UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

FACULTAD DE CIENCIAS

DIVISIÓN DE ESTUDIOS DE POSGRADO

REVISIÓN SISTEMÁTICA DEL GÉNERO USNEA HILL 1753 EN MÉXICO

T E S I S

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTORA EN CIENCIAS (BIOLOGÍA)

P R E S E N T A

MARÍA DE LOS ÁNGELES HERRERA CAMPOS

DIRECTORA: DRA. PATRICIA DOLORES DÁVILA ARANDA

CO-DIRECTOR: DR. THOMAS HAWKES NASH III

1998

INDICE

INTRODUCCIÓN 1

1.- Antecedentes 2

2.- Clasificación del género Usnea (Ascomiceto liquenizado) 5

3.- Delimitación del género Usnea 9

4.- Caracteres diagnósticos 11

5.- Concepto de especie 13

6.- Distribución y ecología 19

MÉTODOS Y MATERIALES 20

RESULTADOS

1.- Especies péndulas de Usnea de los bosques templados México 23

2.- Especies saxícolas de Usnea (ascomiceto liquenizado) subgénero Usnea en Norteamérica 77

3.- El complejo Usnea fragilescens en México 119

4.- Agregado Usnea subfloridana-Usnea madeirensis 180

5.- Especies pigmentadas de Usnea 189

6.- Agregados de especies fértiles de Usnea 196

CLAVE 200

DISCUSIÓN 211

LITERATURA CITADA 213

A mis hijos, Gaby y Alex

AGRADECIMIENTOS

Agradezco profundamente la participación de mi comité tutorial durante el proceso de aprendizaje que llevó a la elaboración de esta tesis: Dra. Patricia Dávila Aranda, Dr Thomas H. Nash III, Dr.Teófilo Herrera y Dra. Adela Rodríguez.

Por la revisión y corrección del manuscrito agradezco al jurado integrado por el comité tutorial, el Dr Claudio Delgadillo, el Dr. Miguel Ulloa y el Dr. Joaquín Cifuentes. En esta revisón también se agradece la colaboración del Dr. Philippe Clerc y el M.en C. Angel Zambrano.

Particularmente, quiero agradecer a la Dra. Patricia Dávila por apoyarme durante las etapas iniciales de este proyecto proporcionando la infraestructura necesaria para los viajes de campo.

Al Dr. Thomas Nash III le agradezco profundamente su continua preocupación en mi formación académica en la liquenología. Muchas gracias por su incansable búsqueda de los fondos necesarios para la realización de este proyecto, y por compartir su rica experiencia en diferentes aspectos de la liquenología.

Al Dr. Philippe Clerc expreso especial agradecimiento por su dedicación, y asesoría en la revisión e identificación de los ejemplares, así como por las múltiples discusiones que hemos sostenido durante los últimos años.

Muchas gracias a Gabriel Flores, Ismael Calzada y Antonio Salinas por su apoyo durante el trabajo de campo. La ayuda de Robin Schramm, Jennifer Biringer y Travis Robbins fue clave durante la fase final del análisis químico de los ejemplares.

A mis compañeros del Laboratorio de Liquenología de ASU: Bill Davis, Connie Klimczack, Steve Goldsmith, Joanne Rogmanii y Angel Zambrano les doy las gracias por sus comentarios y sugerencias. A Mike Thomas por su valiosa ayuda al comienzo de mi trabajo, particularmente con la cromatografía en capa fina. A la Dra Corina Gries le agradezco el compartir conmigo su entusiasmo y experiencia en el manejo de bases de datos. A Bruce Ryan por sus interesantes y formativas charlas, por su disposición continua a responder a mis incontables preguntas sobre líquenes y referencias bibliográficas.

Gracias a mis amigas. A Janet Marsh su constante hospitalidad, sus enseñanzas en el campo, y su continua disponibilidad para ayudar académica y extra académicamente. A

Beth Kantrud, gracias por enseñarme el arte de curar líquenes, por ayudarme en la identificación de los mismos y por revisar mis manuscritos.

A Sara Krichheimer expreso especial gratitud por las innumerables horas de apoyo incondicional y constante en el trabajo cotidiano con la computadora, en la elaboración de tablas, de gráficas, revisión de manuscritos, y en elaboración y manejo de bases de datos, por el soporte personal que siempre me brindó, todas las cenas, charlas y apoyo económico. MUCHAS GRACIAS, SARA.

A Stephie Bond, Kathleen Pigg y a Barb Backes por su colaboración en el trabajo fotográfico.

Al Dr. Kenneth Hoober y a Lynda Krygers agradezco su diligencia y atención durante los procesos burocráticos, siempre presentes, siempre interminables. Su responsible y dedicada labor contribuyeron de manera importante a mi buen desempeño como miembro del Plant Biology Department de ASU.

A la Sra. Ana Eugenia Campos y al Sr. Faustino Parra, mis padres, les doy las gracias por haberse encargado de la titánica tarea de cumplir con los trámites burocráticos nacionales necesarios para la defensa de esta tesis y la obtención del grado, sin su ayuda....no quiero ni pensarlo!

El apoyo financiero para la realización de este proyecto es agradecido a CoNaCyT a través de una beca de doctorado, a PADEP-UNAM que hizo posible la mayoría de los viajes de campo y la adquisición de material básico de laboratorio, a la NSF, a través del financiamiento asignado al proyecto Lichen Flora of the Sonoran Desert, encabezado por el Dr. Thomas Nash III.

RESUMEN

Este trabajo es el primer estudio sistemático de líquenes realizado en México y tiene como objetivo principal la revisión del género Usnea de los bosques templados del país, la cual comprende la descripción de especies y su distribución y la elaboración de una clave para su identificación.

Se llevó a cabo una extensa recolección en los bosques templados de diferentes estados del país localizados en distintas provincias fisiográficas: a) Provincia del Eje Neovolcánico Transversal (Colima, Michoacán, Estado de México, Distrito Federal, Tlaxcala, Puebla, Hidalgo y Veracruz), b) Sierra Madre Occidental (Chihuahua, Sinaloa, Durango y Nayarit); c) Sierra Madre Oriental (Nuevo León, Tamaulipas y San Luis Potosí); d) Sistema Montañoso de Baja California (San Pedro Mártir, Baja California, Sierra de la Laguna, Baja California Sur); e) Sierra Madre del Sur (Guerrero); f) Sistema Montañoso del Norte de Oaxaca (Oaxaca) y g) Macizo Central de Chiapas (Chiapas).

Además del material colectado, se estudiaron ejemplares de herbario de diferentes instituciones nacionales y extranjeras, lo que representa un total aproximado de 2700 ejemplares analizados morfológica, anatómica y químicamente.

Se describen cuarenta y tres especies y cuatro agregados. Cinco son especies nuevas: U. ammannii P. Clerc y Herrera-Campos, U. halei P Clerc, y U. nashii Clerc, Herrera-Campos Usnea santaritae Clerc y Herrera-Campos y U. vitrea Clerc y Herrera-Campos. Diez son nuevos registros para México: U. brasiliensis (Zahlbr.) Mot., U. cornuta Koerb.s. str., U. esperantiana Clerc, U. fragilescens Lynge var. mollis (Vainio) Clerc, U. jamaicensis Ach., U. malmei Motyka., U. ramillosa s. str.Mot.,.U. scabrata Nyl., s. lat., U. subcabrosa Nyl. ex Motyka, U. wirthii Clerc y dos son nuevos registros continentales: U. goniodes (Stirt.) Mot. y U. sanguinea Swinscow y Krog.

Se proponen las siguientes sinonimias: U. amblyoclada (Müll. Arg.) Zahlbr (Syn. nov. U. globularis Mot.), U. ceratina Ach. (Syn. nov. U. solida Motyka.), U. dasaea (Syn. nov.

U. dolosa Mot., U. galbinifera Asah., U spinigera Asah , U. spinulifera (Vain.) Mot., U. undulata Stirt.), U filipendula Stirton (Syn. nov. U. sublaxa Vain. ex Motyka.), U. himantodes (Syn. nov. U. sericea Motyka.), U. malmei Motyka (Syn. nov. U. sorediata (Zahlbr.) Motyka) y U. mexicana Vainio (Syn. nov. U. duriuscula Motyka).

Los resultados obtenidos se presentan como descripciones, mapas de distribución y claves de identificación. Con esta información se ha integrado una base de datos sobre el género en México.

INTRODUCCIÓN

Entre los macrolíquenes fruticosos el género Usnea es uno de los grupos más fácilmente reconocibles; pero su sistemática a nivel de especie se ve complicada por su amplia variación morfológica. Desafortunadamente, son pocos los trabajos que se ocupan de la sistemática de este género, permaneciendo como fundamental la monografía de Motyka (1936-1938) El período moderno del estudio del género está caracterizado por la observación de las poblaciones en su ambiente natural, sin depender únicamente de las colecciones de los herbarios y por el desarrollo y empleo de técnicas modernas de análisis (Clerc 1991).

En el estudio sistemático del género Usnea la especie se define como una combinación única de caracteres morfológicos, anatómicos y químicos, más que por la ausencia o la presencia de los mismos, por lo que en este trabajo se describe dicha combinación para cada una de las especies estudiadas.

El objetivo principal de esta disertación es la revisión del género Usnea en México, la cual comprende la descripción de especies y su distribución, así como la elaboración de la clave para su identificación.

Los objetivos particulares son.

- Definir los caracteres taxonómicos diagnósticos.
- Elaborar un listado florístico de las especies o agregados del género Usnea en México.

Esta disertación responde a la necesidad de generar información básica acerca de las especies de líquenes mexicanos que facilite la realización de diferente tipo de estudios acerca de estos organismos.

Finalmente, esta tesis permite continuar con los trabajos de organización general de la colección liquénica del Herbario Nacional MEXU y es de utilidad para impulsar el intercambio con otros herbarios nacionales y extranjeros y promueve la formación académica en una área de la biología en la cual se requieren especialistas nacionales

1.- Antecedentes

Son pocos los trabajos que se ocupan de la sistemática del género, permaneciendo como fundamental la monografía de Motyka (1936-1938) y diversos estudios de carácter particular que se mencionarán a continuación.

En el "Lichenum Generis Usnea Studium Monographicum" (Motyka 1936-1938) se describen 451 especies de distintas partes del mundo y representa el primer estudio taxonómico exhaustivo del género. Sin embargo, es una publicación de difícil manejo debido a que se basa en caracteres extremadamente polimórficos como el color y la longitud del talo, la densidad de la ramificación, el desarrollo y la densidad de las fibrillas, forma de la papilas y presencia de foveolas, así como el grosor y crecimiento de los ápices. Sin un tratamiento pleno de la variación infraespecífica, Motyka reconoce como nuevas especies a morfotipos con suficientes diferencias exteriores (Clerc 1991; Jørgensen 1977; Swinscow y Krog 1979). Aunque en 1947 Motyka discute algunos de los caracteres considerados al asignar las especies a distintas secciones, no profundiza acerca de su variabilidad

Asahina (1956) describe morfológica, anatómica y químicamente 38 especies, 17 subespecies, 7 variedades y 13 formas de usneas japonesas, pero las arregla de acuerdo a su semejanza morfológica, siguiendo el esquema de Motyka (1936-1938).

Según Clerc (1991), el período moderno del estudio del género está caracterizado por la observación de las poblaciones en su ambiente natural, además de las colecciones de herbaio, y por el desarrollo y empleo de técnicas modernas de análisis. Así el estudioso puede definir mejor los caracteres propios de cada especie al aproximarse a las modificaciones fenotípicas de los individuos de una misma especie expuestos a condiciones ambientales variables.

El tratamiento sistemático y moderno del género se inicia realmente con los trabajos de Swinscow y Krog (1974-1979), quienes revisan los caracteres diagnósticos del género, registran y describen algunas especies de los subgéneros Eumitria y Usnea, colectadas en el este de África. Aportan claves, descripciones de nuevas variedades, sinonimias y enmiendas o adiciones a complejos como U. undulata Stirton, U. bornmuellerii Steiner y U. articulata (L.) Hoffm., entre otros.

Krog (1976) segrega del género Usnea los subgéneros Lethariella y Protousnea y los trata como géneros independientes basándose en su distribución, morfología, anatomía y química. Además presenta una diagnosis de las especies que los integran

Walker (1985) realiza la revisión taxonómica mundial de Neuropogon conservándolo como un subgénero de Usnea.

Por otra parte, el estudio del género en Europa ha sido realizado por Clerc (1984a, b, 1987 a, 1991, 1992), quien describe y discute la ecología, la distribución, la variabilidad y los cambios nomenclaturales de complejos como U. florida (L.) Wigg. emed. Clerc y U. fragilescens Havaas ex Lunge y especies como U. madereirensis Mot. y U wirthii Clerc (Clerc 1984b, Clerc y Diedrich 1991), proporcionando claves para identificar las especies estudiadas en regiones como Escandinavia y las Islas Británicas.

Rogers y Stevens (1988) realizan la descripción morfológica de dos especies del complejo U baileyi (Stirton) Zahlbr. en Australia, mismas que no presentan aparentemente diferencia alguna, sin embargo, encuentran que tienen diferentes compuestos químicos representantes de vías biosintéticas separadas.

Stevens (1991a) discute el origen y la distribución de especies de los géneros Ramalina y Usnea, relacionándolas con la paleogeografia de sus forofitos. Presenta la distribución mundial conocida para las especies estudiadas y establece que las verdaderas especies tropicales son las que crecen a bajas altitudes en los trópicos porque siguen principalmente la distribución de los manglares o crecen en forofitos de origen tropical. En contraste, concluye que las especies de regiones montañosas frías y nubladas se originaron en la Antártida asociadas con fanerógamas como Araucaria y Nothofagus.

Stevens (1991 b) describe una nueva especie endémica de Australia, U. elixii Stevens, con un continuo de morfos desde talos fértiles a únicamente isididados conteniendo ácido protocetrárico. Sin embargo, esta especie comparte semejanzas morfológicas con U. albomaculata Moy y U. submollis Steiner de África, aunque se distinguingue en la química y el hábito de crecimiento.

Stevens (1992) estudia la variación morfológica, anatómica y química de cinco especies del complejo U. scabrida-U. molliuscula y la considera como respuesta al clima. En este sentido, establece que cuando morfos similares coincieden en diferentes regiones geográficas con regímenes climáticos distintos, se trata de subespecies que se intergradan en un grupo de amplia distribución y cuya separación se basa más en una división geográfica que en diferencias morfológicas o químicas. Con este esquema, Stevens propone cambios nomenclaturales por sinonimia y reducción de varias especies a subespecies.

Entre los trabajos de índole nomenclatural podemos citar a James (1979), Awasthi (1985), Awasthi y Awasthi (1985), y Stevens (1990); este último incluye aspectos de la distribución mundial de U. himantodes Stirton.

Siguiendo el esquema planteado por Swinscow y Krog (1974-1979), Awasthi (1986) describe 54 especies de Usnea, subgéneros Eumitria y Euusnea de India, establece sinonimias y reporta varias especies nuevas. Discute detalladamente los caracteres diagnósticos incluyendo comentarios de orden evolutivo y agrupa las especies de cada subgénero, atendiendo en primera instancia a la naturaleza del eje central y al patrón de ramificación. Incluye claves y amplias descripciones que contemplan también la distribución.

Por otra parte, Hale (1962) reconoce la importancia del análisis químico en el entendimiento de la variación en el género al estudiar las razas químicas de U. strigosa (Ach.) A. Eaton.

Fiscus (1972) identifica por cromatografía en capa fina 17 constituyentes químicos en 13 combinaciones distintas de 358 ejemplares del grupo U. florida en Norteamérica.

Dey (1978) estudia los líquenes de los Apalaches del Sur y presenta una clave para reconocer las 10 especies de Usnea colectadas, pero enfatiza que, dadas las características del género, varias de ellas pueden representar en realidad complejos de especies. Así pues, menciona U. subfusca Stirt., U. strigosa (Ach.) A. Eat., U. ceratina Ach., U. subfloridana Stirt., U. hesperina, Mot., U. diplotypus Vain., U. confusa Asah., U. mollis Stirt., U. fulvoreagens (Räs.) Mot., y U. trichodea Ach.

Basándose en la presencia de ácido lecanórico, Culberson et al. (1983) describen una nueva especies , U. lecanorica Culb., Culb. y Fiscus, colectada en el Estado de México.

Tavares (1987) en su trabajo sobre las especies del complejo U. strigosa en el este de Estados Unidos, compara U. florida var. major Michx., U. florida var. intermedia Michx. y U. florida var. rubiginea Michx. con U. strigosa (Ach.) A. Eaton, U. tristis Mot. y U. evansii Mot., y establece dos nuevas combinaciones y un nuevo nombre, U, michauxii, sinónimo de U florida var. intermedia Michx Posteriormente, en 1998, presenta una clave preliminar para identificar las especies de Usnea de California.

Carlin (1986) al analizar las razas químicas de U. lapponica Vain. y U. glabrescens (Nyl.) Vain. en Suecia, cuestiona el valor taxonómico de aquellas sustancias liquénicas que difieren sólo en el grado de oxidación, bajo la suposición de que éste puede deberse más a un estado metabólico que afecte la actividad enzimática del liquen que a diferencias genéticas.

Desde 1979 Czeczuga ha considerado el contenido de carotenos de los talos en estudios taxonómicos y trabaja con especies de los géneros Cornicularia, Evernia, Ramalina y Usnea, continuando los trabajos de Czeczuga y Osorio (1989) con Concamerella fistulata (Taylor) W. Culb. Y C. Culb., U amaliae Mot. y U. densirostra Tayl. y de Czeczuga y Richardson (1989) con Menegazia terebrata (Hoffm) Massal. y U. rubicunda Sirt.

Finalmente, sobre el género en cuestión, en México sólo se cuenta con el trabajo de Guzmán y González de la Rosa (1976) quienes presentan una lista de las especies o formas infraespecíficas de origen mexicano que aparecen descritas en la monografía de Motyka (1936-1938) e incluyen los datos de los herbarios donde se encuentran depositadas.

Por otra parte, Gibert (1935) cita, entre otras especies, once para el género presentes en el Valle de México.

2.- Clasificación del género Usnea (Ascomiceto liquenizado)

Desde el punto de vista sistemático, los líquenes son hongos especializados al igual que los que forman micorrizas (Tehler 1996). Su integración en la clasificación fúngica, principalmente en los Ascomycetes, ocurrió recientemente con su inclusión como hongos liquenizados en el Index of Fungi y el Dictionary of the Fungi en 1971. En el Código de Nomenclatura Botánica (1981) ya no son tratados como un grupo separado y en el trabajo de Erikson y Hawksworth (1983-91), se logra concenso entre micólogos y liquenólogos sobre una clasificación general de Ascomycetes liquenizados y no liquenizados (Tehler 1996; Lutzoni y Vilgalys 1995 a, b).

