable species in appearance depending on its exposure on rock. For instance, the shape of the branches may vary from nearly cylindrical (Fig. 2e) to more or less irregularly swollen and reticulate-foveate (Figs. 2f, g). The frequency of fibrils is variable as well. As they are probably very efficient short distance dispersers, most of the fibrils usually break away quickly leaving scars (fibercles) where soredia may develop. In some individuals, for some unknown reasons, fibrils remain on the branches and give therefore an unusual strigose appearance to these thalli (Fig. 2c). Extreme forms can be seen in exposed habitats and they are extremely depauperate, with thick branches that are conspicuously reticulate-foveate with few ramifications (Figs. 1c, 2f, g). The chemistry is constant, the diagnostic substances always being present. Galbinic acid is rarely missing in North America, whereas it seems to be less frequent in South America (Walker 1985).

Taxonomic remarks.—Swinscow and Krog (1976) considered U. amblyocladula to be conspecific with U. pulvinata Fries. Later they indicated (Swinscow & Krog 1979) that these taxa might represent separate species. Walker (1985) agreed with this latter opinion, and discussed U. amblyocladula in detail. She indicated that galbinic acid occurs in two collections from South America. The identity of the specimen with salazinic, protocollic, and fumarprotocollic acid, mentioned by Walker (1985) needs confirmation. The Usnea bornmuellleri aggr. as discussed by Swinscow and Krog (1976) needs a world revision. Usnea bornmuellleri Steiner has large soralia with isidiosporae, and not true isidia as stated by Walker (1985). Segments are swollen, with a thin cortex and a large and lax medulla. This species is not closely related to U. amblyocladula. The holotype of U. pulvinata has not been seen by us, but it contains usnic acid only (Swinscow & Krog 1976), and has been collected in Australia. The South African material housed at g and labelled U. pulvinata is morphologically, anatomically, and chemically different from U. amblyocladula.

Usnea amblyocladula is closely related to U. dasaea, and other taxa producing norstictic and galbinic acids. In addition to similar chemistries they share a glossy cortex, the capacity to produce spinulose fibrils densely disposed on some part of the thallus, and more or less ridged-foveate branches. For differences, see under U. dasaea.

Ecology and distribution (Fig. 3).—Mainly saxicolous, rarely corticolous. Usnea amblyocladula is present almost everywhere where saxicolous Usnea have been found (except southern California) and consequently has the largest ecological amplitude of all saxicolous Usnea species. It has the largest elevational range, from 300 to 2,800 m. Its distribution area is continuous from the southeast to the southwest of North America. This species can withstand dry conditions and it is so far, together with U. rubicunda, the only Usnea species which has been found on rocks in Baja California where precipitation is low (less than 100 mm), and is the only saxicolous Usnea found so far in the Piedmont in North Carolina. A few corticolous specimens were collected in Arizona on Pinus latifolia in pine-oak forests, and in North Carolina in the Appalachian Mountains on Prunus serotina and Kalmia. Motyka (1936–38) and Walker (1985) recorded U. amblyocladula from South America where the original material was collected. Ongoing investigations on South American species of Usnea (Velisek-Grundlehnner & Clerc, unpublished) will shed new light on the distribution of this species on this continent.


2. **Usnea ammannii** P. Clerc & M. Herrera-Campos sp. nov. (Fig. 4,5)


*Etymology.*—This species is dedicated to Klaus Ammann, Director of the Botanical Garden, Bern, Switzerland. Without his help, support, and encouragement the senior author would never have started and carried on studies of the genus *Usnea.*
Thallus shrubby, 1.5–3.0 cm long (Fig. 4a), grayish-green; branching anisotominc-dichotomous; trunk short, not conspicuous, black pigmented in basal part; branches usually tapered, sometimes ± irregular, with inconspicuous segmentation (3–5 segments/0.5 cm), lateral branches not narrowed at ramification point (Fig. 4c); segments terete to slightly ridged, cylindric to slightly sausage-like; apices short and thick with few ramifications; foveoles absent; transversal furrows present on whole thallus; papillae verrucous (Fig. 4c), irregularly distributed on main branches; tubercles absent; fibres absent; fibrils short spinulous, 1–2(–3) mm long, irregularly distributed on whole thallus; soralia superficial to slightly tuberculat es, as large as the branches when mature (Fig. 4b), sometimes ± encircling the end of branches, circular to transversely oblong, without margin, usually not confluent, arising on cortex ab initio; isidiomorphs small and sometimes black-tipped, mainly on young soralia, usually few on mature soralia (Fig. 4b); apothecia rare; cortex ± smooth and glossy, thin [(5–) 5.5–7%–8.5(–9) (n = 15)]; medulla loose to dense, extruding between segments, especially at ramification points, moderately large [(17–) 21–25%–29(–31) n = 15]; axis moderately thick [(26–)29.5–36.5%–43.5(–52) (n = 15)].