De acuerdo al desarrollo del cuerpo fructífero, se dintinguen dos grupos principales de Ascomycetes· ascohimeniales y ascoloculares, y unitunicados y bitunicados de acuerdo con la presencia de una o dos capas funcionales en las ascas. En el cuerpo fructífero ascohimenial las ascas se forman a patir de un himenio verdadero con paráfisis verdaderas que se desarrollan del tejido basal, mientras que en el ascolocular el desarrollo de las ascas se lleva a cabo en lóculos de un ascostroma preformado que presenta hifas interascales conocidas como parafisoides y pseudoparáfisis formados a partir del tejido del ascostroma (Tehler 1995 a, b, 1996)

El Orden Lecanorales es un taxón cosmopolita que crece en diferentes tipos de sustratos. Representa el orden más grande de euascomicetes, integrado casi en su totalidad por ascomicetes liquenizados, algunas especies son parásitas de líquenes y muy pocas son saprobias. Los talos, según sus formas de crecimiento, pueden ser costrosos, foliosos o fruticosos. Los fotobiontes son principalmente algas verdes unicelulares, comúnmente Trebouxia presente en líquenes más avanzados, aunque también se presentan cianobacterias como fotobiontes asociados (Poelt 1973, Hale 1983, Tehler 1996).

De acuerdo con Poelt (1973) y Tehler (1996), el orden Lecanorales es un grupo muy heterogéneo integrado por líquenes que presentan apotecios de desarrollo ascohimenial, solitarios, con disco redondeado y abierto; paráfisis a menudo con puntas engrosadas; ascas bitunicadas con dehiscencia rostrada, típicamente rostradas, amiloides, I + conspicuamente azul y de paredes gruesas.

Este orden es un grupo parafilético definido por las características de las ascas, sin embargo, estudios recientes de la subunidad del ADN ribosomal en Lecanora, Lecidea y Cladonia apuntan a un origen monofilético (Tehler 1996).

En el suborden Lecanorinaeae el apotecio es biatorino o lecideíno, con margen talino. Las paráfisis son libres, simples, ramificadas o están formando una red. Las ascas presentan un tolus al menos parcialmente I + azul y un cuerpo axial en un rostro apical, sin estructura en forma de capucha; 8 ascosporas por asca, a veces más, hialinas unicelulares, algunas veces bi- o multi-septadas o muriformes, ocasionalmente pigmentadas (Poelt 1973, Tehler 1996).

Es a nivel de familia donde los autores difieren en torno a la posición de Usnea y géneros relacionados. Los caracteres que se interpretan de manera diferente son la forma de crecimiento, la simetría de los talos, la anatomía de la corteza y la distribución geográfica.

Poelt (1973) reconoce dentro de los Lecanorales, entre otras, dos familias altamente heterogéneas. Parmeliaceae y Usneaceae. La primera agrupa líquenes principalmente foliosos, dorsiventrales, bicorticados, con rizinas en la corteza inferior (rara vez ausentes o raducidas), pocos umbilicados, con apotecios ocasionalmente hundidos, más comúnmente laminares, pero también se observan marginales, las ascas con tolus amiloide; las ascosporas pequeñas, rara vez largas; fulcra con células moderadamente largas; conidios cortos baciliformes, rara vez largos y filamentosos. Comprende a los géneros Asahinea, Cetraria, Nephromopsis, Cetrelia, Dactylina, Omphalodium, Pannoparmelia, Parmeliopsis y Plastismatia.

La familia Usneaceae está caracterizada en el esquema de Poelt (1973) por líquenes con talo fruticoso que varía de erecto a péndulo, usualmente pigmentados, con simetría radial, algunas veces dorsiventral; la médula a menudo es laxa, atravesada longitudinalmente por uno o varios cordones; apotecios lecanorinos constrictos, sésiles, laterales o terminales; las esporas unicelulares y hialinas, rara vez muriformes Comprende a los géneros Alectoria, Evernia, Everniopsis, Himantormia, Letharia, Neuropogon, Oropogon, Sulcaria y Usnea. Reconoce que la familia no es homogénea y plantea la posibilidad de la segregación de géneros como Alectoria, Bryopogon, Oropogon y Sulcaria en una familia independiente.

Por su parte, Hale (1983) reconoce tres familias: Alectoriaceae, Parmeliaceae y Usneaceae. La familiaAlectoriaceae está integrada por géneros con talos de simetría radial, sin cordón central, con apotecios lacanorinos con excípulo propio bien desarrollado, 2-4 ascosporas hialinas o cafés por asca, de simples a muriformes. Son principalmente cortícolas y terrícolas y crecen en regiones árcticas templadas y tropicales montañosas. Comprende a los géneros. Alectoria, Bryoria, Coelocaulon, Cornicularia, Pseudephebe y Sulcaria. De acuerdo con este autor, Parmeliaceae es la familia más grande y más colectada entre los líquenes foliosos. Es una familia cosmopolita, con especies cortícolas y saxícolas. Los talos son foliosos y dorsoventrales, con rizinas (excepto en Asahinea); psedocifelados, con epicorteza; los apotecios son lecanorinos y las esporas son unicelulares y hialinas. Compende a los géneros Asahinea, Bulbotrix, Cetraria, Cetrariastrum, Cetrelia, Esslingeriana, Foraminella, Hypotrachyna, Masonhalea, Melanelia, Neofuscelia, Parmelia, Parmelina, Parmeliopsis, Parmotrema, Platismatia, Pseudevernia, Punctelia, Relicina, Tuckermanopsis y Xanthoparmelia.

Finalmente, para Hale, la familia Usneaceae se relaciona con Parmeliaceae por la ontogenia de los apotecios, pero difiere en la simetría radial del talo, a veces ligeramente dorsiventral, y por la presencia frecuente de cordones medulares. Sin embargo, los apotecios también son lecanorinos y las esporas también son unicelulares y hialinas. Comprende a los géneros Dactylina, Evernia, Letharia, Neuropogon y Usnea.

De acuerdo con Krog (1982), la familia Parmeliaceae está delimitada principalmente por las características de los apotecios y los conidios, aunque a nivel de género los apotecios ofrecen pocos rasgos útiles, ya que la mayoría presentan discos simples morenos o negros y ocho esporas por asca. Sin embargo, considerando otros caracteres (anatomía de la corteza, simetría y presencia de tejido de soporte) se pueden reconocer cuatro grupos principales de géneros, a saber: hypogymnioides y parmelioides/cetrarioides que son foliosos y dorsiventrales; alectorioides y usneoides ambos con talos fruticosos y radiales, rara vez dorsiventrales.

Entre los parmelioides *sensu lato* las diferencias en la anatomía de la corteza superior separa a los estrictamente parmelioides de los parmotremoides. Los primeros (igual que los cetrarioides) presentan una corteza paraplenctenquimatosa sin epicorteza, mientras que en los parmotremoides la corteza es plectenquimatosa con una epicorteza con poros.

Los líquenes cetrarioides y los parmeliáceos se distinguen por la posición de los picnidos en el talo, son marginales en los primeros y laminares, con algunas excepciones, en los segundos (Krog 1982) En Usnea, no se ha puesto atención a estas estructuras, sin embargo, en algunas especies se han observado picnidios, pigmentados o no, en las puntas de las ramas terminales.

En la familia Parmeliaceae se reconocen diferentes tipos de conidios con algunas variantes: bifusiforme, sublageniforme, unciforme y filiforme La forma de los conidios se relaciona con las características que definen a los géneros en la familia. Por ejemplo, Usnea, así como algunas especies de Parmotrema y Platismatia, presenta conidios sublageniformes (hinchados cerca de un extremo) de 5 a 8 μm de largo.

Los líquenes alectorioides y usneoides se distinguen de los parmelioides por la presencia de un tejido de soporte, y entre ellos, por la posición de dicho tejido en el talo, el cual en los alectorioides se localiza periféricamente, mientras que en los usneoides es central o interno con respecto a la capa algal.

Krog (1982) considera que las esporas pigmentadas, septadas o muriformes y en número menor a ocho por asca en los alectorioides, los separan de los parmeliáceos -incluyendo los usneoides- en los que las esporas son hialinas, simples y ocho por asca. Por ello, excluye los géneros alectorioides de la familia Parmeliaceae y los incluye en la familia Alectoriaceae. No reconoce la familia Usneaceae por considerarla artificial y deja a los usneoides como parte de Parmeliaceae, con base en la producción de 8 esporas simples hialinas por asca y el tipo de conidios.

Tehler (1996) define las características de Parmeliaceae y Alectoriaceae de la siguiente manera. La familia Parmeliaceae tiene talo folioso o fruticoso, ascocarpo con margen talino, excípulo con hifas anticlinales y anastomosadas e incluye, además de los géneros foliosos, a Usnea, Evernia, Letharia y Lethariella. Éstos fueron considerados por Poelt (1973) como parte de Usneaceae que incluía a los alectorioides, y por Hale (1983) como Usneaceae, familia independiente de Alectoriaceae.

La familia Alectoriaceae comprende líquenes con talo fruticoso, ascas grandes fuertemente amiloides; parafisoides anastomosadas, ascosporas aseptadas, largas y pigmentadas y con perisporio hialino; son cortícolas o saxícolas y comprende a los géneros Alectoria, Oropogon y Sulcaria, los cuales eran parte de Usneaceae (Poelt 1973) y de Alectoriaceae (Hale 1983).

3.- Delimitación del género Usnea

Motyka (1936-1938) en su monografía mundial del género incluye todos aquellos parmeliáceos con cordón central y los sudivide en subgéneros y secciones.

Los subgéneros son Protousnea, Neuropogon, Lethariella, Chlorea, Eumitria, Euusnea (=Usnea s. str.). Euusnea está dividido en varias secciones:

Foveatae, Articulatae, Barbatae, Setulosae, Elongatae, Straminae, Glabratae, Dendriticae y Laevigatae.

Sin embargo, dicha división agrupa especies muy disímiles en una misma sección y no explica las relaciones entre ellas. Además, fue hecha con base en caracteres que resultaron imposible de aplicar prácticamente, como el cambio de color de los ejemplares en el herbario, el cual ocurre en ocasiones después de varios años.

Algunos de estos subgéneros han sido segregados de Usnea y erigidos como géneros independientes. La subdivisión de Usnea en secciones no ha resultado de utilidad en la taxonomía del género, por lo tanto, no se presenta discusión alguna al respecto.

Con base en características apoteciales de color y pruinosidad, relacionadas con las tendencias químicas y de distribución, Krog (1976, 1982) segrega a Protousnea y Lethariella como géneros independientes y Chlorea como subgénero de Lethariella, confirma a Neuropogon como género independiente cercano a Usnea s. str.

Usnea s. str. tiene apotecios discoides de color claro y pruinosos; Neuropogon y Lethariella tienen disco opaco de café a negro, en Letharia y Protousnea el disco es brillante de café a café obscuro. En Usnea s. str., Letharia y Neuropogon el excípulo talino presenta fibrillas, mientras que en Lethariella y Protousnea carecen de ellas. En todos estos géneros las esporas presentan muy poca variación; son simples, hialinas, subglobosas o elipsoides cortas, ocho por asca de 3-5 X 5-8 µm, ligeramente más largas en Usnea s. str.

Algunos ejemplares fértiles de Protousnea y Letharia presentan picnidios negros; Usnea y Neuropogon tienen picnidios con aberturas claras y en Lethariella no son conocidos.

El eje central muestra considerable variación entre estos géneros y en los subgéneros de Lethariella. En Usnea subgen. Usnea, Protousnea y Lethariella subgen. Nipponica el eje es sólido y elástico. En Eumitria el eje es tubular, total o parcialmente hueco, o sólido con fisuras longitudinales, flexible o rígido. En Neuropogon y Lethariella subgen. Lethariella el eje central es parecido a Eumitria. En Lethariella subgen. Chlorea consiste de tejido condroide atravesado ocasionalmente por fibras longitudinales de pseudoparénquima hifal localizadas hacia el centro del eje, el cual es de diámetro variable, aunque regularmente muy grueso, flexible a rígido, no elástico, tubular en las partes basales y sólido en el resto del talo.

En Usnea y Neuropogon las papilas, pseudocifelas y fibrillas son comunes, pero Lethariella y Protousnea normalmente no las presentan. Una particularidad de Lethariella es la estructura cortical, la cual varía de poco organizada, más o menos fibrosa, reticular y con costillas, hasta claramente acanalada.

Los metabolitos secundarios medulares de Usnea s. str. son de la serie ß-orcinol, mayormente ß-orcinol depsidonas, pocas ß-orcinol depsidas y rara vez ß-orcinol paradepsidas, pero nunca ácido divaricático. Neuropogon sólo produce pocas ß-orcinol depsidonas. Protousnea presenta principalmente ácido divaricático. Lethariella produce meta- y para-orcinol depsidas, ß-orcinol depsidonas y una terfenil-quinona; Lethraria carece de sustancias medulares, pero en ocasiones el ácido norestíctico (ß-orcinol depsidona) es detectado en los apotecios.

En la corteza, Usnea, Neuropogon y Protousnea producen ácido úsnico, aunque en algunas especies la atranorina también puede ser detectada; en Lethariella y Letharia la atranorina sustituye totalmente al ácido úsnico. Lethariella (incluyendo el subgénero Chlorea) a veces produce el pigmento ácido canariónico y Letharia debe su color amarillo sulfúreo a la presencia de ácido vulpínico

El último carácter considerado por Krog (1976, 1982) en esta segregación es el de las diferencias en la distribución geográfica. Usnea s. str. es un género de distribución cosmopolita; Neuropogon presenta una distribución bipolar, más extendida en la Antártida; Protousnea se limita al suroeste de América del Sur y a las Islas Malvinas; Lethariella tiene una distribución fragmentada en Europa, Asia Central y Japón, y Letharia con el centro de distribución en el oeste norteamericano.

Walker (1985) no acepta la segregación de Neuropogon porque considera que los caracteres en que está basada no son suficientemente confiables, particularmente la pigmentación del talo y el hábitat, aunque también menciona que probablemente ni las características apoteciales sean suficientes para distingir dichos taxa.

4.- Caracteres diagnósticos del género Usnea

Una opinión generalizada entre los liquenólogos es que Usnea es uno de los géneros más compliejos taxonómicamente debido a que sus caracteres morfológicos son muy plásticos y confusos. El mismo Motyka (1947) decía: "... c'est un genre extraordinairement variable, abondant en formes et très difficile à distinguer du point de vue systèmatique ..."

Debido a la confusión que surgió con el estudio de Motyka, se hizo necesaria la revisión crítica de los caracteres que definen su delimitación de las especies. Ésta fue realizada por Herre en 1963 y sirvió de base a Swinscow y Krog (1974) para considerar la amplia variación morfológica y química de los distintos complejos de especies. Las especies son delimitadas por la combinación de caracteres de valor relativo, y no a por la presencia o ausencia de uno u otro carácter (Swinscow y Krog 1975).

A continuación se enlistan los caracteres diagnósticos reconocidos por los especialistas actuales.

1.- Caracteres morfológicos: patrón de ramificación; tronco o base (longitud, forma y color); ramas principales y secundarias (forma y diámetro); segmentos de las ramas (forma tanto en sección longitudinal como transversal); papilas (forma, densidad y localización); tubérculos (densidad y localización); fibérculos (densidad y localización); fibrillas (forma, longitud y permanencia); soralios (origen, posición relativa a la corteza, características de la superficie soredial, tamaño, forma, densidad, margen y localización en el talo); isidiomorfos o isidios (tipo, densidad y localización); apotecio (diámetro y tipo de acuerdo a la posición en la rama) (Clerc 1984a; 1987a, b; Clerc y Herrera-Campos 1997; Halonen et al. 1998; Herrera-Campos et al. 1998; Stevens 1992; Swinscow y Krog 1974-1979).

2.- Caracteres anatómicos: corteza (pigmentación, textura, dureza, grosor relativo al ancho total de la rama, presencia y tipo de grietas); médula (pigmentación, tipo de acuerdo a su densidad y grosor relativo al ancho total de la rama); eje (pigmentación, tipo de acuerdo a la constitución del mismo y grosor relativo al ancho total de la rama). Las dimensiones mencionadas de la corteza, la médula y el eje son referidas en la literatura como CMA (cortex, medulla, axis) y expresadas en porcentaje del total de la rama (Clerc 1984a, 1987a; Herrera-Campos et al. 1998).

Las esporas (forma y dimensiones) son otro carácter anatómico por considerar; sin embargo, hasta la fecha no existe un estudio que demuestre su importancia a nivel específico. Clerc (1984) menciona una ligera diferencia entre las esporas de algunas especies del complejo U. florida (L.) Wigg. emend. Clerc en Europa. Se requiere de un estudio comparativo profundo de las especies fértiles en el que se considere también el estudio de las características himeniales.

3.- Caracteres químicos. El tipo de metabolitos secundarios producidos por los líquenes es un carácter diagnóstico a diversos niveles taxonómicos (Brodo 1986; Culberson 1969, 1970, Culberson y Culberson 1976; Elix 1996; Hafellner 1988; Hawksworth y Hill 1984). Su importancia particular en la taxonomía del género Usnea es discutida en el capítulo sobre el complejo Usnea fragilescens Havaas ex Lunge en México.

5.- Concepto de especie

La taxonomía liquénica se basa en el concepto biológico de especie, definida como un grupo interfértil de organismos con un acervo genético común. Sin embargo, las descripciones de las especies liquenológicas corresponden básicamente a morfoespecies y se fundamentan en la evaluación de las semejanzas y diferencias. Teóricamente la biosespecie y la morfoespecie debieran ser idénticas, pero esto raramente sucede en la práctica (Jahns 1989 a). Los caracteres evaluados son principalmente fenéticos, como la morfología y la química de los talos, aunque recientemente se han incorporado criterios vinculados a la genética de los organismos como las características de las proteínas, las isoenzimas y el ADN; cuyo análisis conjunto desde un enfoque cladístico permite la elaboración de un concepto filogénetico de especie en líquenes (Jahns 1989 b; Kilias 1987).

Según Poelt (1994) hay tres tipos de especies liquénicas: especies sexuales estables, especies sexuales genéticamente variables y especies apomícticas. Las primeras se reproducen regularmente por ascosporas que necesitan combinarse con el (los) fotobionte (s) adecuado (s). Estas especies muestran gran plasticidad debido a factores ecológicos, son monomórficas y distinguibles de otras especies relacionadas. Estos líquenes presentan variación genética a lo largo de áreas muy extensas, por ejemplo entre Europa y Norteamérica.

Las especies sexuales genéticamente variables son comunes entre los líquenes costrosos saxícolas que desarrollan apotecios abundantes así como espermogonios. Forman poblaciones grandes que se mezclan espacialmente con otros líquenes creciendo en la misma roca. Bajo condiciones ecológicas idénticas, desarrollan talos parecidos en los caracteres principales, pero marcadamente variables en caracteres menos importantes, que a su vez, pueden presentarse en una gran variedad de combinaciones. Tales poblaciones parecen ser genéticamente homogéneas y los intentos por describir categorías infraespecíficas han sido inútiles pues todas las combinaciones de caracteres ocurren sin una clara delimitación. En estas especies los caracteres no han estado sujetos a fuertes presiones de selección y son interpretados como neutrales en la evolución. Ejemplos de este tipo de especies son: Fuscidea cyathoides (Ach.)V. Wirth y Vezda, F kochiana (Hepp) V. Wirth y Vezda, Graphis scripta Adanson em. Müll. Arg., Rhizocarpon geographicum (L) D C. y Bellemerea alpina (Sommerf) Clauz y Roux. En géneros como Lecidea la situación se complica considerablemente ya que además de la variabilidad morfológica existe una considerable variabilidad química. Umbilicaria cylindrica (L.) Del. Ex Duby y Parmelia omphalodes (L.) Ach. son ejemplos entre los líquenes foliosos. Finalmente, las especies apomícticas son aquéllas que se reproducen asexualmente a través de diasporas como filidios, isidios o soredios. La formación de ascocarpos es rara, o de ocurrir no culmina en la producción de ascas y/o ascosporas maduras.

Otro concepto ampliamente aceptado en taxonomía liquénica es el concepto de par de especies planteado por Poelt (1972). Este concepto establece que los pares están integrados por una especie sorediada o de reproducción asexual y una especie fértil o de reproducción sexual. Según Mattson y Lumbsch (1989), la primera referencia a los criterios que definen un par de especies fue hecha en 1924 por DuRietz, quien discutió la importancia taxonómica de las diasporas y el hecho de que frecuentemente, entre taxa relacionados, los sorediados y los fértiles presentan diferencias ecológicas. En 1963 Poelt introdujo los términos primario y secundario para designar los taxa fértiles y los taxa soredio-isidiados, respectivamente, y postuló que las diferencias en frecuencia y distribución de los mismos en Europa Central se deben a que la recolonización postglacial se llevó a cabo principalmente por poblaciones sorediadas o isidiadas. En 1970 postuló que cada taxón sorediado se originó a partir de uno fértil, y considera que los sorediados son líneas evolutivas muertas. Sin embargo no fue hasta 1972 cuando atribuyó la categoría de especie a cada uno de los taxa integrantes del par (Mattson y Lumbsch 1989).

El concepto de par de especies es rechazado por algunos liquenólogos, por ejemplo Robinson (1975) y Tehler (1982). El primero considera que en realidad se trata de especies panmícticas Mientras que el segundo postula que los taxa sorediados son formas correspondientes de los fértiles y no especies distintas. Tehelr (1982) asume que entre ellos no existen diferencias genéticas suficientes para separlos y no reconoce la utilidad distribución geográfica en dicha separación.

Tanto Poelt como Tehler coinciden en afirmar que los taxa fértiles dan origen a los sorediados y que éstos conservan los caracteres ancestrales. Sin embargo, Mattson y Lumbsch (1989) consideran que las poblaciones apomícticas tienen la variabilidad genética suficiente para que la selección pueda seguir operando en el proceso evolutivo e inclusive mencionan la posibilidad de que un taxón estéril dé origen a otro, cuestionando así la afirmación de que todos los taxa sorediados hayan tenido necesariamente un ancestro fértil y que representan líneas evolutivas finales.

Los mismos Mattson y Lumbsch aceptan la importancia del aislamiento y la separación como mecanismos de especiación y de la distribución geográfica en el reconocimiento de verdaderos pares de especies. Presentan cinco casos de distribución geográfica y el rango taxonómico en cada uno:

1. Ambos componentes del par tienen una distribución simpátrica con la existencia de formas intermedias, en donde los soredios sólo representan una modificación, no deben separarse taxonómicamente.

2. Los dos componentes tienen una distribución alopátrica, o pero presentan formas intermedias cuando son simpátricas, entonces se considera el taxón sorediado como subespecie.

3 Si el par es simpátrico, sin formas intermedias, es probable que no se trate de un par de especies.

4.- Cuando ambas contrapartes son alopátricas sin formas intermedias, se trata de dos especies.

5. En el caso en que sólo la especie secundaria es conocida, evidentemente es considerada como especie.

Por otra parte, Hale (1965) observó que en algunos casos las "contrapartes" fértiles presentan una distribución reducida en las áreas tropicales, mientras que las sorediadas son pantropicales. En otros casos la especie sexual tiene una distribución pantropical mientras que la contraparte asexual se extiende a regiones templadas.

Un concepto que ha resultado muy controvertido es el de especies hermanas, definidas en liquenología como aquellas razas que integran un agregado morfológicamente uniforme pero que varían en la presencia de metabolitos secundarios, fisiología o ecología (Culberson 1986b). De acuerdo a esta definición, el grupo Ramalina siliquosa se considera integrado por siete especies que se distinguen principalmente por sus metabolitos secundarios. Rogers (1989) rechaza este enfoque y considera que dicho grupo en realidad está integrado por dos especies que presentan variación química. Para él, la relación entre la química y la distribución y/o ecología no es de utilidad taxonómica. El carácter químico importante en taxonomía debe ser la ruta metabólica y no los productos finales, ya que variaciones en una estructura molecular básica no puede demostrar aislamiento genético ni discontinuidad biológica.

La opinión contraria es defendida por Feige y Lumbsch (1995), quienes sostienen que son precisamente los diferentes quimiotipos de la misma ruta metabólica los que tienen significado taxonómico y no sustancias de distintas rutas metabólicas cuya ocurrencia aislada o poco común.

El problema de interpretar y ponderar la variación química de los líquenes no es nuevo. Hawksworth (1976) establece algunos lineamientos para interpretar la variación química. Los quimiotipos biogenéticamente cercanos son considerados especies si están relacionados con diferencias morfológicas y de distribución. Si dichas diferencias son sólo geográficas locales, o condiciones ecológicas o microambientales, el rango correspondiente es el de variedad. En caso de que los quimiotipos sean biogenéticamente distantes, se les asigna el rango de especie si están relacionados con diferencias morfológicas y/o ecológicas; o con diferencias geográficas mayores.

Culberson y Johnson (1988) proponen los estudios de flujo de genes como alternativa a la discusión morfología *versus* química. Concluyen que si no se detecta flujo de genes entre los quimiotipos, sean éstos biosintéticamente cercanos o no, puede asumirse que se trata de especies reproductivamente aisladas. Por el contrario, si ocurre flujo de genes, los quimiotipos representan un tipo de polimorfismo dentro de una población, particularmente cuando no se detecta alguna relación entre caracteres morfológicos y caracteres químicos.

En el género Usnea las especies son definidas por la combinación de distintos caracteres morfológicos, anatómicos y químicos, en la cual al menos dos de estos caracteres independientes se correlacionan Por ejemplo, la morfología de los soralios y la química del talo, o ésta última y la anatomía (Herrera-Campos et al 1998). Es importante también incluir los patrones de distribución geográfica en la caracterización y definición de las especies.

La delimitación de la especies se complica debido a la variedad de quimiotipos y morfotipos que existen en el género y por numerosas formas intermedias entre especies cercanamente relacionadas En este estudio, a los quimiotipos de morfología idéntica no se les reconoce rango taxonómico a menos que se compruebe que sus diferencias químicas se correlacionan con otro carácter anatómico o con diferencias en la distribución geográfica, o cuando distintas rutas sintéticas están involucradas.

En Usnea, la intergradación morfológica entre especies que crecen juntas, que parece ser más la regla que la excepción, hace mucho más difícil su separación y la delimitación de la combinación de caracteres distintivos (Stevens 1992; Swinscow y Krog 1979). Particularmente interesantes son los morfos intermedios; son ejemplares con caracteres mezclados de dos especies morfológica, anatómica y químicamente distinguibles, como en los casos de U. subfloridana Stirton y U wasmuthii Räs. (Clerc 1992), U. fragilescens y U. cornuta Koerb. (Tavares 1997), y U. fulvoreagens (Räs.) Räs. y U glabrescens (Nyl. Ex Vain.) Vain. (Halonen et al. 1998). Tales ejemplares han sido considerados como posibles "híbridos vegetativos" (Brodo 1978; Clerc 1992; Fahselt 1996; Halonen et al. 1998) aunque la hibridización liquénica aún no ha sido entendida.

6.- Distribución y ecología

Usnea es un género cosmopolita cuyas especies se desarrollan principalmente en sitios húmedos, fríos o templados y bien iluminados. Son principalmente epífitas, tanto en coníferas como en árboles caducifolios, pero también pueden crecer en otros sustratos como madera muerta o roca, aunque son muy pocas las especies totalmente saxícolas.

De acuerdo a la distribución geográfica conocida, las especies mexicanas de Usnea podrían agruparse en boreales y templadas, tropicales y endémicas. Aunque, refiriéndose al origen de las especies encontradas en los trópicos, particularmente en Australia y las islas de la región oeste del Pacífico, Stevens (1991) considera como tropicales únicamente a aquellas especies que crecen a altitudes bajas siguiendo la distribución de los manglares o creciendo en forofitos de origen tropical. Las especies que se desarrollan en elevaciones altas, en condiciones húmedas y frías tienen un origen templado ya que inicialmente migraron de la Antártida siguiendo a géneros como Araucaria y Notophagus y deben referirse como especies templadas.

La mayoría de las localidades mexicanas están ubicadas entre los 1200 y los 4000 msnm en bosques de coníferas puros o mixtos y mesófilos de montaña, aunque hay dos localidades a altitudes bajas (360 m y 670 m) en las cuales ocurren bosques de Pinus-Quercus en las inmediaciones de bosques tropicales. Tales comunidades son consideradas de afinidades holárticas pero con una capacidad inusual de penetrar en zonas de condiciones climáticas más cálidas y secas (Rzedowskii 1981).

Se recolectó material en distintas localidades del Desierto Sonorense donde sólo unas cuantas especies están bien representadas, pero también se estudiaron algunos ejemplares de herbario procedentes de localidades con vegetación tropical o subtropical. Los forofitos más comunes son Abies, Pinus, Quercus y Alnus, en menor grado Pseudotsuga y Cupressus; unas cuantas especies están limitadas a rocas. No se encontró relación entre la altitud y el sustrato, como la establecida por Swinscow y Krog (1978) en el este de África, ni tampoco preferencia alguna por un tipo de árbol como es mencionado por Halonen et al. (1998) en Columbia Británica.

Las especies de más amplia distribución y de mayor amplitud altitudinal son: a) entre las especies péndulas, U. ceratina Ach. (1300-3920 msnm), que es epífita, sólo ocasionalmente saxícola, sigue claramente la distribución de los bosques templados del país, pero no ha sido colectada en Baja California. b) U. dasaea Stirt. , especie arbustiva que crece tanto en árboles como en roca, es la que tiene la mayor amplitud altitudinal, desarrollándose en zonas sitios con vegetación xerófila de Baja California (30-200 msnm) hasta el bosque mesófilo de montaña y bosque de coníferas entre 1550 m y 3000 msnm. Este tipo de distribución sólo es igualado por U. rubicunda, la cual también es principalmente cortícola y ocasionalmente saxícola. U. cirrosa Mot., especie arbustiva apoteciada que alcanza los 3650 m de altitud presenta una distribución similar a U. ceratina, pero está mejor representada en los bosques secos de Chihuahua.

Las especies de distribución restringida corresponden a especies que alcanzan los límites de distribución en nuestro país, como es U. scabrata Nyl. que fue recolectada en muy pocas localidades en zonas subalpinas del Eje Neovolcánico, siendo éste el límite sur de su distribución en el continente. U. papillata. Mot. encontrada únicamente en una localidad, y reportada para Brasil, para la que México podría representar el límite norte de su distribución. U. esperantiana Clerc y U. wirthii Clerc han sido colectadas tan esporádica y escasamente que no se puede caracterizar su distribución.

Entre las especies conocidas sólo para México, U.cristatula Mot. es la que tiene la más amplia distribución comparada con U. sanctaritae Clerc y Herrera-Campos, U. vitrea Clerc y Herrera-Campos, U. nashii Clerc y Herrera-Campos y U. ammannii Clerc y Herrera-Campos.

U. angulata Ach. y U. transitoria Mot son ejemplo de especies morfológicamente muy similares, químicamente distintas y con distintas tendencias de distribución. U. angulata tiene un rango altitudinal más estrecho que U transitoria y ha sido encontrada principalmente al este y sur del país en la Sierra Madre Oriental, Sistema Montañoso del Norte de Oaxaca y en el Macizo Central de Chiapas; mientras que U. transitoria se recolectó principalmente en el oeste, centro y norte de México en la Sierra Madre Occidental, Eje Neovolcánico Transversal y en las partes altas del Sistema Montañoso de Baja California, la Sierra de San Pedro Mártir al norte, y la Sierra de La Laguna al sur de esa península.

Se recolectaron alrededor de 4000 ejemplares de Usnea en las principales zonas montañosas del país, en los bosques templados de las siguientes provincias fisiográficas: a) Eje Neovolcánico Transversal (Colima, Distrito Federal, Estado de México, Jalisco, Michoacán, Hidalgo, Puebla, Tlaxcala y Veracruz), b) Sierra Madre Occidental (Chihuahua, Sinaloa, Durango y Nayarit), c) Sierra Madre Oriental (Nuevo León, Tamaulipas y San Luis Potosí), d) Sistema Montañoso de Baja California (San Pedro Mártir, Baja California y Sierra de la Laguna, Baja California Sur); e) Sierra Madre del Sur (Guerrero); f) Sistema Montañoso del Norte de Oaxaca (Oaxaca) y g) Macizo Central de Chiapas (Chiapas).

Cerca de 2700 ejemplares se usaron en los análisis anatómicos y químicos. En el estudio se incluyeron numerosos ejemplares recibidos en préstamo de los siguientes herbarios: ASU, BERN, COLO, DUKE, ENCB, FH, H, G, IBUG, LAM, LE, LUB, MEXU, NY, O, S, TUR, UPS, VT y W.

La agrupación inicial de todo el material se hizo con base al hábito de los ejemplares, al tipo de reproducción (sexual o asexual) y al tipo de médula, corteza y eje que presentan. Se reconocieron tres grupos artificiales principales: a) péndulos, b) arbustivos sorediados y/o isidiados y c) arbustivos apoteciados. En cada uno de estos grupos se separararon los ejemplares pigmentados y los no pigmentados.

Los análisis morfológicos y anatómicos fueron realizados en un estereoscopio, los caracteres analizados se describen en los capítulos siguientes. La anatomía fue estudiada siguiendo el método de Clerc (1984a). En la parte más ancha de la rama más gruesa del talo, se hizo un corte longitudinal cuyo espesor sea la mitad del diámetro de la rama misma, exponiendo la corteza, la médula y el eje. Estas estratos se midieron y cada uno se refirió relativamente como porcentaje del diámetro total de la rama. Las tres mediciones corresponden a lo que se conoce como CMA. En las descripciones de las especies (n) representa el número de ejemplares analizados. En los artículos publicados, los porcentajes referidos para cada una de estas estructuras son los valores promedio ± desviación estándard; sin embargo, después del análisis estadístico de las especies del complejo U. fragilescens, se decidió hacer la comparación de los valores porcentuales promedio considerando el error estándar de la media y no la desviación estándard.

Los metabolitos secundarios fueron analizados siguiendo la técnica de cromatografía de capa fina estandarizada por Culberson y Ammann (1979) y modificada por Culberson y Johnson (1982). Se practicaron las pruebas de tinción convencionales (Hale 1979) practidas sobre la corteza y la médula expuestas en un corte longitudinal; ocasionalmente éstas se practicaron directamente sobre los soralios

La técnica de cromatografía en capa fina utilizada fue la siguiente. Primeramente se extrajeron de los ácidos liquénicos en tres cambios de acetona al 100%, llevando a sequedad cada uno de ellos. Al extracto se le añaden unas cuantas gotas de acetona para colocar las muestras en placas de gel de sílice para cromatografía en capa fina (BAKER Si25OF) de 250 µm de espesor, y de 10X10 cm. En cada una de las placas se incluyeron de dos a tres controles de composición conocida y que servieron como referencia en la identificación de las sustancias.

Los cromatogramas y los pretratamientos se corrieron en tanques de vidrio bien sellados y en una campana de extracción.

Las mezlas de disolventes utilizadas fueron A, B y C. La mezcla C fue usada principalmente por ser la de más amplio espectro, mayor durabilidad y fácil manejo. Las otras dos se utilizaron en los casos en que se necesitara información adicional sobre una sustancia. La composición de los disolventes fue la siguiente:

A: tolueno-dioxano-ácido acético (180:45:5)

B: hexano-dietil éter-ácido fórmico (120:90:20)

C: tolueno-ácido acético (200:30)

Después de prepararlas, fue necesario esperar por lo menos dos horas antes de usar las mezclas, a fin de que fueran homogéneas. Las mezclas A y B debieron ser usadas y descartadas el mismo día en que se prepararon. Asímismo, cuando se utilizaron las mezclas B y C se requirió practicar un pre-tratamiento a las placas. Cada placa se colocó en ácido fórmico al 60% durante 5 minutos, si se utilizó la solución B, y en ácido acético al 100 % cuando se utilizó la solución C.

La solución se dejó correr por la placa hasta que el frente alcanzó aproximadamente 1 cm menos de la longitud de la placa. Ésta se leyó bajo luz ultravioleta de onda corta (254 nm) y de onda larga (366 nm). Se marcaron las manchas observadas y se registraron su fluorescencia, color e intensidad de las mismas.

Se utilizó ácido sulfúrico al 10% como revelador, aplicándolo a la placa con una brocha de esponja. Se dejó secar ligeramente y la placa fue colocada en un horno a 100 C, durante aproximadamente ocho minutos, o hasta que los colores de las manchas se hicieron visibles. Estos colores fueron registrados y se realizó una segunda lectura en UV de onda larga, anotando la fluorescencia, la intensidad y el color de las manchas. Cada mancha en la placa corresponde a una sustancia liquénica la cual es identificada con la información anterior y el Rf de cada una de ellas. Esta información se compara con la base de datos Mactabolites para verificar la identificación de las sustancias liquénicas.

El tamaño relativo de la corteza, la médula y el eje con respecto al grosor de la rama principal, fue comparado de manera separada con ANOVA. Fue necesaria una transformación logarítmica de los valores porcentuales de la corteza, y la elevación al cuadrado de los del eje, para normalizar los datos. La prueba de Tukey HSD se usó para comparar las medias de cada especie después del ANOVA.

La exploración adicional de las similitudes y diferencias interespecíficas usando los mismos caracteres, se llevó a cabo con un análisis discriminatorio (Sharma 1996). Este tipo de análisis ha sido practicado con éxito en problemas taxonómicos (e. g. Hess y Stoynoff 1998). Para este análisis se emplearon 68 especímenes de U. cornuta s. lat., 60 de U. brasiliensis, 66 de U. cirrosa, 38 de U. ramillosa s. str. y 44 de U. glabrata. Se usaron los valores reales de las tres variables en lugar de los porcentuales, aunque fue necesaria una transformación logarítmica para satisfacer los requerimientos de normalidad. Además, debido a que la suposición de la igualdad de las matrices de varianza-covarianza fue rechazada (prueba de Bartlett), se usó como regla de clasificación una función discriminante cuadrática en lugar de una función lineal. El análisis fue hecho con un programa SAS, haciendo uso de los procedimientos DISCRIM y CANDISC (SAS 1990). De acuerdo con la regla min {G-1, p}, donde G es el número de grupos (5 especies en este caso), y p es el número de variables (3 caracteres), se trabajó con tres funciones discriminatorias.