Chemistry.—Usnic and salazinic acids (n = 18).

Variation.—Compact forms have been collected and are characterized by small, pulvinate thalli that are densely branched in the apical part. Some variation exists in frequency of isidiomorphs that can be numerous to nearly absent. More collections are needed to have a good idea about the variation of this taxon.

Taxonomic remarks.—The lateral branches that are not narrowed at ramification point makes this taxon distinct from all species of the U. fragiliscens agg. Characteristic are the large and ± circular soralia with few isidiomorphs when mature. Usnea substerilis Motyka has the same type of soralia, but has different ecology, a mat cortex, and normally no isidiomorphs in mature soralia. Nevertheless, morphology of soralia does not seem to be a good indicator of phylogenetic relationship in Usnea and these two species are probably not closely related. Usnea lapponica and U. fulvoreagens have large soralia as well, but they are deeply excavate, reach the central axis, and never produce isidiomorphs.

Ecology and distribution.—Usnea ammannii was
found in only three localities where it occurs on rocks, between 1,950m and 2,800m. So far *U. ammannii* is endemic to Mexico (Fig. 5), but more collections are needed to understand its distribution pattern.

**Figure 4.** *Usnea ammannii.* — a. Thallus small, shrubby, holotype. — b. Terminal branch with soralia, holotype. — c. Branch with verrucose papillae and fibrils, May 22, 1992, *Herrera-Campos* (MEXU). Scale bars: Fig. b–c = 1 mm.

**Type:** MEXICO. CHIHUAHUA. Al E de San Rafael, 27°30'N, 107°53'W. Bosque de *Pinus-Quercus-Arbutus*, 2,000 m, 2.10.1992, *Herrera-Campos* 3292 (MEXU; holotype, 8SU, 2, isotypes). %C/M%A: 5.5/26.5/35. Chemistry: usnic and salazinic acids.

*Additional specimens examined.*—MEXICO. CHIHUA-
3. **Usnea halei** P. Clerc, sp. nov.  (Fig. 6, 7)


**Etymology.**—This species is dedicated to M. E. Hale who contributed so much to the knowledge of the lichen flora of North America and was the first who recognized *U. herrei* nom. illeg. as a distinct species (Hale 1979).

**Thallus** shrubby to subependent (Fig. 6a), 2–15 cm long, grayish to brownish green; **branching** isotomic-dichotomous at least in apical parts; **trunk** usually short (0–1 mm), branching at once, mostly with reddish brown pigment or of the same color as main branches, with conspicuous annular cracks (Fig. 6b); **branches** usually tapering, sometimes slightly irregular, lateral branches not or slightly to distinctly narrowed at ramification point; **segments** terete to slightly ridged, cylindric to slightly sausage-like, with slightly inturned ends; **apices** thin and loosely branched (except in compact forms); **foveolae** sometimes present; **transversal furrows** sometimes present; papillae low, verrucous, sparsely and unevenly distributed; **tubercles** present, verrucous, sparsely and unevenly distributed; **fibracles** absent; **fibrils** 2–4 mm, slender; sparsely and unevenly distributed close to basal part, absent in upper parts; **soralia** punctiform to large, slightly tuberculous, first smaller than half diameter of branches (Fig. 6c), but often soon enlarged (Fig. 6d), few to numerous (16–)18–27–36–44 soralia/0.5 mm² (n = 25), arising on low tubercles in lower part of thallus, and on cortex *ab initio* on apices; **isidiomorphs** almost only on soralia, mostly visible on young soralia but sometimes densely covering mature, large, and capitate soralia (Fig. 6d), never single on plain cortex, rarely slightly blackened at tips; **cortex** (Figs. 6e, f) thin to thick [(4–)5.5–7%–8.5–(13.5)] (n = 77), mat, distinctly transversely cracked at base of main branches, edges of cracks even or slightly inturned; **medulla** (Figs. 6e, f) thick [(13.5–)23–28.5%–34–(37.5), n = 77], compact to dense, and rose pigmented periaxially; **axis** (Figs. 6e, f) moderately thick [(14–)20–29%–38–(58)] (n = 77), almost always pink-pigmented.