Finalmente se integraron dos bases de datos, la primera conteniendo la información de herbario y la segunda de la composición química de los ejemplares estudiados.

Herrera-Campos, M. A., P Clerc, y T H Nash III 1998. Pendulous Species of Usnea from the Temperate Forest in Mexico. The Bryologist 101 (2): 303-329.

Especies péndulas de Usnea de los bosques templados de México

RESUMEN

Este estudio representa el primer paso hacia un tratamiento moderno completo del género Usnea en México. Se describen las características morfológicas, anatómicas y químicas y la distribución geográfica de diecisiete especies péndulas mexicanas procedentes de bosques templados, cuyo espectro altitudinal fluctúa entre 1300 y 1400 m Se reportan cuatro nuevos registros: U. goniodes (Stirt.) Mot. nueva para el continente americano; U. malmei Motyka., U. scabrata Nyl., s. lat. y U. subcabrosa Nyl. ex Motyka nuevos registros para México. Se proponen las siguientes sinonimias: U. ceratina Ach. (Syn. nov. U. solida Motyka.), U. filipendula Stirton (Syn. nov. U. sublaxa Vain. ex Motyka.), U. himantodes (Syn. nov U. sericea Motyka.), U. malmei Motyka (Syn. nov. U sorediata (Zahlbr.) Motyka) y U. mexicana Vainio (Syn. nov. U. duriuscula Motyka).

Usnea santaritae Clerc & Herrera-Campos y U. vitrea Clerc & Herrera-Campos son descritas como nuevas especies.

En este artículo se definen e ilustran los caracteres diagnósticos del género y de las especies tratadas en particular; se incluye la descripción de cada una con comentarios acerca de la variación morfológica y química, tanto intraespecífica como interespecífica. Se presenta una clave para identificarlas, así como los mapas de su distribución en México.

Herrera-Campos, M. A., P. Clerc, y T. H. Nash III 1998. Pendulous Species of Usnea from the Temperate Forest in Mexico. The Bryologist 101 (2): 303-329.

Especies péndulas de Usnea de los bosques templados de México

RESUMEN

Este estudio representa el primer paso hacia un tratamiento moderno completo del género Usnea en México. Se describen las características morfológicas, anatómicas y químicas y la distribución geográfica de diecisiete especies péndulas mexicanas procedentes de bosques templados, cuyo espectro altitudinal fluctúa entre 1300 y 1400 m. Se reportan cuatro nuevos registros: U. goniodes (Stirt.) Mot. nueva para el continente americano; U. malmei Motyka., U. scabrata Nyl., s. lat. y U. subcabrosa Nyl. ex Motyka nuevos registros para México. Se proponen las siguientes sinonimias: U. ceratina Ach. (Syn. nov. U. solida Motyka.), U. filipendula Stirton (Syn. nov. U. sublaxa Vain. ex Motyka.), U. himantodes (Syn. nov. U. sericea Motyka.), U malmei Motyka (Syn. nov. U. sorediata (Zahlbr.) Motyka) y U. mexicana Vainio (Syn. nov. U. duriuscula Motyka).

Usnea santaritae Clerc & Herrera-Campos y U. vitrea Clerc & Herrera-Campos son descritas como nuevas especies.

En este artículo se definen e ilustran los caracteres diagnósticos del género y de las especies tratadas en particular; se incluye la descripción de cada una con comentarios acerca de la variación morfológica y química, tanto intraespecífica como interespecífica. Se presenta una clave para identificarlas, así como los mapas de su distribución en México.

Pendulous Species of Usnea From the Temperate Forests in Mexico

MARIA ANGELES HERRERA-CAMPOS
Arizona State University, Plant Biology Department, Tempe, AZ 85287, U S.A

PHILIPPE CLERC
Conservatoire et Jardin Botaniques, Case postale 60, 1292 Chambésy, Switzerland

THOMAS H. NASH III
Arizona State University, Plant Biology Department, Tempe, AZ 85287, U.S.A

ABSTRACT. This study is the first step towards a modern, thorough treatment of the genus Usnea in Mexico Morphological, anatomical, and chemical features as well as distribution of seventeen Mexican pendulous species from temperate forests (1300 to 4000 m) are described U. malmei Mot , U. scabrata Nyl. s. lat., and U subscabrosa Nyl. ex Motyka are new records for the country. U. goniodes (Stirt.) Mot. is new for the American continent. The following synonyms are proposed: U. ceratina Ach. (Syn nov. U. solida Motyka), U. filipendula Stirton (Syn nov. U. sublaxa Vain. ex Motyka), U. himantodes (Syn. nov U. sericea Motyka), U. malmei Motyka (Syn. nov. U. sorediata (Zahlbr.) Motyka), and U. mexicana Vainio (Syn. nov U. duriuscula Motyka).

Usnea santaritae Clerc & Herrera-Campos sp. nov., and U. vitrea Clerc & Herrera-Campos sp. nov are described.

A key for Mexican pendulous species of Usnea is provided

The genus Usnea is one of the most easily recognized of the fruticose lichens, yet it remains poorly understood at the species level due to the spectacular plasticity of such characters as color, length of the thallus, density of ramification, development and density of fibrils, shape of papillae, presence of foveolae, and thickness and growth of apices (Clerc 1991). Motyka's monograph represents the only exhaustive taxonomical study of the genus. However, it is mainly based on the variable characters mentioned above. In many cases what may be simply morphological variants of one species are treated as multiple species (Clerc 1991; Swinscow and Krog 1978)

Recent papers dealing with taxonomy of Usnea have put more weight on less variable characters, such as chemistry (Clerc 1987a; Swinscow and Krog 1978, 1979) morphology of soralia (Clerc 1987b), and several other morphological features (Swinscow and Krog 1975, 1976, Clerc 1992). Attempts have also been made to include spore length (Clerc

1984), thickness of anatomical features, such as cortex, medulla, and axis (Clerc 1984, 1994) as well as climatic and geographic data (Stevens 1992).

The literature available for Mexican species of Usnea is limited to scattered reports of species in floristic investigations, such as those from Bouly de Lesdain (1914, 1929, 1933) who reported for Mexico approximately thirty three species identified by Motyka. Gilbert (1935) mentions eleven species of Usnea from the Mexican Valley. Imshaug (1956) listed forty six species (subspecies, varieties, and forms were not considered). Guzmán and González de la Rosa (1976) published a list of the Mexican species and infraspecific forms that were cited by Motyka (1936-1938) From different localities in the country, González de la Rosa and Guzmán (1976) reported five species of Usnea, including the pendulous species: U. angulata Ach , U. cavernosa Tuck, and U. trichodea Ach. Coutiño and Mojica (1982; 1985) respectively, reported five species of this genus on their study of corticolous lichens from Hidalgo and listed six different Usnea from the region Perote-Xalapa in Veracruz. In the latter two papers U. dasypoga (Ach.) Motyka was the only pendulous species mentioned. None of these publications used TLC in the identification of the lichen substances; consequently, the determination of all these specimens needs revision. Culberson et al. (1983) described a new shrubby species from the Estado de México, U. lecanorica W. Culb , C. Culb. & Fiscus based on the presence of lecanoric acid in the medulla.

This paper is the first of a series to discuss Mexican species of Usnea. For practical reasons, species have been first grouped artificially according to their growth habit and the presence or absence of apothecia versus soralia and/or isidiomorphs, following the general approach of Swinscow and Krog (1978, 1979) The main purpose of this paper is to describe the pendulous species, characterized by pendulous or subpendulous thalli with parallel branches on most of their length. These species occur typically in coniferous (Abies or Pinus dominated), mixed forests (Pinus-Quercus), or montane cloud forests.

MATERIALS AND METHODS

The specimens examined are primarily the senior author's personal collections made from numerous field trips to the temperate forests of the primary montane areas of different physiographic provinces in Mexico (Rzedowski 1981, Fig. 1) between 1992 and 1996. Materials from the following herbaria are also included in this study: ASU, BERN, COLO, DUKE, ENCB, FH, H, G, IBUG, LAM, LE, LUB, MEXU, NY, O, S, TUR, UPS, VT, and W. Most of the types of the 140 Usnea species reported from the Americas, and all of the species occurring in Europe (Motyka 1936-1938) have been studied as well.

The specimens were morphologically and anatomically analyzed under a stereomicroscope. Anatomical analyses were performed following Clerc (1984) by measuring the relative thickness of the cortex, medulla, and axis (CMA) at the widest part of the main branch under the stereoscope at 40X, and are expressed as percentage of the total width of the branch In the descriptions, (n) stands for the number of individual thalli measured.

The chemistry was studied by TLC following the technique standardized by Culberson and Ammann (1979) and modified by Culberson and Johnson (1982). The usual spot tests (Hale 1979) were performed on the exposed medulla of a longitudinal section of the main branch

SPECIES CONCEPT

In lichens, genetic evaluation of characters by crossing experiments is thus far impossible for technical reasons. Therefore, lichenologists have no choice but to seek discontinuities in characters that are assumed to be independent and genetically fixed. Each species accepted in this paper is a unique combination of morphological, anatomical, and chemical characters The correlation of at least two characters that are postulated to be independent (e.g. soralia morphology and chemistry, or cortical structure and chemistry) is the minimum condition for a population or a group of populations displaying these characters to be considered as good species. As a consequence, we do not consider morphologically identical chemotypes to be good species but to result from chemical variation within a taxon. In their revolutionary, for lichenology, gene flow study in Cladonia, Culberson et al. (1988) showed that closely related secondary metabolites are not necessarily an indication of close association. So, without experimentation, it makes no sense to overburden nomenclature by describing chemical races as species.

One exception to this taxonomic species concept is used when considering primary versus secondary species (Poelt 1970, 1972). For these pairs, the unique difference is sometimes the presence versus the absence of soralia or isidiomorphs in secondary species and primary species respectively. For such cases, we agree with Durietz (1924) and Mattson and Lumbsch (1989) that looking at the distribution patterns of the fertile and asexual morphs in a species pair is an important step when considering how to rank them. The general distribution pattern of each one of the species pairs discussed here is given in Fig 2 Although many uncertainties remain due to lack of knowledge or differences in the taxonomic concepts used in previous studies, it is evident (Table 1) that in four out of the six species pairs considered, the asexual morph has a much wider distribution than the sexual morph. Each morph is given species rank. The same concept is applied to the two species pairs (U. himantodes/U. mexicana and U. goniodes/U transitoria) where reliable information about their world distribution is not yet available.

MORPHOLOGY

Thallus

Species described in this paper are up to 250 cm long with well developed points of attachment, except in U. cavernosa which often hangs loosely on twigs. Some species, such as U ceratina and U. subscabrosa, also have shrubby forms whose length ranges from 3 to 15 cm. Thallus color varies from pale yellow-green to dark olive green. Sometimes older branches become darker (e.g. U. filipendula). Although few species display a characteristic color, perception and description of this character are very subjective. Therefore, we agree with Swinscow and Krog (1978) that it is not an important diagnostic character in Usnea.

Ramification

Branching pattern in pendulous species is mostly isotomic dichotomous or filamentosic-dichotomous (Hawksworth 1972), with branches running parallel to each other. Density of ramification of the thallus (i e number of branches) strongly affects its general appearance (habit) and has been used in the past as a very important diagnostic feature (Clerc 1991). However, this feature is also very variable within Mexican species; therefore it is not regarded here as a good specific character.

Trunk

The trunk (Fig. 3) is defined as the part of the thallus which extends from the point of attachment to the main ramification. It may be very short and thus indistinct or well developed, or short (3-5 mm) to long (up to 28 mm). It is variously pigmented at the base, a diagnostic character regarded as very important. For instance, well developed black pigmented trunk occurs in U. filipendula, whereas an orange-reddish pigmented base often occurs in U. subscabrosa and U. hesperina.

Branches

Branches in Usnea are usually more or less conspicuously segmented. In some species the frequency of segmentation is a good taxonomical character. Branches are i) tapered with the diameter slowly and regularly decreasing towards the apices, ii) cylindrical with a constant diameter over most of the length but decreasing rapidly close to the apices, or iii) irregular with the diameter varying along the length of the branch.

Main branches are those which arise directly from the trunk and are usually the thickest ones (Swinscow and Krog 1978). Their shape in cross section is terete as in U. merrillii, U. hesperina, and U subscabrosa (Fig. 4a), flattened (Fig.4b), striated (i.e.

delicately ridged without deforming the segments) as sometimes in U. scabrata; irregular (i.e. deforming the segments) as in U. cavernosa (Fig. 4c), ridged as in U. transitoria (Fig. 4d), or alate as in U. angulata (Fig. 4e). In longitudinal secton the segments are cylindrical as in U. hesperina, U. subscabrosa, and U. filipendula (Fig. 5a,b,e), ridged as in U. transitoria (Fig. 5c), trapezoidal as in U. angulata (Fig. 5d), ± "sausage-like" i.e. swollen in the middle part as in U. scabrata (Fig. 5f). Finally, the segments can be deformed by the presence of depressions in the cortex like foveolae or transverse furrows as in U. cavernosa (Fig. 5g).

Papillae and tubercles.

The distinction made by Swinscow and Krog (1979) between papillae and tubercles is also followed in this study: papillae as protuberances of cortical material, whereas tubercles are composed of cortical and medullary material. It is common to find both structures on the same thallus. The presence, type, and distribution of these structures is variable among species; some being commonly papillate and/or tuberculate (U. ceratina, U. subscabrosa, and U. transitoria) (Fig. 6 a, b). Other species are rarely papillate or tuberculate (U. hesperina), yet others lack papillae and tubercles entirely (U. cavernosa). Shape and frequency of papillae have been found to be of no taxonomical significance.

Fibrils.

Fibrils are lateral appendages composed of cortex, medulla, and a central axis that may function as diaspores (e.g. U. filipendula). Their average length is 3-5 mm, but may reach up to 15 mm. In the pendulous species, it is particularly common to find the so called "fish-bone" pattern of arrangement, in which fibrils are more or less regularly distributed on both sides of the branches, giving an appearance of vertebrae of a fish. This pattern is particularly clear in U. angulata, U. filipendula, and U. transitoria (Fig. 5 d, e).

Fibercles

These structures are basically the scars left after the fibrils detach (Clerc and Herrera-Campos 1997), and as with the fibrils, they are composed of cortex, medulla, and central axis. Fibercles may also become sorediate and/or isidiate. Among the pendulous species studied they are characteristic of U. filipendula (Fig. 8 e).

Pseudocyphellae.

In Usnea we restrict the use of the word pseudocyphellae to those structures that are thin, elongated, fusiform discontinuities of the cortex that do not develop into soralia. Pseudocyphellae are constant and conspicuous in U. cavernosa and U. malmei, and may sometimes be inconspicuous in other species (Fig. 7).

Soralia

Soralia in these species produce farinose or granular soredia, usually in the gaps left after the detachment of isidiomorphs.

Soralia provide reliable characters, because their production and morphology correlate with variations of chemistry, distribution, and several morphological and anatomical features (Clerc 1987b). The following features are considered: origin (cortex, tubercles or papillae, fibril scars, cracks in the cortex, or nodules); situation with respect to the cortex (superficial, raised, or excavate); surface (plane, concave, convex, or capitate); size relative to the width of the branch bearing them (small, less than half of the branch, more than half of the branch, or surrounding the whole branch), shape (punctiform, circular, longitudinally and/or transversely oblong, irregular); density (separated, partially confluent, or totally confluent); margin (present or absent), location (on main branches, secondary branches, terminal branches, or fibrils) (Fig. 8 a-k).

Isidiomorphs

The thin and small isidia-like structures observed in Usnea are not homologous to the isidia s. str. found in other lichens. They are morphologically and anatomically identical with the "isidiod spinules" in Bryoria (Brodo & Hawksworth 1977) and may grow in the soralia (Hawksworth 1972; 1984), cracks of branches and rarely on cortex. Except for U. cavernosa, all sorediate species treated in this paper have the potential to produce isidiomorphs mainly on soralia; rarely on cortex or on cracks of the branches.

Apothecia

Usnea filipendula, U. subscabrosa, and U. merrillii were never found with apothecia. In most other sorediate species, apotheciate specimens were rare; however, in few specimens apothecia were abundant, as in U. transitoria (caperatic acid strain). When present, apothecia are terminal, subterminal, lateral, or serial (Fig. 9 a-d), with pruinous, circular to somewhat irregular discs, located on terminal or tertiary branches, or on fibrils.

ANATOMY

The cortex, medulla, and central axis have various characteristics that are often diagnostic in species delimitation (Clerc 1984, 1987).

Cortex

Cortices vary from mat and soft as in U. hesperina; to shiny and hard as in U. ceratina; or to vitreous as in U. subscabrosa, which has the thickest cortex (14% of the total width of the branch). U. mexicana and U. cavernosa have the thinnest cortex (5.5%) (Table 1, Figs. 10) Some specimens of U. subscabrosa have a reddish pigment in the cortex distributed as discrete points, but this feature is of no taxonomical value.

Longitudinal and transverse cracks in the cortex may occur in several species, sometimes with calcium oxalate (?) excretions. Similar excretions also occur between segments, as at the base of main branches in U. hesperina.

Medulla

Medullary tissues (Clerc 1987) may be loose with few separated and conspicuous hyphae (Fig. 10 b), dense with agglutinated and individually visible hyphae (Fig. 10 a), or compact with agglutinated but not individually visible hyphae (Fig 10 c and d).

Usnea transitoria and U. angulata have a compact and thin medulla, which is sometimes hard to see. These species have the thinnest medulla among all the species observed: 11% and 15%, respectively. On the other hand, U. scabrata has the widest medulla (31%) (Table 1). Pink or yellow pigments are usually present in the medulla of U. ceratina, although they may be patchy

Central Axis

The thickness of the central axis is inversely proportional to the thickness of the medulla in the species studied.

The axis may be sinuous as it is often the case in U. cavernosa or straight as in all other species. Sometimes the axis is fistulose as occurs in U. transitoria (Fig. 10 c) and in U. mexicana, but it is solid in other species The brownish to ochraceous central axis of U. mexicana is a constant and characteristic feature for this species. The medullary pink/yellow pigment of U ceratina sometimes extends into the axis.

CHEMISTRY

To the best of our knowledge, we provide the first report on the chemistry of pendulous Usnea in Mexico (Table 2). Usnic acid is present in large amount in the cortex of all species. These species produced mainly depsidones, of which salazinic acid was found in thirteen species. Protocetraric acid was detected in three species. U. hesperina, U. subscabrosa, and U. mexicana. This latter species, with three chemotypes, showed the largest chemical variability. Norstictic acid is diagnostic for U. angulata

Other secondary products included caperatic acid, the fatty acid found in U. transitoria. The ß-orcinol paradepsides diffractaic and barbatic acids are present only in U. ceratina and U. mexicana.

The species that showed a distinct chemistry were U. ceratina, U. cristatula, U angulata, U. malmei, and U. papillata.

The large infraspecific chemical variation found by Swinscow and Krog (1978) for the pendulous Usnea in East Africa, was not observed in the Mexican species, except for U. mexicana.