**Chemistry.**—Usnic, salazinic, norstictic, and ± protocetraric acids (n = 62).

**Variation.**—Most of the variation affects the shape of the branches, which may be more or less distinctly segmented and swollen or tapered and slightly but distinctly constricted (or not) at their base. Some thalli are conspicuously ridged and foveolate. Ridges, depressions, and foveoles seem to be a response to environmental stress. Furthermore, depressions or foveoles are especially seen in species or individuals with a thin cortex like for instance in *U. hirta* (L.) Wigg. or in *U. cavernosa* Tuck. It is noteworthy that species have been described on the base of such modifications e.g., *U. foveata* Vain., which is a synonym of *U. hirta* (L.) Wigg. (Clerc 1992, 1997; see, however, Halonen & Puolasmaa 1995). The soralia show variation as well. They are close to the *U. cornuta*-type (Clerc 1987a, b), but enlarge in many individuals reaching sometimes the same width as the branches supporting them (Fig. 6d).

**Taxonomic remarks.**—Usnea halei is most probably the taxon which has been called *U. herrei* nom. illeg. by Hale (1979). Superficially, *U. halei* resembles *U. amblyocladula* but has a dull cortex, a different type of soralia with a different ontogeny, fibrils that are never spinulous but slender, low papillae (although sometimes difficult to see), and different chemistry. *Usnea cornuta* has lateral branches more distinctly constricted at the attachment points, usually more inflated branches, an isometric-dichotomous ramifications type, a thinner and shiny cortex, and occurs principally on bark. The most closely related species seems to be the European *U. flamma* (Clerc 1987a), which however, differs in its type of soralia, chemistry, and ecology.

**Ecology and distribution.**—Mostly saxicolous, sometimes corticolous. The distribution of *U. halei* is disjunct in North America (Fig. 7). In the southeast, in the Appalachian area, it is the most frequent saxicolous Usnea, occurring only in the mountains, between 800 and 2,000 m. In the southwest, this species is much rarer and replaced by *U. ambly-
oclada. It was found only once in southern Arizona, in the Santa Rita Mts, and a few times in northern Mexico where its elevation range (2,000–2,300 m) is narrower than that of other saxicolous Usnea. This, and the frequent occurrence in the Appalachian Mountains together with its absence in lower and drier habitats, suggests that this species requires more humid conditions than the other saxicolous species. So far, this species is only known from Mexico and the United States.


4. **Usnea nashii** P. Clerc & M. Herrera-Campos, *sp. nov.* (Fig. 8, 5)


*Etymology.*—This species is dedicated to Thomas Nash, III (ASU) in recognition of his continuing support for the investigation of the Mexican lichen flora.

*Thallus* shrubby (Figs. 8a, b), rigid, 2–12 cm long, yellowish green; branching anisometric-dichotomous; *trunk* short (1–3 mm), variously pigmented but never jet black, sometimes barely developed, often rugose to ± decorticated (Fig. 8d); *branches* usually tapering, conspicuous with few ramifications, distinctly segmented (especially the main branches) with conspicuous everted medulla between segments, lateral branches sometimes slightly narrowed at ramification point; *segments* terete to slightly ridged, cylindric to slightly sausage-like; *apices* thick and short with few ramifications, axis nearly 90°; foveoles absent; transverse furrows sometimes present; *papillae* minute, hardly distinct; *tubercles* absent; fibers of large (7–10 × 10–20 μm), conspicuous and numerous on whole thallus (Fig. 8c); *fibrils* of mature length rather rare and only present near basal part, short (1–3 mm), ± slender; short (0.5 mm) isidiomorphic fibrils produced (sometimes in bundles) on top of fibers (Fig. 8c); *soralia* absent; *isidiomorphs* absent; *cortex* ± glossy, distinctly longitudinally and transversely cracked, with conspicuous everted medullary tissues emerging from cracks (Fig. 8d), moderately thick [(4.5–)5.5–7.5%–9.5(–11) (n = 28)]; *medulla* dense, moderately thick [(22–)26–30%–34(–37) (n = 28)]; *axis* sometimes fistulose, ± thin [(15–)18–24%–30(–41) (n = 28)].

*Chemistry.*—Usnic and protocetraric acids (n = 14).

*Variation.*—More collections are needed to have a good idea of the variability of this species; however, the few specimens collected show remarkable
variability in the thallus appearance. Some specimens are long, appearing depauperate, with conspicuous main branches and few ramifications (Fig. 8a); other specimens are more compact and more or less densely branched with numerous fibrils (Fig. 8b). Intermediate thalli can be found between these two extreme morphotypes.

Taxonomic remarks.—Usnea nashii seems to have a somewhat isolated position in the genus Usnea and does not seem, so far, to have close relatives. Characteristic, unique, and curious at the same time, are the large fibrils producing short isidiomorph-like fibrils at their summit.

Ecology and distribution (Fig. 5).—Similar to Usnea ammannii


Additional specimens examined.—MEXICO. CHIHUAHUA. Cascada de Basaseachic, Herrera-Campos 2454 (MEXU); Sierra Tarahumara, E of San Rafael, Herrera-Campos 3293 (MEXU); El Creel, Herrera-Campos 3203 (MEXU). DURANGO. La Michilúa, Cerro Blanco, 5.12.1992, Zambrano (MEXU)—all paratypes.

Primarily Corticicolous Species, Rarely Collected on Rocks


For a detailed description of the species, see James et al. (1992) and Herrera-Campos and Clerc (in press).

This species is characterized by tuberculate soralia, vitreous cortex, more or less pinkish pigmented and compact medulla, pale base sometimes with a yellowish hue, and production of diffractaic and barbatic acids in the medulla that reacts C+ and CK+ yellow orange. It is rarely found growing on rocks. The specimen cited here was growing on “mostly steep to overhanging northeast-facing sandstone”. In the United States and southern Canada, U. ceratina is reported to have a disjunct distribution in the western and the eastern parts of these countries (Hale 1979). In Mexico, U. ceratina occurs throughout the country except for the most arid parts, from 670 to 4,000 m, mainly on Abies, Quercus, Pinus, Alnus, and Pseudotsuga (Herrera-Campos & Clerc, in press).


6. USNEA CORNUTA Koerber, Parerga Lichenol. 2. 1859, s. lat.

For a detailed description of the species and synonyms, see Clerc (1987a).

Most of the specimens collected on rocks in southern California are here tentatively assigned to this species. They are characterized by small, erect-bushy thalli with constricted branches, and a thin, glossy cortex. The basal part is blackened or not. Soralia are quite variable from minute to enlarged and from even to ± tuberculate, with or without isidiomorphs. The chemistry is quite variable and the following chemotypes have been found 1) salazinic, ± constictic, and ± protocetraric acids; 2) psoromic acid; 3) norstictic, ± salazinic, and ± stictic acids; 4) thamnolic, and protocetraric acids; 5) fatty acids; and 6) protocetraric, and ± psoromic acids.

When a primarily corticolous species occurs on rocks, many distinctive characters (e.g., soralia) can be modified. Since corticolous species of the U. fragilis agg. (incl. U. cornuta) in the western and southwestern parts of North America are poorly understood and need a thorough revision which is outside the scope of this paper, it is difficult to interpret and correctly identify their saxicolous relatives.