ECOLOGY AND DISTRIBUTION

All species occur commonly on Abies, Pinus, Quercus, and Alnus, and to a minor extent on Pseudotsuga and Cupressus. Occasional saxicolous specimens of U. ceratina, U. hesperina, and U. subscabrosa can also be found (Clerc and Herrera-Campos 1997).

Most collection sites ranged from 1300 to 4000 m (Fig. 11), although there were two lower collection sites (360 and 670 m) at which Pinus-Quercus forests occurred. The latter communities have holarctic affinities, and are unusual in their ability to penetrate into zones where warmer and dryer climatic conditions prevail (Rzedowskii 1981).

Usnea ceratina has the widest geographic and altitudinal (1300-3920 m) distribution, although it is not found in the forests of Baja California (Figs. 11, 12 c). One species with a very restricted distribution is U. scabrata, which is found mainly in subalpine localities at 3800 m in the Eje Neovolcánico (Figs. 11, 12 b). U. angulata and U. transitoria are superficially similar species that are chemically distinct and have clear differences in their geographical and altitudinal distribution. U. angulata's altitudinal range is narrower that of U. transitoria (Figs. 11, 12 j, l). The former species is found mainly in the east and south of the country in the Sierra Madre Oriental, Sistema Montañoso del Norte de Oaxaca, and Macizo Central de Chiapas. U. transitoria was collected in the west, center, and north of Mexico at Sierra Madre Occidental, Eje Nevolcánico Transversal, and the highlands of Sistema Montañoso de Baja California. Distributional overlap is so far limited to just one locality.

KEY TO MEXICAN PENDULOUS USNEA

1. Soralia (sometimes immature, and looking like small circular pseudocyphellae), and/or isidiomorphs present; apothecia absent or rare 2
1. Soralia, pseudocyphella-like structures, or isidiomorphs lacking; with few to many apothecia 11

2. Central axis ochraceous brown, brittle .... 11 U. mexicana
2. Central axis not ochraceous brown 3

3. Medulla with pink or yellow pigment (sometimes very faint); CK$^+$ deep yellow-orange, diffractaic acid present .... 3. U. ceratina
3. Medulla without pigments; CK- or CK+, never with diffractaic acid 4

4. Medulla K-, P+ red-orange; protocetraric acid as the main secondary substance 5

4. Medulla K+ yellow or red, P+ yellow or red, or K- P-, protocetraric acid never present 6

5 Cortex vitreous and hard, base often tinged with red................. 15. U. subscabrosa

5. Cortex mat and soft; base often tinged with orange............................. 8. U hesperina

6 Branch segments distinctly ridged or angulate; medulla very thin (10-15%), and compact; axis very thick (45-65%).. 7

6 Branch segments without distinct ridges or wings, at most striate; medulla thicker (20-30%), dense to compact; axis thinner (30-40%)......................... 8

7. Branch segments distinctly alate, with trapezoid-like segments; edges of wings eroded, opening longitudinally, and exposing the medulla; norstictic acid present.. 1. U. angulata

7. Branch segments not alate but distinctly ridged, edges of segments not opening longitudinally, medulla not visible; salazinic acid or caperatic acid present .... 16. U. transitoria

8. Branches regularly and conspicuously segmented, with distinct regeneration areas between the segments 9

8. Branches irregularly segmented, without regeneration areas between segments10

9 Pseudocyphellae conspicuous, often in patches on main branches; longitudinal cracks present; cortex vitreous and hard; stictic acid or unknown secondary substances UP1 and UP2 present.. 9.U. malmei

9. Without conspicuous pseudocyphellae; longitudinal cracks absent, cortex mat to shiny, and soft, salazinic acid present .... 10 U. merrillii

10. Branches irregular; segments slightly to distinctly swollen; soralia on low tubercles; fibrils few to numerous, irregularly disposed on branches .... 14. U. scabrata

10. Branches tapering; segments cylindrical; soralia on fibercles; fibrils numerous in fish-bone pattern .... 5. U. filipendula

11. Longitudinal cracks with involute edges .... 18 U sp 1
11. Longitudinal cracks without involute edges or absent 12

12. Branches distinctly foveate; papillae absent, cortex thin (4-8 %); central axis often sinuose .... 2 U. cavernosa
12. Branches not foveate; papillae usually present; cortex thicker; axis rarely sinuous 13

13. Central axis ochraceous brown, brittle .... 20. U. himantodes
13. Central axis neither ochraceous brown nor brittle 14

14. Medulla with pink or yellow pigment (sometimes very faint); CK+ deep yellow orange, diffractaic acid present .... 4. U. cristatula
14. Medulla not pigmented; C-, CK-, or CK+ reddish orange; diffractaic acid absent.. 15

15. Medulla K-, protocetraric acid as main secondary substance 16
15. Medulla K^+ yellow or red, protocetraric acid never present 17

16. Cortex mat and soft; base conspicuously annulated, tinged with orange . . .. 6. U. firma.
16. Cortex vitreous and hard; base not conspicuously annulated, tinged with red . . .. 17. U vitrea.

17. Branch segments distinctly ridged or angulate; medulla very thin (10-15%) and compact; axis very thick (45-65%).. 18
17. Branch segments without distinct ridges or wings; at most striate; medulla thicker (20-30%), dense to compact; axis thinner (30-40%) 19

18. Branch segments distinctly alate, with trapezoidal segments, edges of wings eroded, opening longitudinally and exposing the medulla; norstictic acid present ... . 19. U. alata
18. Branch segments not alate but distinctly ridged, edges of segments not opening longitudinally, medulla not visible; salazinic acid or caperatic acid present ....7 U. goniodes

19. Pseudocyphellae conspicuous , often in patches on main branches, with longitudinal cracks; cortex thick, vitreous, and hard; papillae frequent; unknown secondary substances UP1, and UP2 present .... 12. U papillata

19. Conspicuous pseudocyphellae and longitudinal cracks absent, cortex thin, mat and soft; salazinic acid present .... 13 U. sanctaeritae

TAXA

1. Usnea angulata Ach. Synops. Lich.: 307. 1814. TYPE. America septentrionalis, Muhlenberg (holotype, H-ACH 1800!). %C/%M/%A: 8/4.5/74. Chemistry: usnic, and norstictic acids (thin layer chromoatography by O. Vitikainen).

Usnea sulcata Lich. Gen. Usnea Stud. Monogr. Pars Syst. 2: 478. 1938. TYPE: BRASILIA. Minas Geraës, Sitio, 1885, Vainio (holotype, TUR-V 00450 !) %C/%M/%A. 8.5/14.5/55. Chemistry: usnic, and norstictic acids.

Thallus pendulous 10-90 (160) cm long, rigid, glossy, sparsely to moderately branched with anisotomic dichotomous and parallel branches; often with many points of attachment; trunk indistinct, sometimes up to 10 mm long, brownish, concolorous with or paler than the branches; branches [(0.4)-0.50-0.7-0.9-(1.7)] mm thick (n = 35), cylindrical, tapering only close to the apices, distinctly segmented; segments weakly to strongly alate, trapezoidal when optimally developed, edges of wings eroded and opening longitudinally exposing the medulla, apices thin, with few ramifications; papillae absent to numerous especially on main branches, large, cylindrical to truncate-conical; tubercles absent; fibrils numerous, 2-4 (6) mm, spinulous, in fish-bone arrangement; pseudocyphellae thin and elongated, inconspicuous, scattered; soralia arising on small and low elevations on the cortex of fibrils and small lateral branches, almost circular to longitudinally oblong, punctiform to wider than half of the branch, slightly to distinctly tuberculate, with a conspicuous cortical margin when mature; isidiomorphs on soralia, sparse, and not conspicuous; cortex thin [(4.5)-6-8.5 %-11-(15), n = 35], vitreous, sometimes producing schizidia, especially on the wings; medulla thin [(2)-8-14 %-20-(28.5), n = 35], compact; axis thick [(31)-41-53 %-65-(83), n = 35]; chemistry: usnic, and norstictic acids (n = 35).

Variation .– The variable features of U. angulata are the frequency of papillae and the development of soralia from absent to well developed

Distinctive features – Among the sorediate pendulous Usneae, this species is the only one having typically alate and trapezoidal segments that open at the top exposing the medulla. Other typical features are the glossy cortex, the anisotomic dichotomous branching pattern with fibrils in a fish-bone pattern, the very thick central axis, and the presence of norstictic acid as a main secondary substance.

A very similar species, U. transitoria, differs mainly in its branch segments, which are more frequently ridged rather than trapezoidal, thinner medulla (11%), type of soralia, and the presence of salazinic acid or caperatic acid as main medullary secondary substances.

Distribution and ecology.– The synonym U. sulcata, a very robust morphotype, is reported from Cuba, Jamaica, Mexico, Honduras Costa Rica, Colombia, Ecuador, Venezuela, Peru, Brasil, Argentina, Paraguay, and Africa (Motyka 1938). Two other taxa, U. asahinai, and U torquescens, given as synonyms by Awasthi (1986) are reported from Japan, New Zealand, Australia, and Tasmania (Motyka 1938, Asahina 1971). U angulata has also been reported from Mexico and United States (Motyka 1938; Fink 1971; Hale 1979), and India (Awasthi 1986). In Mexico it was collected in Chiapas, Guerrero, Hidalgo, Jalisco, Nuevo Léon, Oaxaca and San Luis Potosí (Fig. 12 j). Although it is predominately epiphytic on Quercus, Pinus, and Pyrus, it has also been found growing on Prosopis in tropical deciduous forests. Its altitudinal range is (360 m) 1500-2200 m (Fig. 11).

Exsiccatae examined.– Lich. Exs. COLO 316 (ASU); Lich. Can Exs. CANL 218 (ASU); Kurokawa and Kashiwadani, Lich Rar. et Crit. Exs. 350, 450, 550 (ASU).

Selected specimens examined.– MEXICO. CHIAPAS. km 11 of the road to Huiztlán, Herrera-Campos 4889 (MEXU). GUERRERO. Zihuaqueo-Filo Mayor, Hinton 9300 (COLO). HIDALGO. 100 km S of the bridge at Tamazunchale, along hwy. 85, Hellwigh 1240 (DUKE) JALISCO. North of Talpa, García 226. (IBUG). NUEVO LEON. Galeana, Hinton 18664 (ENCB); Cumbres de Monterrey. Puerto El Tejocote, Zambrano 11/29/1992. OAXACA. Along Pan-American Highway (km. 493-4), Iltis et al. 3039 (ENCB); Cerro del Veinte, Herrera-Campos 4884 (MEXU).

2. Usnea cavernosa Tuck., Agassiz, Lake Superior, p. 171. 1850. TYPE: America Septentr. ad oras Lacus superioris, Tuckerman (holotype, F!) %C/%M/%A: 3 5/36/21 (thallus a), 4/35/22 (thallus b). Chemistry: usnic acid (both specimens).

Thallus pendulous with parallel branches, up to 60 cm, isotomic dichotomously branched, flaccid, hanging loosely on branches and twigs, sometimes with several attachment points; trunk indistinct to short (1-2 mm long) paler than or concolorous to the branches; branches thick [(0.3)-0.45-0.6-0.75-(0.85)] mm (n = 39), cylindrical to irregular, tapering very slowly, commonly conspicuously foveolate; segments terete, striate, or weakly ridged, cylindrical; apices long, capillary, and sinuous; papillae absent; tubercles absent; fibrils absent to scarce and irregularly distributed, 1-3 (5) mm long;

pseudocyphellae fusiform to elongate-sinuous; soralia and isidiomorphs absent; cortex thin [(2 5)-4-6 %-8-(10.5), n = 39], shiny and smooth, with thin transverse cracks; medulla [(10.5)-19-25 %-31-(40.5), n = 39], dense, axis thick [(7.5)-27.5-38 %-48.5-(62.5), n = 39], straight to typically sinuous, apothecia rare, small (1-3 mm diam) subterminal; spores subglobose, (5)7-11 X 5-9 µm; chemistry· usnic acid and salazinic acid (n = 45).

Variation.– The shape of the branch segments is the most variable character of U. cavernosa; specimens from dryer areas seem to be more foveolate with irregularly deformed segments in cross section, in contrast with specimens from more humid, probably more protected areas, which have terete and distinctly striate segments with almost no foveolae.

Distinctive features.– The distinctive features of U cavernosa have mostly slender branches with numerous elongate-sinuous pseudocyphellae not developing into soralia and lacking papillae

Some thalli may look superficially similar to U. trichodea and U. merrillii, which differ in their distinctively and regularly segmented branches with cylindrical, not foveolate segments, straight axis, and the presence of fibrils, soralia, and isidiomorphs. The colored axis and the chemistry also make U. trichodea different.

Distribution and ecology.– Usnea cavernosa is a circumpolar, boreal to temperate species (Thomson 1984), reported from Central Europe to Northern Central Asia, and North America from Alaska to Mexico, and Cuba (Motyka 1938; Thomson 1984) However James et al. (1992) mention that reports of this species for the British Isles may be based on specimens collected outside the isles. Halonen et al. (1998) report this species from British Columbia scattered along the coast at low elevations under 500 m and less frequent towards inland areas. Hale (1979) refers it from the conifers from the northeastern United States and Canada, and also from the front ranges of the Rocky Mountains through Colorado, New Mexico, and Arizona.

In Mexico, it grows on Pinus, Abies, and Alnus from 1800 to 3900 m (Fig. 11), and ranges from northern Baja California, northwestern Sierra Madre Occidental (Chihuahua, Sonora, Sinaloa, and Durango) to the Eje Neovolcánico Transversal (Estado de México, Jalisco-Colima, Michoacán, and Puebla). Its southern limit is in the southern Sierra Madre Oriental (Hidalgo) (Fig. 12 a). Its presence in Baja California Norte is consistent with that flora's affinities to western North America, as clearly established for vascular plants by Rzedowskii (1981, 1993) and for mosses by Delgadillo (1993).

Selected specimens examined.– MEXICO. BAJA CALIFORNIA NORTE. San Pedro Mártir, Nash 14656. (COLO); Herrera-Campos 4581 (MEXU). DISTRITO FEDERAL. Mountain Tlaloc, Antipovich 121 (COLO). NUEVO LEON Vertiente NE del Cerro

Potosí Mpio. de Galeana, Rzedowski 27163-A (ENCB) CHIHUAHUA, Nash 36435 (ASU). Road Basaseachic-San Juanito, Herrera-Campos 2427 (MEXU). ESTADO DE MEXICO. Volcán Popocatepetl, Ruiz Oronoz 6/8/1957 (MEXU). 8 km from El Paso de Cortés, Herrera-Campos 2332 (MEXU). SONORA, Felger et al. 92857 (ARIZ). PUEBLA. Pico de Orizaba, Smith 2/24/1892. (LAM). DURANGO 2 km from the border with Sinaloa, 1 km from Barranca de Liebre, Herrera-Campos 2574 (MEXU).

3. Usnea ceratina Ach Lichen. Univ 610. 1810. TYPE: (Poland) Silesia, Mosig (holotype, H-ACH 1890 !). %C/%M/%A: 9.5/23/35. Chemistry: usnic, diffractaic, barbatic, and squamatic acids.

Usnea solida Motyka, Lich. Gen. Usnea Stud. Monogr Pars. Syst. 2: 382. 1938. TYPE: MEXICO, Veracruz, Jalapa, 1840, Galeotti (holotype,W !). %C/%M/A%: 12.5/21/33. Chemistry: usnic, diffractaic, and barbatic acids, and several unknown substances from the diffractaic group

Thallus erect to pendulous, 3-70 cm long, isotomic to anisotomic dichotomously ramified, branches divergent or parallel; trunk 2 5-13 mm, rarely up to 25 mm, concolorous with or paler than the branches, or yellow to dark brown pigmented, branches [(0 5)-0.7-1.0-1.3-(2.3)] mm thick (n = 123), cylindrical to irregular, slightly or conspicuously foveate or transversely furrowed; segments terete, striate, or weakly ridged; cylindrical or slightly swollen; apices short and thick to long and slender; papillae absent to numerous, from indistinct to verrucose; tubercles always present, usually abundant, conspicuous; fibrils numerous, spinulous (1-3 (4) mm) and long (10 mm), irregularly distributed; pseudocyphellae absent; soralia arising from the cortex, on tubercles or striations, located mainly on the fibrils, plain to convex, frequently capitate, occasionally excavate, punctiform to wider than half of the bearing branch, with margin, rarely confluent, when crowded curving the tips of fibrils; isidiomorphs mainly on soralia, also cortical, and along the edges of longitudinal cracks; cortex [(3)-6.5-9 %-11.5-(18), n = 123] thick, shiny to vitreous, hard, smooth to densely cracked; medulla [(12.5)-19-24 %-29-(38.5), n = 123] thick, dense to compact, rarely loose, pink, and/or yellow pigmented; axis [(9)-26.5-34.5 %-42.5-(57), n = 123] thick, white, translucent, wine red, pink or yellow pigmented; apothecia rare, terminal or subterminal, 1.5-5 mm diameter; chemistry: usnic, diffractaic, ± barbatic, ± squamatic acids, ± unknown fatty acid (C: 3-4), ± unknowns C· 1-2, 5 (n = 75).

Variation.— This is the most polymorphic of the sorediate pendulous species. The variable features include the growth habit, ramification pattern, thickness of the branches, segment shape, and abundance of tubercles, soralia, isidiomorphs, and fibrils The general appearance of the thallus varies from extremely coarse to slender, and its consistency from rigid to flaccid. There is a continuum of morphs from very rigid, coarse, erect thalli to long, slender, pendulous ones, that may have isotomic, anisotomic or filamentous dichotomous ramification The segments of the branches vary from terete to moderately ridged in cross section, and in longitudinal section they may be circular, swollen or sometimes deformed by the presence of depressions in the cortex like transverse furrows. The soralia vary in size from punctiform to very broad, with more than half of the branches bearing them. The isidiomorphs, besides being present on the soralia, can also develop on the cortex or along the edges of longitudinal cracks. The concentration of the pigment in the medulla and axis is also variable.

Distinctive features.– Usnea ceratina is characterized by the rigidity and coarseness of the thallus, its very hard and shiny to vitreous cortex, the presence of conspicuously sorediate tubercles, its pinkish pigmented medulla and axis, and the occurrence of diffractaic acid as the main secondary substance.

The pendulous thalli of U. ceratina can be distinguished from U. filipendula in that the latter species has smaller soralia arising on fibril scars (fibercles) that are distributed over the entire thallus, its softer, and mat cortex, its unpigmented medulla, and the occurrence of salazinic acid as the main secondary substance in the medulla.

Usnea subscabrosa also is similar to U ceratina, but the medulla of the former species is never pigmented, the soralia are smaller and do not arise on large tubercles, the basal part is often reddish, and protocetraric acid is produced as the main secondary substance.

Under non-favorable conditions, such as in polluted environments, the shrubby forms of U. ceratina resemble normal thalli of U. cornuta Körber, with typically curved apices (James et al. 1992). This was observed in collections from environs of Mexico City. U. cornuta is a small, shrubby species that has a very characteristically loose unpigmented medulla and thin axis, and it does not produce diffractaic acid.

Usnea solida is a morphotype in which the medullary pigment is not visible.

Distribution and ecology.– Usnea ceratina has a wide world distribution. In the Northern Hemisphere, it occurs in Europe from the British Islands (James et al. 1992) to Russia (Motyka 1938; Schindler), and in North America from Canada to Mexico (Hale 1979, Halonen et al. 1998; Motyka 1938), and in Asia (Asahina 1965, 1973).

Its synonym U. solida has been cited for México, Costa Rica (Motyka 1938), and from Venezuela (López 1986).

In Mexico, U. ceratina has the widest geographical and altitudinal distribution of all the species considered herein. Although it is not found in the forests of Baja California, it clearly follows the distribution of the mainland temperate forests in the physiographic provinces described by Rzedowski (1981) (Fig. 1). Although it grows better in the more humid woodlands in the Eje NeovolcánicoTransversal, and Sierra Madre Oriental, it has occasionally been found in subtropical forests. It has been collected in Chiapas, Chihuahua, Durango, Estado de México, Hidalgo, Jalisco, Jalisco-Colima, Mexico City, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tlaxcala, and Veracruz (Fig. 12 c). Its altitudinal range is (670) 1300-3920 m (Fig. 11) mainly on Abies, Quercus, Pinus, Alnus, Pseudotsuga, members of the Compositae, Prunus and Pyrus, and occasionally on rocks (Clerc and Herrera-Campos 1997).

Selected specimens examined.– MEXICO. OAXACA. Mpio. Ixtepeji. Sierra Juárez, Iltis 27180. (MEXU). MORELOS. Serranía del Ajusco, Iltis et.al. 1666 (ENCB). PUEBLA. Esperanza, 2400 m, Arsène 4268. (COLO) HIDALGO. El Chico, Ruiz-Oronoz 1948; Herrera-Campos 657, 4369 (MEXU); Nash III 38038 (ASU). DISTRITO FEDERAL. Desierto de Los Leones, Herrera-Campos 1452 (MEXU). ESTADO DE MEXICO. Road to Sultepec 2 km from La Guacamaya, Herrera-Campos 1602.4 (MEXU). MORELOS. Lagunas de Zempola. Camino Santiago Tianguistengo-Huitzilac, 6 km from the detour to Huitzilac, Herrera-Campos 1723 (MEXU). DURANGO. 2 km from the border with Sinaloa, 1 km from Barranca de Liebre, Herrera-Campos 2568 (MEXU). MEXICO. Volcán de Colima, Kerba 3015 (BERN).

4. Usnea cristatula Motyka Lich. Gen. Usnea Stud. Monogr. Pars. Syst. 2: 641. 1938. TYPE: MEXICO, Michoacán, Morelia, Cerro Azul, 3300 m, Brouard (holotype, LUB !). %C/%M/%A: 13/16.5/41. Chemistry: usnic, diffractaic, and squamatic acids.

Thallus erect to pendulous, 3-70 cm long, isotomic to anisotomicaly dichotomous ramified, branches divergent or parallel; trunk 2.5-13 -(25) mm, concolorous with or paler than the branches, yellow to dark brown; branches [(0.6)-1-1.4-1.8-(2.1),n = 27] mm thick, cylindrical to irregular, slightly or conspicuously foveate and/or transversely furrowed; segments terete, striate to weakly or strongly ridged, cylindrical, slightly swollen or trapezoidal; apices short and thick to long and fine, papillae absent to numerous, from indistinct to verrucose; tubercles always present, regularly abundant, conspicuous; fibrils numerous, spinulous (1-3 (4) mm) and long (10 mm), irregularly distributed; pseudocyphellae punctiform, elliptical, on the cortex or on top of tubercles; cortex [(6)-8.5-11.5 %-14.5-(16.5), n = 27] thick, shiny to vitreous, hard, smooth to very cracked; medulla [(12)-17-21.5 %-26-(33), n = 27] thick, dense to compact, rarely loose, pink and/or yellow pigmented; axis [(21.5)-27-34 %-41-(48.5), n = 27] thick, white, translucid, wine red, pink or yellow pigmented; apothecia terminal or subterminal, 1.5-5 mm diameter; chemistry: usnic, diffractaic, ± barbatic, ± squamatic acids, ± unknown fatty acid (C: 3-4), ± unknowns C: 1-2, 5 (n = 27).

Variation.— Except for those characters related to soralia, U. cristatula has similar variation to that found in U ceratina.

Distinctive features.— The pigmented medulla together with the presence of large tubercles, shiny to vitreous cortex, and distinct chemistry make this species easily recognizable among the pendulous taxa without soralia. We consider U. cristatula to be the primary species of U. ceratina.

Distribution and ecology.— Usnea cristatula is only known from Mexico (Motyka 1938). Among the pendulous primary species, U. cristatula has the widest distribution range in the country. As might be expected, U. cristatula has a slightly more restricted distribution than U. ceratina. Both were collected in the same localities and substrata in all physiographic provinces, except in Chiapas, where U. cristatula was not found (Figs. 11, 12 d).

According to their known worldwide distribution in Fig. 2, it is probable that U. cristatula and U. ceratina have arisen in Mesoamerica and only U. ceratina succeeded in invading other continents.

5. Usnea filipendula Stirton, Scott. Naturalist 6: 104. 1881, s. lat. TYPE: America borealis. Roy (holotype BM, not seen).
Usnea sublaxa Vain. ex Motyka, Ann. Univ. Marie Curie-Sklodowska, Sect. 3, Biol. I, 9: 217, 1936 TYPE. FINLAND Tavastia· Lammi, Evo. In betulis, Norrlin (holotype, TUR-V 34747 !). %C/%M/%A: 10/21/38. Chemistry· usnic acid.

Thallus pendulous, up to 60 cm long, with anisotomic to isotomic dichotomous branching, and parallel branches; trunk usually well developed, over 1-15 mm, with distinct annular cracks sometimes attenuated at point of attachment, distinctly jet black pigmented, branches [(0.35)-0.5-0.75-1.0-(1.25)] mm thick (n = 35), tapered to cylindrical, distinctly segmented, often exposing the medulla or the axis, main branches distinctly darker than the rest of the thallus; segments terete and cylindrical; apices clearly anisotomic dichotomous, often capillary, with few ramifications; papillae cylindrical to conical, sparse to numerous, mostly on main branches; tubercles absent; fibercles abundant; fibrils 2-10 mm long, numerous and conspicuous, arranged in fish-bone pattern, frequently detaching and leaving fibercles; pseudocyphellae inconspicuous, linear on small branches; soralia arising from fibercles, ± punctiform, rarely enlarging, and reaching more than half of the bearing branch, plane to convex, circular, without margin, rarely confluent; isidiomorphs conspicuous and numerous, mostly on young soralia; cortex [(6.5)-7.5-9 5

%-11 5-(13), n = 35] thick, mat to slightly shiny; medulla [(11)-17-22 %-27-(30 5), n = 35] dense to compact; axis [(21.5)-26.5-36 5 %-46.5-(58), n = 35] thick; apothecia absent; chemistry usnic acid, and salazinic acid (n = 51).

Variation.– Usnea filipendula is a very variable species with many different morphotypes that vary in characters such as the thickness of the branches, the pattern of ramification, the abundance of isidiomorphs, soralia, papillae, and fibrils as well as the density of the medulla, and the appearance of the cortex. A world revision of this group is necessary to decide if it includes different species or not.

Distinctive features.– Usnea filipendula s lat. is characterized by a black base, main branches that are distinctly darker than the rest of the thallus, cylindrical segments, fish-bone pattern of the fibrils, numerous fibril scars or fibercles on which isidiomorphs and soralia develop (Clerc and Herrera-Campos 1997). Pendulous thalli of U. madeirensis resemble U. filipendula but have distinct and numerous annular cracks at the base, a thinner, and more compact medulla, and larger soralia arising ab initio on the cortex, and not on fibril scars. U. scabrata is sometimes difficult to separate from U filipendula but it has irregular branches often with weakly sausage-like segments, a different type of soralia mainly arising on small eroded tubercles, and fibrils that are not in fish-bone pattern.

Distribution and ecology.– The distribution of this species is circumpolar in boreal to northern temperate regions (Thomson 1984). It has been reported from southern to northern Europe, northern Asia (Siberia), western North America, and Mexico (James et al. 1992; Motyka 1936-38). In the United States (Hale 1979 as U. dasypoga) it is present on the west coast and other inland locations, as well as in the northeastern part of the country where it is coastal, down to the southern Appalachians.

Thomson (1984) mentions that this species occurs more commonly on the West coast than on the East coast, but in Mexico it was collected mainly along the eastern side of the country, in the Eje Volcánico Transversal (Jalisco-Colima border, Morelos, Estado de México, Mexico City, Estado de México-Michoacán border, Hidalgo, Puebla, and Veracruz) Sierra Madre Oriental (Veracruz and Nuevo León), and Sistema Montañoso del Norte de Oaxaca as its southern limit (Fig. 12 i).

Selected specimens examined.– MEXICO. DISTRITO FEDERAL. Desierto de los Leones, Ruiz-Oronoz January 1940 (MEXU). VERACRUZ. Nash 35775 (ASU). HIDALGO Presa Jaramillo, Rzedowski 29-VII-1978 (ENCB). El Chico, Herrera-Campos 678 (MEXU). Laguna de Atezca, Herrera-Campos 281 (MEXU). ESTADO DE MEXICO. Road to Sultepec, 2 km from the detour to La Guacamaya, Herrera-Campos 1689 (MEXU). 8 km from El Paso de Cortés 2350 (MEXU). VERACRUZ. Cofre de Perote, Nash 35775 (ASU).

6 Usnea firma Motyk, Lich. Gen. Usnea Stud. Monogr Pars. Syst. 2: 410. 1938.
TYPE· BRAZIL. Teresiopolis, Wawra (W, holotype, not seen; LBL nr 005218! isotype). %C%M%A. 8/17/59. Chemistry: usnic and protocetraric acids.

Thallus pendulous up to 55 cm long, isotomicaly to anisomicaly dichotomous branched, with branches mostly parallel; trunk conspicuously annulate, 2-12 mm long, usually orange-brown pigmented; branches [(0.6)-0.8-0 9-1 0-(1.1) mm thick (n = 12), distinctly annulated in the basal parts, cylindrical, tapering very slowly, segmented, segments terete and cylindrical, apices thick, papillae absent; tubercles absent, fibrils long (5) - 10-20 -(30) mm, curved, few, and irregularly distributed to numerous, and in a fish-bone arrangement; pseudocyphellae absent; soralia absent; isidiomorphs absent; apothecia lateral, (1.5)-2.5-12.5 mm diameter, on small branches and fibrils; spores 7 5-10 5 X 4.5-7.5 µm; cortex [(7)-8-10.5 %-13-(13.5), n = 12] thick, mat; medulla [11)-12-14.5 %-17-(19), n = 12] thick, compact; axis [(43 5)-46 5-50 %-53.5-(55), n = 12] thick; chemistry· usnic and protocetraric acids (n = 8).

Variation.–The variation of the characters is the same as in U hesperina, with the exception that soralia that are absent in U. firma.

Distinctive features.– Usnea firma is the primary species of U. hesperina. It has a very similar morphology, anatomy, and chemistry. Among the other pendulous, esorediate species, it is fairly well characterized by the cortex, orange-brown annulated base, cylindrical and terete segments, and by the production of protocetraric acid as the main secondary substance in the medulla. U. vitrea has the same chemistry, but has a thick and vitreous cortex and a not so conspicuously annulated base with a dark reddish pigment.

As in U hesperina, U. firma is characterized by a thick axis, mat cortex, orange-brown annulated base, cylindrical segments, and protocetraric acid as the main secondary medullary substance.

It is distinguished from U. vitrea, which may have the same chemistry and a does have reddish base, mainly because U firma has a mat, and soft cortex and lacks soralia.

Distribution and ecology.– It is collected in Chiapas, Hidalgo, Oaxaca, and Veracruz in conifer and oak forests on Alnus, Quercus, and Abies at an altitudinal range of 1500-2730 m (Fig. 11, 12- h).

Selected specimens examined.– MEXICO. HIDALGO. Parque Nacional El Chico, Herrera-Campos 637, 4554, 4555 (MEXU). VERACRUZ. Cruz Blanca, Herrera-Campos 14 (MEXU). Santa Rita, Herrera-Campos 396, 403, 5482 (MEXU). Road Naolinco-Misantla, detour to Landero, and Coss, Herrera-Campos 260 (MEXU).

7. Usnea goniodes (Stirt.) Motyka, Lich. Gen. Usnea Stud. Monogr. Pars. Syst. 2 396. 1938.

Usnea angulata Ach. subsp. goniodes Stirt., Scott. Nat. 6: 108. 1881. TYPE: SOUTH AFRICA, Bolus s n et d. (holotype, BM!). %C/%M/%A: 5.5/15/59. Chemistry: usnic and caperatic acid. Thallus pendulous, up to 250 cm long, rigid, poorly to moderately branched, with anisotomic dichotomous and parallel branches; often with many points of attachment; trunk indistinct, sometimes up to 10 mm long, brownish, concolorous with or paler than branches, annulate; branches [(0 3)-0.5-0.8-1.1-(1.7)] mm in diameter (n = 30), cylindrical, tapering only close to the apices, sometimes areolated, and cracked, rarely with erose cortex; segments ± weakly to strongly ridged, slightly alate, cylindrical to slightly trapezoidal; apices thin, with few ramifications; papillae absent, tubercles conspicuous, abundant, large, cylindrical to truncate-conical, paler at the top, often eroded, irregularly distributed on main and secondary branches; fibrils short (0.5-2 mm), and long (3-10 mm), mostly spinulouse, in a fish-bone arrangement; pseudocyphellae linear, inconspicuous; soralia absent; cortex [(1.5)-5.5-8.5 %-11.5-(15), n = 30] thick, shiny, medulla [(1.5)-4-9.5 %-14 5-(26), n = 30] thin, compact; axis thick [(18.5)- 49 5-64 5 %-79.5-(94), n = 30], often fistulose at the base of main branches; apothecia up to 2 cm in diameter, lateral; spores 10.5-12.5 X 7μ chemistry: 1, usnic acid and salazinic acid, 2, usnic and caperatic acid (n = 34).

Variation.— The thickness of the main branches and the density of fibrils are quite variable in this species. A gradation can be observed between segments being from weakly to strongly ridged, sometimes slightly alate in cross section, and longitudinally cylindrical to trapezoidal.

Distinctive features.— Usnea goniodes is the primary species of U. transitoria, from which is differentiated by the absence of soralia and isidiomorphs. Swinscow and Krog (1978) did not separate the species. Their figure 26, showing thalli with soralia and isidiomorphs suggests U. transitoria, which may then be new for Africa. Among the non-sorediate pendulous Usneae, U. goniodes is characterized by segment shape, anisotomic dichotomous branching with fibrils arranged in fish-bone pattern, a thick axis, and salazinic acid or caperatic acid as the main secondary substance.

Distribution and ecology.— Usnea goniodes has been reported previously only for Africa (Motyka 1938; Duvigneaud 1952, Dodge 1956, 1957; Herre 1960; Swinscow, and Krog 1978), and is first reported here for the American continent. The connection between the African and Mexican flora is recognized for bryophytes and phanerogams (Delgadillo 1993; Rzedowski 1993).

In Mexico U. goniodes has a more restricted distribution than its secondary species U. transitoria. It is only found in few localities where the latter species has not been collected, for example north in Monterrey, and further south in Oaxaca Both species are the only pendulous ones present in Baja California Sur (Figs. 11, 12 l and m)

Selected specimens examined.– MEXICO. BAJA CALIFORNIA SUR. Sierra de Laguna, Herrera-Campos 4667 (MEXU); JALISCO. Volcán Nevado de Colima, Herrera-Campos 4662, 4664 (MEXU); Real Alto La Bufa, Y. Mexia 1603-a (G). MICHOACAN. Volcán Tancítaro. Barranca del Cuartel, Herrera-Campos 4665 (MEXU); 33 km E of Uruapan on the road to Patzcuaro, Culberson and Culberson 18078 (DUKE).

8 Usnea hesperina Motyka, Lich. Gen. Usnea Stud. Monogr Pars. Syst. 2: 383. 1938.
TYPE: ESPAGNE [SPAIN], ILES CANARIES, Tenerife, La Laguna, Monte Las Mercedes, Lomo del Boqueron, 740-780 m, dans la pente boisée en exp. SW, Laurisylva-Fayal-Brezal, sur les branches de Laurus, 12 september 1986, P. Clerc (neotype, G !). %C/%M/%A. 9.5/24/34 Chemistry: usnic, and protocetraric acids. (Clerc, 1997).

Usnea subgracilis Vainio, Ann. Acad. Sci. Fenn., Ser. A. 6. 7. 1915. TYPE. Jamaica, in ramibus arborum, 1906, Boergesen (holotype, TUR-V 513 !) %C/%M/%A: 12 5/16/43 Chemistry: usnic, and protocetraric acids

Note - U. hesperina is a laater hoonym of U. subgracilis (Clerc 1997) and a proposal to conserve U. hesperina will be made elsewhere.

Thallus pendulous up to 55 cm long, isotomic to anisotomic dichotomously branched with branches mostly parallel; trunk conspicuously annulate, 2-12 mm long, usually orange brown pigmented, branches [(0.5)- 0.55-0.70-0.85-(1.12)] mm (n = 53), segmented, tapering very slowly, distinctly annulated in basal parts; segments terete and cylindrical; apices thick; papillae absent; tubercles absent; fibrils long (5)- 10-20 -(30) cm long, curved, few, and irregularly distributed to numerous, and in a fish-bone pattern; pseudocyphellae absent; soralia punctiform, arising at the surface of the cortex often on small elevations and then very slightly tuberculated, convex, sometimes confluent, often immature and resembling pseudocyphellae, rarely mature and enlarged; isidiomorphs very small, on young soralia and regenerative parts; apothecia absent or rare, on small branches and fibrils, subterminal; cortex [(3.5)-8 5-11.5 %-14.5-(20.5), n = 53] thin, mat; medulla [(6.5)-10 5-14.5 %-18.5-(23), n = 53] thin, compact; axis [(27)-37-47.5 %-58-(80), n = 53] thick; chemistry: usnic and protocetraric acids (n = 44).

Variation.– In U. hesperina the most variable characters are the frequency, and arrangement of fibrils, from nearly absent and irregularly distributed to frequent and in fish-bone pattern, the presence of everted medulla rings, (calcium oxalate ?), and the density and development of soralia from absent to enlarged with isidiomorphs.

Distintive features._ Morphologically, anatomically, and chemically U hesperina is a very distinctive species in the genus. It is mainly characterized by cylindrical branch segments, mat and soft cortex, thick axis, conspicuously annulated base that usually is orange-brown, and the production of protocetraric acid as main secondary substance in the medulla.

In comparison with U subscabrosa, which may have the same chemistry and a reddish base, it is mainly distinguished on the basis of cortex and different type of soralia.

Distribution and ecology ._ Motyka (1936-1938) reported U hesperina from western Europe, some Atlantic islands (Canary and Madeira Islands), from eastern North America, and Jamaica Clerc (1997) reported that this species was new for Africa and South America (protocetraric strain) as well as for Asia (stictic acid strain). It has also been collected on conifers in British Columbia in very maritime conditions (Halonen et al. 1998).