Saxicolous specimens examined.—MEXICO. El Chico, Herrera-Campos (chemotypes 1, 3, and 6). U.S.A. CALIFORNIA. SANTA BARBARA CO., Hollister Ranch, Clerc & Hilburn, 19.09.1989, (ο) (chemotypes 1, 2, 4, and 5); Santa Rosa Is., 2.01.1994, Ryan (ASU) (chemotypes 2, and 3); SAN MATEO CO., San Bruno Mountain, Ryan 21986 (herb. Ryan) (chemotype 2). NORTH CAROLINA. ALLEGHANY-WILKES CO., Doughton Park, Dey 556 (DUKE) (chemotype 3); AVERY CO., Grandfather Mountain, Dey 1855, 1856 (DUKE) (chemotype 3); JACKSON CO., Whiteside Mountain, Egan 12566 (MIN) (chemotype 6); MITCHELL CO., Roan Mountain, Dey 2266 (DUKE); TRANSYLVANIA CO., Horsepasture River Gorge, Moore 1674c (DUKE) (chemotype 3).


(Figs. 9, 10, 11)


Morphology.—Thallus shrubby (Figs. 9b, c) to subependent (Fig. 9a), 2–15 cm long, grayish green; branching isotomic- or anisotomic-dichotomous; trunk short (1–3 mm), paler or of the same color as main branches, without conspicuous cracks; branches tapering or irregular; lateral branches often slightly to distinctly narrowed at attachment points; segments terete or slightly ridged, cylindric; apices mostly thin; foveoles absent or present; transverse furrows present; papillae absent; tubercles absent; fibercles present, mainly on main branches, verrucous, low; fibrils 1–2(–3) mm, usually conspicuous, spinulinous (Figs. 10a, b), easily breaking away, usually densely disposed on some parts of the branches, especially close to basal part, rarely on whole length of branches, giving spinulose appearance to this part of thallus (Figs. 9a, 10a); soralia punctiform to slightly elliptic longitudinally (especially on terminal branches), raised, smaller than half diameter of main branches (Fig. 10c) where they mainly arise from fibercles; typically enlarged on apices (Fig. 10d) where they mainly arise on cortex ad initio, and appearing ± fusiform; isidiomorphs occurring on soralia only, not blackened at tips; cortex thin [(2.5–)5–6.5%–8(–13)] (n = 77), foveoles, not conspicuously cracked; medulla large [(13–)21–26.5%–32(–37.5)] (n = 77), compact to dense, perixially pinkish pigmented; axis moderately thick [(14–)24–34%–44(–57)] (n = 77), often pinkish pigmented, thick.

Chemistry.—Usnic, salazinic, norstictic, and galbinic acids (n = 42) or norstictic and salazinic acids (n = 1).

Variation.—The length of the thallus, density of branches, and ramification type are the main sources of variation for this species in North America. However the typical and spinulose fibrils may be sometimes absent or present only on a few short segments of branches. As a matter of fact, these fibrils are in this species most probably efficient propagules, and as such break away quite easily, thus obscuring what is, beside chemistry, the most significant taxonomic character of U. dasaea among the U. fragilens agg. More than 100 specimens from Europe and North America have been analyzed with TLC, and chemistry has been found to be constant. Galbinic acid was absent in only one specimen.

Taxonomic remarks.—The ‘Usnea undulata ag-
gregates’ in East Africa was discussed by Swin-
scow and Krog (1975). They emphasized the diffi-
culty in delimiting species in this group. Especial-
ly difficult was the separation of U. leprosa Motyka from U. undulata Stirr., and they illustrated this by showing a table (Swincock & Krog 1975, Table 2) where ‘transitional and mixed forms of a single population’ were listed. However the characters chosen by Swincock and Krog (inflated branches, lax medulla, and presence of papillae) to separate these two taxa are highly variable, and therefore not relevant in this case. Usnea leprosa, which is a syn-
onym of U. hirta (L.) Wigg. em Motyka (Clerc 1997), differs from U. undulata by soralia, which are minute, numerous, and never enlarged, with a high density of isidiomorphs; lateral branches which are not narrowed at attachment points; and a thinner cortex (4.5%). The chemistry is different as well, but this may not be the case in East Africa. A reinterpretation of all chemotypes given by Swin-
cow and Krog (1975) in the light of the characters mentioned above seems to be necessary. Examina-
tion of the holotype of U. undulata shows that there are no essential differences from U. dasaea, and therefore U. undulata is here considered syn-
onymous with U. dasaea.