Its distribution in Mexico is mainly on the east side in the Sierra Madre Oriental (Nuevo León, San Luis Potosí, Hidalgo, Puebla, and Veracruz), Sonora, central and eastern part of Eje Volcánico Transversal (Morelos, Estado de México-Puebla border), Sistema Montañoso del Norte de Oaxaca, and Sierra, and Macizo Central de Chiapas (Fig. 12 g). It is mostly corticolous, although a few specimens were found growing on rocks; it was collected mainly in Quercus forests and Liquidambar cloud forests, Pinus, and mixed forests at altitudinal range of 1500-3690 m, and at 360 m in a relic Pinus-Quercus forest adjacent to a tropical rain forest. This distribution pattern suggests that it is a species that reflects Mexican flora affinities with eastern North America and the Caribbean area, a pattern also described for vascular plants (Rzedowski 1981) and bryophytes (Sharp 1939; Delgadillo 1993).

Selected specimens examined _ MEXICO. COAHUILA. Cd. Acuña. Heeds April 1949. ex. L. H Bailey Hortorium. (NY). -PUEBLA. Huachinango, Fröderstròm and Hultén. 12/20/1932. (COLO). PUEBLA-ESTADO DE MEXICO. Los Volcanes. Paso de Cortés, Herrera-Campos 1972 (MEXU). HIDALGO. El Chico, Herrera-Campos 636 (MEXU). Zacualtipán, Herrera-Campos 1366 (MEXU). MORELOS. Lagunas de Zempoala. Ocoyotongo, Herrera-Campos 1726 (MEXU). NUEVO LEON. Cumbres de Monterrey. El Tejocote, Zambrano 11/29/1992 (MEXU). SAN LUIS POTOSI. El Potosí. Cañada Grande, Zambrano 11/28/1992 (MEXU). VERACRUZ. Cruz Blanca, Herrera-Campos 5 (MEXU).

9. Usnea malmei Motyka, Lich. Gen. Usnea Stud. Monogr. Pars. Syst 2: 381. 1938. TYPE. BRAZIL. Rio Grande do Sul, Hamburgerberg, 26.X.1892, Malme (holotype, UPS !). %C/%M/%A:13.5/13.5/45. Chemistry· usnic, salazinic, and norstictic acids, unknown sibstances UP1, UP2

Usnea sorediata (Zahlbr.) Motyka Lich Gen. Usnea Stud. Monogr. Pars. Syst. 2: 382. 1938. TYPE: BRAZIL. Mono de St. Sebastiano, Serra do Proto, Damazio (holotype,W 7446!). %C/%M/%A· 17/7.5/51. Chemistry: usnic, stictic, constictic, cryptostictic acid, and norstictic (trace?) acids, unknown substances UP1, UP2

Thallus pendulous with parallel branches up to 75 cm, anisotomic dichotomously branched, rigid; trunk 1-5 (7) mm, annulate, paler than main branch to brownish; branches [(0.7)-0.7-0.8-0.9-(.0.95)] mm thick (n = 5), cylindrical, tapering very slowly, with numerous transverse cracks (3-7 cracks/0.5 cm), distinctively paler margins (regenerating cortex), and short longitudinal cracks connected to the transverse ones; segments terete and cylindrical; apices slender with few ramifications; papillae indistinct to verrucose, irregularly distributed; tubercles absent; fibrils sparse, on main and secondary branches, long 3-15 (20) mm; pseudocyphellae very abundant and conspicuous, somewhat irregularly distributed in patches, irregularly shaped, punctiform, fusiform to elongate; soralia punctiform, slightly tuberculate, plane to convex, ± circular, without margin, sometimes confluent; arising on cortex or at the edge of annular cracks; isidiomorphs on mature soralia sparse; cortex thick [(6.5)-8-13 %-18-(18), n = 5], vitreous; medulla compact, hardly distinct [(9.5)-9-14.5 %-20-(24 5), n = 5]; axis thick [(32.5)-35-45 %-55-(60) n = 5]; apothecia absent; chemistry: usnic acid, unknowns UP1, and UP2, terpenes, ± stictic acid gr.

Variation.— The variable features of U malmei are the density of ramification and fibrils, the size of its main branches, and the length of the mature thalli.

Distinctive features.— Among the pendulous species, U. malmei is easily recognized by its very hard and vitreous cortex, its conspicuous pseudocyphellae characteristically arranged in patches, its soralia type, its very thin and compact medulla, and the presence of the unknowns UP1 and UP2 in the medulla.

Usnea subscabrosa also has vitreous and hard cortex, but lacks the type of pseudocyphellae present in U. malmei, and its main secondary substance is protocetraric acid. U. ceratina as well may have a very thick, and vitreous cortex but also lacks the pseudocyphellae, and has a larger pink-pigmented medulla, a different type of soralia, and a different chemistry. In addition, U. papillata is mainly distinguished from U. malmei by the absence of soralia and the presence of apothecia.

Distribution and ecology.— U. malmei and its synonym U. sorediata had previously only been known from Brazil (Motyka 1938). Thus, U. malmei is new for Mexico where it has been collected at an altitudinal range of 1500-2500 m in coniferous and cloud forests in Chiapas, Guanajuato, Hidalgo, Jalisco, Oaxaca, and Veracruz, states which also have important stands of more tropical vegetation (ie. tropical deciduous or rain forests). U malmei and U mexicana have their northern limit at the Eje Neovolcánico. In contrast to U mexicana and U angulata, U malmei was not found growing in tropical woodlands (Figs. 11, 12 p).

Selected specimens examined.— MEXICO CHIAPAS. Grutas SE from San Cristóbal de las Casas, Herrera-Campos 5483 (MEXU); km 11 road to Huixtán, Herrera-Campos 2748 (MEXU). JALISCO. Manantlán. Las Joyas, Herrera-Campos 5484 (MEXU). OAXACA. Cerro del 20, Barranca del Aguacatillo, Herrera-Campos 2754 (MEXU)

10. Usnea merrillii Motyka, Lich. Gen. Usnea . Stud. Monogr. Pars. Syst. 2. 371. 1938. TYPE USA, Maine, Matinicus Island, viii. 1909 G. K. Merrill, Lich. Exs. G. K. Merrill Nr. 64, U. ceratina (lectotype, W 4785 !) %C/%M/%A: 13/16/41. Chemistry usnic, and salazinic acids.

Thallus decumbent to pendulous with parallel branches, up to 50 cm, isotomic dichotomously branched, flexible, hanging loosely on branches and twigs or with several attachment points; trunk indistinct to long (up to 7 mm), sometimes annulate, concolorous with or paler than the branches, sometimes blackish; branches thin [(0.35)-0.45-0.56-0.67-(0.85),] mm (n = 60), cylindrical, all of them almost of the same diameter, tapering very slowly, distinctly sinuous, densely segmented and annulately cracked (up to 12 cracks/0.5 cm), with areas of regeneration of the cortex in between segments looking like irregular beads; segments terete and cylindrical; apices long, capillary, sinuous, anisotomic dichotomous; papillae absent to scattered, indistinct; tubercles absent; fibrils long (5-12 mm), irregularly distributed; pseudocyphellae irregularly fusiform; soralia arising on cortex or on eroded papillae, punctiform, slightly tuberculate, convex, circular to irregular, rarely confluent; isidiomorphs on soralia, inconspicuous, sparse, cortex thin [(6)-10-13 %-16-(21), n = 60] mat to slightly shiny; medulla thin [(7.5)-14-18 %-22-(28.5), n = 60], compact, axis thick [(25)-32-38.5 %-45-(53), n = 60]; apothecia rare; chemistry: usnic and salazinic acids, ± unknown yellow C: 5-6 (n = 66).

Variation.— The most variable characters of U. merrillii are the frequency of soralia from few to numerous, the size of the thallus, the density of branches, and the degree to which regeneration areas between segments are developed.

Distinctive features.– The characteristic features of this species are its entangled growth habit with many attachment points, its slender, cylindrical, conspicuously segmented branches with terete segments, its very distinct pattern of cortical regeneration between the segments, and its slightly raised, small, convex soralia.

Usnea merrillii shares the same segmentation pattern as U. malmei, with bead-like cortical regeneration among the segments, but it differs from the latter species by its growth form (decumbent with many attachment points), its absence of large pseudocyphellae, its non-vitreous cortex, and its chemistry. U. merrillii resembles U. trichodea, but the latter species has an ochraceous axis, a branch segmentation pattern without conspicuous regeneration areas, and a different chemisty. U. merrilli may also be similar to U. hesperina, but the latter species does not have multiple attachment points, and has thicker branches, a segmentation pattern without conspicuous regeneration areas, a mat cortex, and protocetraric acid as main secondary substance in the medulla.

Distribution and ecology.– Usnea merrillii has been reported from Canada, eastern and southern United States (Motyka 1938). Asahina (1965) also mentions it from southern Mexico (Chiapas) and Japan, but he wrote that U. merrillii "coincides completely" with U. cribrosa Asah. However, the latter species is a synonim of U. malmei (Clerc unpublished). Therefore, the specimens of U. merrillii reported herein are thus the first verified material for Mexico This species shows the affinities between Mexican and eastern United States flora, a pattern that is well documented for vascular plants and bryophytes. In the absence of reports from other areas, it is assumed that U. merrillii originated on the American continent, perhaps in tropical latitudes, and then migrated northwards. It is known that some tropical bryophytes have extended their distribution in eastern North America into formerly glaciated territory (Sharp 1939).

In Mexico, its distribution range is on the east slope of the country, where more humid and warmer climatic conditions prevail. Typically, it occurs in cloud forests characterized by the presence of the genus Liquidambar, which is restricted to areas protected from wind and intense insolation, but it also occurs in places where Quercus is dominant. Although it seems to be a mesophilic species, it can also tolerate the colder conditions of some Abies and southern Pinus forests (Figs. 11, 12 n).

Selected specimens examined.– MEXICO. VERACRUZ. Mpio. Yecutla, Barranca del Sedral, Gutiérrez (MEXU). El Volcancillo, Juárez 8/15/1979 (ASU). Santa Rita, Herrera-Campos 378 (MEXU). Road Noalinco-Misantla, detour to Landero y Coss, Herrera-Campos 246 (MEXU). Cruz Blanca, Herrera-Campos 1 (MEXU). HIDALGO. Zacualtipán, Herrera-Campos 1361 (MEXU); 5 km N de Tlalchinol, Rzedowski and

Madrigal 29433 (ENCB). PUEBLA Encimadas, Zacatlán, Castorena 51. (ENCB). SAN LUIS POTOSI. El Potosí, Cañada Grande. Zambrano 11/28/1992.
Exsiccatae examined.– Lich Exs. COLO 488 (COLO, O).

11. Usnea mexicana Vain. Dansk Botanisk Arkiv. 4· 3. 1926. TYPE: MEXICO, Paso de Doña Juana, in arboribus, 2 1241, Liebman 7703 (lectotype, here selected, TUR-V 381!). %C/%M/%A· 5.5/6.5/76. Chemistry usnic, diffractaic, and constictic acids.
Usnea duriuscula Motyka, Lich. Gen Usnea Stud. Monogr. Pars. Syst. 2· 401. 1938 TYPE. BRAZIL, Serra de Caldas, ad arbores loco aprico, 1895, Mosén (holotype UPS!). %C/%M/%A: 4.5/11.5/68/ CHEMISTRY· usnic and protocetraric acids.

The syntypes of U. mexicana are mixed collections of two species. One has a pale axis and protocetraric acid in the medulla, and the other a brown pigmented central axis and diffractaic acid in the medulla. Both taxa are included in the protologue: "Axis albidus aut pallescens aut saepe demum, obscurus" (Vainio 1926). The former species is U hesperina and we decided lectotypify U mexicana on the specimen with pigmented axis and diffractaic acid in the medulla.

Thallus pendulous, up to 80 cm, stiff, barely ramified, anisotomic dichotomously ramified with parallel branches, often with multiple attachment points; trunk indistinct to long (2.5-3 cm), concolorous with the branches, brownish or even black, branches [(0.5)-0.6-0 8-1 0-(1.1)] mm thick, cylindrical, only narrowing towards the apices, distinctly segmented, with eroded edges; segments terete, slightly ridged to weakly alate, smooth to conspicuously cracked and areolated, with an eroded cortex in some places, and cylindrical; papillae indistinct to conical, irregularly distributed on the thallus, from scattered to abundant, tubercles low, and ± subhemispherical, scattered to abundant, irregularly distributed; fibrils abundant, long 5-15 (20) mm, usually in fish-bone pattern; pseudocyphellae long and narrow on thin branches, inconspicuous; soralia arising on eroded tubercles or papillae, usually slightly tuberculate, punctiform; isidiomorphs on cracks and erose parts; cortex thin [(2)-3-6 5 %-10-(15)] (n = 10), mat to shiny; medulla [(12)-16-20 %-24.5-(26)] (n = 10) thin, compact; axis [(30)-36.5-48 %-59.5-(71 5)] (n = 10) thick, ochraceous brown, fistulose in the thickest branches, brittle; apothecia mostly absent or rare, lateral, 3 mm diameter; chemistry: l. usnic, diffractaic, ± salazinic, ± constictic acids; 2. usnic, salazinic acid, ± protocetraric (accessory) acids, 3. usnic, and protocetraric (main) acids (n = 10).

Variation.– The most variable characters of U. mexicana are the shape of the branch segments, the frequency of papillae and tubercles, and the chemistry, similar to those characters discussed for U. gigas and U. himantodes by Swinscow and Krog (1978) and Stevens (1990)

Distinctive features.— In our concept, U mexicana is a secondary species, and U. himantodes is the corresponding primary species, both characterized by their brown pigmented and fistulous central axes, which distinguish them from all other species, primary or secondary, treated in this study.

Distribution and ecology.— Motyka (1938) reported U. mexicana from Mexico, Belize, Costa Rica, and Cuba. Its synonym, U. duriuscula, is recorded for Mexico, Costa Rica, Jamaica, Brazil, and Paraguay (Motyka 1936-1938, Weber 1993).

In Mexico it is found between 1200 and 1850 m in Chiapas, Jalisco, Oaxaca, and Guadalupe Island (Figs 11, 12 k). It occurrs on vegetation types ranging from Pinus-Quercus forests to Quercus forests, and in tropical deciduous forests, which are comparable with the humid monzonic woodlands of Asia (Rzedowskii 1981). The presence of U mexicana in vegetation of tropical characteristics suggests that its distribution range in Mexico probably would be wider if collections were extended to the tropical forests of the country.

Exsiccatae examined.— Lich. Can. Exs. CANL 221 (O).

Selected specimens examined.— MEXICO OAXACA. Cerro Gavilán, Cuyamecalco, Distrito de Cuicatlán, Conzatti y Gómez 3493. (MEXU); JALISCO Entre Los Lobos y Arroyo Verde, González Tamayo 575 (ENCB, MEXU); MANANTLAN. Las Pilitas, Herrera-Campos 4671, 4673 (MEXU). CHIAPAS.Tuxtla Gutiérrez. El Sumidero, Ortega and Ruiz Oronoz 5/24/1954 (MEXU); La Trinitaria, Parque Nacional Lagunas de Montebello, J Wolf and H. Sipman 2142 (B). MICHOACAN-GUERRERO, Monte de las Seneguias, De Candolle 85 (G). BAJA CALIFORNIA NORTE, Isla Guadalupe, Howell 36 (COLO).

12 Usnea papillata Motyka, Lich. Gen. Usnea Stud. Monogr. Pars. Syst. 2. 376. 1938. TYPE: BRASILIA, Minas Geraés, Regnell (holotype, UPS L-72218!). %C/&M/%A: 4.5/12.5/66. Chemistry: usnic, stictic, constitctic, cryptostictic, menegazziaic, norstictic acids, unknown substances UP1, and UP2.

Thallus pendulous with parallel branches up to 15 cm, anisotomic dichotomously branched, rigid; trunk indistinct, 1 mm long, paler than the main branch; branches [0 7-0 9] mm, cylindrical, tapering very slowly, annulated, with numerous transverse cracks with exposed axis; segments terete and cylindrical; apices slender with few ramifications; papillae verrucose, numerous, regularly distributed, often whitish at the top; tubercles absent; fibrils abundant, (3- 15 (20) mm long; pseudocyphellae rare, inconspicuous, fusiform; cortex thick (12 %, n = 1), vitreous, medulla compact, hardly distinct (20 %, n = 1); axis thick (36 %, n = 1), apothecia up to 11 mm diameter; spores 7-9 x 5.5-6 μ, chemistry: usnic acid, UPI, and UPII

Variation.— Although similar variation to that found in U malmei might be expected in U papillata, we do not have with enough material to confirm it.

Distinctive features.— The characteristics that distinguish this species from other esorediate pendulous Usnea are its pseudocyphellae; the cracking pattern of its cortex, its vitreous and thick cortex, its very thin medulla, and the presence of UPI and UP2, two unknown secondary products. It is inferred that U papillata is primary species of U malmei. This is supported by the morphological similarity and chemical unknowns exclusive to these two taxa. U. subscabrosa also has a vitreous cortex, but it lacks the type of pseudocyphellae mentioned, and its main secondary substance is protocetraric acid.

Distribution and ecology.— Collected only in Veracruz in a mountain cloud forest at 1500 m. (Figs. 11, 12 q).

Observed specimen.— MEXICO. VERACRUZ. Santa Rita, Herrera-Campos 409 (MEXU).

13 Usnea sanctaeritae Clerc & Herrera-Campos sp. nov.

Speciei Usnea merrillii Mot. similis, sed soralia desunt. Apothecia 1-5 mm diametro, lateralia et serialia. Sporae 9-12 x 5-7μ. Substantiae lichenum: Acida usnica et salazinica, substantia ignota lutea (TLC C: 5-6).

Similar to U. merrillii except: soralia absent; apothecia 1-5 mm in diameter, lateral to serial; spores 9-12 X 5-7 μ; cortex [(8)-10-13 %-16-(17), n = 20], medulla [(12)-14-17 %-20-(22.5), n = 20]; axis [(30)-33-39.5 %-46-(53), n = 20]; chemistry: usnic and salazinic acids, ± unknown yellow C: 5-6, n = 20.

Variation.— The only feature that actually varies in this species is the frequency of apothecia. Except for soralia and isidiomorphs, the other characters vary as in U. merrillii.

Distinctive features.— We consider U. sanctaeritae to be the primary species of U. merrillii, since the only difference between them is the absence of soralia. For differences with other pendulous taxa, the reader is referred to the discussion under U. merrillii.

Distribution and ecology.— U. sanctaeritae was collected only in two localities in mesophilic cloud forest, growing epiphytic on Quercus and Alnus (Figs. 11, 12 o).

TYPE: MEXICO. VERACRUZ. Santa Rita. 19°50'N, 96°49'W. Bosque mesófilo de montaña. 1500 m. Cortícola. 18. 01. 1992. Herrera-Campos 364 (MEXU, holotype; ASU, G, isotypes). %C/%M/%A: 8/21/42 (holotype). Chemistry: usnic and salazinic acids, ± unknown yellow C: 5-6.