The original material of all species cited in the synonymy share the following characters, which are diagnostic for U. dasaea: the same soralia type (Fig. 10 c,d); lateral branches slightly to distinctly narrowed at attachment points; some branches with densely disposed spinulose fibrils on some part of them; a thin and glossy cortex; and salazinic, norstictic, and galbinic acids (except in U. spinigera) in the medulla. The names U. spinulifera and U. spinigera suggest the characteristic numerous spinulose fibrils, which are the main morphological charac-
ter segregating U. dasaea from other species in the U. fragilens agg. Due to its large variability, this species has been described many times, and U. chilenensis Motyka, U. feeeana Motyka, U. filamentosa Motyka, U. furfuroula (Zahlbr.) Motyka, U. spilotoideus Dodge, and U. strigosella Steiner are probable synonyms of U. dasaea.

Specimens with red pigment in the medulla have been collected in Florida. The first author will dis-
cuss them in a future paper dealing with the species from the eastern part of the United States.

Usnea dasaea is closely related to U. amblyoclada, and they differ morphologically mainly through their different types of soralia and isidiomorphs. When fibrils are absent and soralia not well developed, this species is difficult to separate from U. cornuta without the help of TLC (galbinic acid in U. dasaea). In Europe, this species has not been well understood and has been confused with U.
cornuta (Hawksworth et al. 1980; Motyka 1936–38).

Distribution and habitat.—As indicated by the list of synonyms this mainly corticolous species is distributed worldwide. Usnea dasaea is mentioned here for the first time to North America, South America, Africa, and Asia. Australasia is the only region from which we have not seen specimens. In North America (Fig. 11) and in Europe, U. dasaea has a scattered distribution, mainly in the southern part of the continents.

Selected specimens examined.—Saxicolous: MEXICO, CHIAPAS. San Cristobal de las Casas, Herrera-Campos 3070 (MEXU). CHIHUAHUA. Sierra Tarahumara, Herrera-
Figure 10. Usnea dasaea. — a. Branch with spiny fibrils, Culberson 6152 (DUKE). — b. Close up of spiny fibrils and idiomorph-like fibrils, Culberson 6152 (DUKE). — c. Branch with more or less minute soralia, Culberson 4865 (DUKE). — d. Branches with large soralia, Culberson 4865 (DUKE). Scale bars = 1 mm.


For a detailed description of the species, see Clerc (1997) and Herrera-Campos and Clerc (in press).

Rarely found on rocks, this species is well characterized by a pendulous thallus, cylindric branches with distinct annulation close to the basal part, the absence of papillae, long and curved fibrils, a mat cortex, minute pseudocyphella-like soralia which may enlarge and bear isidiomorphs, and protoconiaric acid in the medulla. The distribution of *U. hesperina* in Mexico is treated by Herrera-Campos and Clerc (in press).

*Saxicolous specimens examined.*—U.S.A. NORTH CAROLINA. BATH CO., Shenandoah Mountains, Clerc 88/63 (g); BUNCOMBE CO., vicinity of Montreat, Standley & Bollman 10146 (US); HAYWOOD CO.—JACKSON CO., Richland Balsam Mountain, Egan 12431 (MIN); SWAIN CO., Blue Ridge Parkway, Clerc 89/715 (g).


For a detailed description of the species, see Clerc (1994).

The minute soralia with isidiomorphs, pale base, lateral branches that are not narrowed at attachment points, absence of papillae, wine red pigment in the medulla, thin, shiny cortex, and the chemistry (fatty acids of the murolic acid group) make this species distinct among other taxa in the genus. *Usnea mutabilis* is morphologically and chemically closely related to *U. hirta*. Unpublished data from the first author show that *U. mutabilis* is one of the most frequent corticolous *Usnea* species on lowlands in the eastern United States and that it is much rarer in the western part of the country. *Usnea mutabilis* is rarely found on sandstone.


For a detailed description of the species, see James (1979) and James et al. (1992).

Easily distinguished by the reddish pigmentation of the cortex (especially close to the basal part of...
the thallus), pale trunk, soralia with numerous isidiomorphs, and chemistry (stictic, ± constictic, ± norstictic acids or salazinic, norstictic, and ± constictic acids), this species can be found only rarely on rocks. *Usnea rubicunda* is morphologically extremely variable.


For a detailed description of the species, see Clerc (1992) and Herrera-Campos and Clerc (in press).

*Usnea subscabrosa* is a conspicuous species. The main diagnostic characters are the thick and vitreous cortex, minute soralia with or without isidiomorphs, pale trunk often with a reddish hue, and chemistry (protocetraric acid). Morphologically, it is variable with shrubby to pendulous growth forms. In the United States, it is found only in the eastern part where it sometimes occurs secondarily on rocks. In Mexico, it is found throughout the country, between 1,300 and 1,400 m, mainly on *Pinus, Quercus*, and *Abies* (Herrera-Campos & Clerc in press).

*Saxicolous specimens examined.—*U.S.A. NORTH CAROLINA. DADE CO., Lookout Mountain, Clerc 88/260 (G); SWAIN CO., Blue Ridge Parkway, Clerc 89/714 (G).


For a detailed description of the species, see Clerc (1984b) and Clerc and Diederich (1991).

Since its first discovery in North America (Clerc & Diederich 1991), this species has been found many times in the northern part of the western coast, especially in British Columbia (Halonen et al., in press). The saxicolous specimens collected for the first time by B. Ryan on Santa Barbara Islands agree well with the main characteristics of *U. wirthii* i.e., the yellow pigment in the medulla and axis, the small-sized thalli (1–4(–6) cm), pale trunk, constricted branches at ramification points, red spotted cortex, and chemistry (norstictic acid chemotype). Only the soralia are somewhat different as they fuse together and cover the extremities of the branches as in *U. esperantiana* P. Clerc (Clerc 1992); this might be, however, an effect of the saxicolous habitat.

*Saxicolous specimens examined.—*U.S.A. CALIFORNIA.

SANTA BARBARA CO., Santa Rosa Island, Ryan 31090 (hb. B. Ryan).

**Excluded Species**


Because the original material of this species was collected on rocks, Motyka (1936–38) considered this taxon as being exclusively saxicolous. However, as stated by Clerc (1987a), *U. diploypus* is mainly a corticolous taxon growing secondarily, and rarely on stone. Based on specimens collected on rocks, Thomson (1956) reported this species new for North America. Later, Hale (1958) examined the type material of *U. diploypus* and rejected the use of this name for North American *Usnea* population growing on rocks. Indeed, Hale was right, and the saxicolous material of North American *Usnea* does not correspond with *U. diploypus*. This species has a trunk which is often black pigmented; minute soralia with numerous isidiomorphs; verrucous to cylindrical papillae; and salazinic, ± barbatic acids, or alectorial acid in the medulla. In North America, *U. diploypus* has been found to occur on trees in British Columbia in Canada (Halonen et al., in press). All collections cited by Wetmore (1976) as *U. diploypus* are most probably *U. amblyocladia* with galbinic acid, and not stictic acid as mentioned here. Specimens cited by Dey (1978) under *U. diploypus* are *U. cornuta* and *U. halei*.


It is not possible from the description given by Hale (1979) to decide whether this taxon corresponds to *Usnea halei* or to *U. amblyocladia*. Most herbarium specimens identified as *U. herrei* belong either to *U. halei* or to *U. amblyocladia*.


This name was used the first time for saxicolous North American *Usnea* by Motyka who identified a population collected on sandstone cliffs in Arkansas and distributed by M. E. Hale in his American Exsiccata (Hale 1956). Later Hale (1958) and Wetmore (1976) expressed some doubts about this concept. Dey (1978), in his study of the lichens of the Southern Appalachians, restricted the use of *U. subfusca* to corticolous specimens of the *U. strigosa* agg. producing salazinic acid in the medulla which is not pigmented. He was followed by Hale (1979). *Usnea subfusca* is indeed a corticolous species whose distribution is so far restricted to eastern North America. This species belongs to the *U. florida* agg. sensu Fiscus (1972), a group of sexually reproducing *Usnea* with numerous
and conspicuous apothecia. This group needs a thorough revision which is under way. Preliminary results show, however, that this species is not closely related to the *U. strigosa* agg. It differs from the latter by its black base, mat cortex, large papillae, and chemistry (salazinic acid).

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**LITERATURE CITED**


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