Additional specimens studied.– MEXICO VERACRUZ. Santa Rita, Herrera-Campos, 365, 366, 367, 370, 372, 373, 375, 763 (MEXU). Road Naolinco-Misantla, detour to Landero y Coss, Herrera-Campos 252, 251 (MEXU)–all paratypes.

14. Usnea scabrata Nyl., Flora 58: 103 1875, s lat. (Incl. U. alpina Mot., U. barbata (L.) Wigg., U. prostrata Vain., U. scabiosa Mot.) TYPE: [AUSTRIA] TIROLIA, Waldrast. An Fichtenzweigen, 5200', 9. 1874, Arnold (holotype, H-Nyl 36517!). %C/%M/%A· 5.5/33/23. Chemistry: usnic, and salazinic acids.

Thallus pendulous, up to 55 cm long, with mixed branching pattern and parallel branches; trunk from 1 to 30 mm long, concolorous with branches or black pigmented near the attachment point; branches cylindrical to irregular; deformed by foveolae, papillae, or tubercles; with segments of various lengths, annular cracks conspicuous, exposing the axis, or with regenerating cortex; segments terete to striated, irregular and slightly swollen or sausage-like in longitudinal section; apices long, ± sinuous, often isotomic dichotomously branched at the ends, or running parallel and densely packed; papillae numerous, indistinct to verrucose, often eroded and turning into soralia, sometimes confluent and forming striations; tubercles sparse to abundant, often eroded; fibrils short (0 5-4 mm), often appearing as very small (0.5 mm) spinules, few to numerous, irregularly disposed along the branch; pseudocyphellae absent; soralia punctiform, irregularly shaped, slightly raised, arising on top of eroded papillae or tubercles; isidiomorphs present on young soralia, not conspicuous; cortex thin [(5)-6-9 %-13-(19), n = 20], mat to slightly shiny; medulla [(21)-25-30.5 %-36-(41.5), n = 20] thick, loose to dense; axis thin [(12)-20-29.5 %-39-(49), n = 20]; apothecia infrequent, subterminal, 1-12 mm in diameter; spores globose to subglobose, or elliptical, 5.5-9 X 4-7 μ; chemistry: usnic acid and salazinic acid (n = 20).

Variation.– Usnea scabrata is a very variable species, especially in the following characters: the ramification pattern, the shape of the branches and segments, the frequency and development of papillae, tubercles, soralia, foveolae, and striations. Although many different morphotypes are apparent, they are connected by transition forms.

Distinctive features – Usnea scabrata is considered here in a broad sense.

Among the sorediate and salazinic acid producing species, the characteristic features of U scabrata are its irregular and slightly swollen branch segments with papillae that turn into isidiate soralia, and its thin axis

Some collections have a very smooth cortex with sparse papillae only on main branches and without soralia; these specimens look very much like U. cavernosa, which differs from U. scabrata in the total absence of papillae and the irregular angulate branches which are not swollen

Distribution and ecology.- According to Galloway's definition (1996), U. scabrata is a boreal/arctic alpine species known from central and northern Europe, western Siberia, and western North America (Motyka 1936; Thomson 1984)

In Mexico, it is an uncommon species collected mainly in areas with subalpine type of vegetation like Pinus hartwegii forests at the limits of Puebla and Veracruz. In Sierra Madre Occidental at high altitudes in Chihuahua and in Abies forests in Morelos. Although older herbarium materials indicate its presence in the environs of Mexico City, we have not found recent collections from that area. Its altitudinal range is 3450-3800 m (Figs. 11, 12 b).

Usnea scabrata is clearly a holarctic species, for which the Eje Neovolcánico Transversal in Mexico appears to represent the southern distribution limit. New to this country.

Selected specimens examined.-MEXICO. CHIHUAHUA. Cascada de Basaseachic. Herrera-Campos 2410 (MEXU). DISTRITO FEDERAL. Desierto de los Leones, Cuarto Dinamo, García 338 (ENCB). ESTADO DE MEXICO. Road to Coatepec, detour to La Piñuela, Herrera-Campos 1589 (MEXU). MORELOS. Lagunas de Zempoala, Los Alumbres, Ruiz-Oronoz 10-XI-1957 (ENCB, MEXU). VERACRUZ. Cofre de Perote, Herrera-Campos 5467, 5468 (MEXU).

Exsiccatae examined.- Lich. Exs. COLO 298 (COLO, O).

15. Usnea subscabrosa Nyl. ex Motyka, Lich. Gen. Usnea. Stud. Monogr. Pars. Syst. 2: 313. 1937. TYPE: PORTUGAL. 1877 Newton (holotype, H!). %C/%M/%A: 14/13.5/45. Chemistry: usnic acid, and protocetraric acid

Thallus erect to pendulous, up to 22 cm long, anisotomic or isotomic dichotomously ramified with branches divergent or parallel; trunk annulate, 9-11 mm long, red-brown pigmented at the base, rarely partially black; branches [(0.4)-0.7-0.9-1.1-(1.3)] mm diameter (n= 72), tapered, segmented; segments terete and cylindrical; apices fine, short or long, divergent; papillae absent to abundant, verrucose or cylindrical; tubercles present; fibrils absent to numerous, mostly spinulous, short 3-5 mm or long 5-10 (12) mm, irregularly distributed; pseudocyphellae ellipsoid or linear, inconspicuous; soralia punctiform to half the width of the branch bearing them, arising from the cortex and/or the tops of papillae or tubercles, plane, convex or capitate, rarely slightly concave, circular, irregular, transversely or longitudinally oblong, totally confluent or remaining individual sometimes with numerous isidiomorphs; isidiomorphs absent to abundant, on young and mature soralia, seldom on cortex; apothecia absent, cortex [(9)-11.5-15 %-18.5-(24.5)] thick, vitreous, and smooth, occasionally with longitudinal cracks, seldom red-spotted; medulla [(4.5)-7-9.5 %-12-(15)] thick, compact, rarely dense; axis [(21.5)-33-40.5 %-48-(55)] thick (n = 72); chemistry: usnic and protocetraric acids, ± fumarprotocetraric, ± hypoprotocetraric, ± barbatic acids, ± unknown fatty acid (C: 5-6) (n = 82).

Variation.— The variable features are the growth habit from shrubby to pendulous (Clerc 1992); the relative abundance of papillae, tubercles, fibrils, and isidiomorphs, and the shape of the soralia which vary from circular or punctiform to transversely or longitudinally oblong.

Distinctive features.— Usnea subscabrosa is characterized by a mostly thick, hard, and vitreous cortex, compact medulla, frequent reddish pigmentation of the base, cylindrical branch segments, and the presence of protocetraric acid as the main substance.

The differences among U. subscabrosa, U. ceratina, and U. hesperina are mentioned under the descriptions of those species.

Usnea glabrata chemically similar, differs from U. subscabrosa in its bushy-erect habit, lax medulla, large soralia that usually wider than half of the branch (Clerc 1992), and lateral branches distinctly constricted at the attachment points.

Distribution and ecology.— According to Clerc (1992), the world distribution of U. subscabrosa is similar to that of U. hesperina. However, U. subscabrosa has not yet been reported from the West Indies and the west coast of United States. It has been reported from British Columbia by Halonen et al. (1998) and from Cuba and Jamaica by Clerc (1997).

This is the first report of U. subscabrosa from Mexico. It is mainly epiphytic, rarely saxicolous, and found mostly in the western mountains from 1300-3910 m (Figs. 11, 12 e).

Selected specimens examined.— MEXICO. DISTRITO FEDERAL. Desierto de los Leones, Bautista. (ENCB). -HIDALGO. Camino a Tlahuelompa 2 km NE from junction with road 115, Johansen y Mojica 6/19/1981. (MEXU). DURANGO. Sierra Madre Occidental. El Salto, Herrera-Campos 2570 (MEXU). ESTADO DE MEXICO. Road to Coatepec, detour to La Piñuela, Herrera-Campos 1588 (MEXU). CHIAPAS. Grutas SE from San Cristóbal de las Casas, Herrera-Campos 4672 (MEXU). OAXACA. Cerro del 20, Barranca del Aguacatillo, Herrera-Campos 4526 (MEXU). JALISCO. Manantlán. Las Joyas, Herrera-Campos 4521(MEXU).

16. Usnea transitoria Motyka, Lich. Gen. Usnea . Stud. Monogr. Pars. Syst. 2: 375. 1938. TYPE. COSTA RICA, Santiago de Cartago, 1200 m, potrero supra Rio Birris, 1929,

Dodge (holotype, LBL!) %C/%M/%A· 2/6/84. Chemistry usnic, stictic, constictic, cryptostictic, menegazziaic, and norstictic (faint) acids.

Thallus pendulous, up to 250 cm long, rigid, poorly to moderately branched, with anisotomic dichotomous and parallel branches, often with many points of attachment; trunk indistinct, sometimes up to 10 mm long, brownish, concolorous with or paler than branches, annulate; branches [(0.4)- 0.5-0.7-0.9-(1.5)] mm thick (n = 32), cylindrical, tapering only close to the apices, with small to extensive areas where the cortex is erose; segments weakly to strongly ridged, cylindrical to slightly trapezoidal, apices thin, with few ramifications, papillae absent, tubercles conspicuous, abundant, largely cylindrical to truncate-conical, paler at the top, often eroded, irregularly distributed on main and secondary branches; fibrils short (0.5-2 mm), and long (3-10 mm) mostly spinulous, in a fish-bone arrangement, pseudocyphellae linear, inconspicuous; soralia arising on the cortex or tubercles and/or ridges; punctiform, circular to irregularly shaped, often becoming confluent and thus looking like large convex to capitate soralia, without a definite margin; isidiomorphs on both young and mature soralia, conspicuous; cortex [(2.5)-4-8 %-12-(20), n = 32] thick, shiny; medulla [(2 5)-6-11 %-16-(29.5), n = 32] thin, compact; axis thick [(27.5)-49-62 %-75-(88), n = 32], often fistulose at the base of main branches; apothecia up to 6 mm in diameter, spores 6-8 X 10-12 μ; chemistry: 1. usnic acid, and salazinic acid, 2, usnic and caperatic acid (n = 32).

Variation.– The most variable characters of this species are the degree of development of the ridges along the branch segments, density of the fibrils, soralia, and isidiomorphs, and the degree of erosion of the cortex. The chemistry seems to be variable as well, since, including the type, there are at least three chemotypes known.

Distinctive features.– Among the species studied, U. transitoria has the thickest axis (up to 88% of the branch) and is characterized by ridged segments with an erose cortex, punctiform confluent soralia, anisotomic dichotomous branching, fibrils arranged in fish-bone pattern, and salazinic or caperatic acid as the main secondary product. U. angulata has segments which are distinctly trapezoidal, with open margins at the edge, broader marginate soralia, and norstictic acid as the main secondary product in the medulla. Furthermore, U longissima is not known from Mexico, has a completely eroded cortex, cylindrical segments, mostly a different chemistry, and is only very rarely sorediate.

Distribution and ecology – Usnea transitoria is known from Mexico, Central America, and the Caribbean Islands (Motyka 1938). In Mexico, it was collected mainly on the Sierra Madre Occidental and, together with U. goniodes, it is the only pendulous species found in Sierra de La Laguna, Baja California Sur, a region considered floristically related to Sierra Madre Occidental (Rzedowski 1981). It is also known from Isla Socorro, in the

Revillagigedo Islands U. transitoria has a more restricted distribution than U. angulata, which grows in Mexico mainly in Sierra Madre Oriental

Usnea transitoria is not known to occur further south than the Eje Neovolcánico. In spite of its more restricted distribution, U goniodes, the corresponding primary species, is found south to Oaxaca (Figs 11, 12 l and m).

Selected specimens examined.– MEXICO. MICHOACAN. Bosques de San Francisco, Iltis et al. 1816. (ENCB); Morelia. Cerro San Miguel, Arsène 8249. (COLO); Arsène 12/1910 (LAM), Müller A 1855 (NY); VolcánTancítaro Barranca del Cuartel, Herrera-Campos 4669 (MEXU) PUEBLA. Honey, Castorena 4 (ENCB). SAN LUIS POTOSI. El Potosí Cañada Grande, Zambrano 11/28/92 (MEXU); CHIHUAHUA. Sierra Tarahumara. Divisadero El Gallego, Herrera-Campos 4670 (MEXU). JALISCO Nevado de Colima, Herrera-Campos 4668 (MEXU); Pringle 28 (VT, MEXU).

Exsiccatae examined – Zahlbruckner and Redinger, Lich Rar Exs. 356 (BERN); Lich. Exs. COLO 51 (MEXU, O, VT).

17. Usnea vitrea P. Clerc & M A. Herrera-Campos sp. nov.

Speciei Usnea subscabrosa ex Nyl., Mot. similis, sed soralia desunt. Apothecia 2-7 mm diametro, subterminalia. Sporae 8-12 x 5-8 μ. Cortex crassus,vitreus, durus. Medulla crassa, compacta, raro densa. Axis crassus. Substantiae lichenum: Acida usnica et protocetrarica, adsunt; acida fumarprotocetrarica, hypoprotocetrarica et barbatica, adsunt vel desunt; acidum aliphaticum, ignotum adest (TLC C: 5-6).

Thallus erect to pendulous, up to 30 cm long, anisotomicaly or isotomicaly dichotomous ramified with divergent or parallel branches; trunk annulate, 9-11 mm long, red-brown pigmented at the base, seldom black; branches [(0.6)- 0.6-0 9-1 2-(1.6)] mm diameter, tapered, segmented; segments terete and cylindrical; apices fine, short or long, divergent; papillae absent to abundant, verrucose or cylindrical; tubercles present; fibrils absent to numerous, mostly spinulous, short (3-5 mm) also long 5-10 (12) mm, irregularly distributed; pseudocyphellae ellipsoid or linear, inconspicuous; apothecia subterminal 2-7 mm diameter; spores 8-12 X 5-8 μm, colorless, elliptical; cortex thick [(9.5)-13-18 %-24-(27) n = 8], vitreous, occasionally with longitudinal cracks, sometimes with red spots; medulla thin [(11)-12.0-14 %-15 5-(16.0), n = 8], compact, rarely dense; axis thick [(24.5)-26-35.5 %-45-(50), n = 8]; chemistry· usnic and protocetraric acids, ± fumarprotocetraric, ± hypoprotocetraric, ± barbatic acids, ± unknown fatty acid C: 5-6, n = 8.

Distribution and ecology.– It is collected in Pinus-Quercus forests at Oaxaca-Chiapas border at 360 m, and in the coniferous and cloud forests of Durango and Hidalgo between 1300 and 2500 m. Epiphytic on Pinus and Quercus (Figs. 11, 12 f).

TYPE: MEXICO HIDALGO. Zacualtipán. Turbera. 20° 37'N, 98° 39'W. Bosque de Pinus-Quercus. 1800 m. En pino. 26 01 1992, Herrera-Campos 1376 (MEXU, holotype). %C/%M/%A: 10/7/66.5. Chemistry usnic and protocetraric acids, ± fumarprotocetraric, ± hypoprotocetraric, ± barbatic acids, ± unknown fatty acid C: 5-6.

Additional specimens studied.– MEXICO. DURANGO. 9 km WSW from El Salto, Herrera-Campos 2573 (MEXU). HIDALGO. Zacualtipán, Herrera-Campos, 1375 (G) 1377 (ASU); Laguna de Atezca, Herrera-Campos 1249 (MEXU). Highway 105 to Tlahuelompa, June 19, 1981. Johansen and Mojica (MEXU). OAXACA-CHIAPAS. Herrera-Campos 5485 (MEXU)–all paratypes.

18. Usnea sp 1

An undetermined morphotype characterized by the presence of longitudinal craks with involute edges, thin and shiny cortex, and salazinic acid as the main medullary substance We do not have enough material to make any conclusive determination.

Excluded species

19. Usnea alata Motyka, Motyka Lich. Gen. Usnea. Stud. Monogr. Pars. Systm 2:395. 1938. TYPE: BRAZIL, MINAS GERAES, Chequeira, 1885 (holotype, TURKU!). %C/%M/%A. 9/15/52. Chemistry: usnic, norstictic, connorstictic acids.

This South American taxon is the primary species of U. angulata. It has not been found so far in Mexico, but it is included in the key.

20. U. himantodes Stirton Scott. Natur. 7:75, 1883. TYPE: AUSTRALIA, NEW SOUTH WALES, Illawarra, 1882, Kirton (holotype, BM!). %C/%M/%A: 8.5/13.5/56. Chemistry: stictic, menegazziaic, cryptostictic, constictic, trace norstictic and usnic acids.

U. sericea Motyka, Lich. Gen. Usnea Stud. Monogr. Pars. Syst. 2: 413. 1938. TYPE: MEXICO, Los Baños, heisse Schwefelquellen, 18 Meilen gen Vera Cruz, feucht und warm, an Bäumen 1000'. Heller, (holotype, W !). %C/%M/%A: 9.5/10.5/60. Chemistry: usnic acid, constictic acid, diffractaic acid.

U. himantodes, considered here to be the primary species of U. mexicana, has not been collected so far in the temperate forests in Mexico, but it is included in the key since its synonym U. sericea Mot. is reported from a warm location in Veracruz (Motyka 1936-1938). No recent collections were available during this study.

Usnea longissima Ach., Lich. Univ 626. 1810

This taxon was mentioned for Mexico by Gómez-Peralta (1992). The specimens proved to be U ceratina and U transitoria. Therefore, U. longissima is considered so far not to occur in Mexico.

Usnea trichodea Ach., Method. Lich. 312. 1803.

The reporting of this exclusively eastern North American species in Mexico (De Lesdain 1929; González de la Rosa and Guzmán 1976) was based on misidentifications of U. hesperina, U. mexicana, and U merrillii. Therefore, this species is also excluded from Usnea species occurring in Mexico

ACKNOWLEDGEMENTS

María Angeles Herrera-Campos deeply acknowledges the support received from Departamento de Botánica, Instituto de Biología, UNAM through Patricia Dávila Aranda, the grants 190/92/PADEP/68 from UNAM, and CoNaCyT financial support. All the authors akcnowledge the grant BSR-920-1111 from NSF. We also are very grateful to the curators and owners of the herbaria listed in the text for loan of specimens. Special thanks to Christian Scheuer, University of Graz for his help with the Latin descriptions, and to S Kirchheimer and K. Pigg from Arizona State University for their invaluable assistance.

LITERATURE

ASAHINA, Y. 1965. Lichenologische Notizen 201 Journal of Japanese Botany 40: 353-357.

ASAHINA, Y 1971. Lichenologische Notizen 245-247 Journal of Japanese Botany 46: 257-262.

ASAHINA, Y. 1973. Lichenologische Notizen 252-253. Journal of Japanese Botany 48: 33-35.

AWASTHI, G. 1986. Lichen Genus Usnea in India. Journal of the Hattori Botanical Laboratory 61: 333-421.

BOULY DE LESDAIN, M. 1914. Lichens du Mexique (Etats de Puebla et de Michoacan) recueillis par le Frére Arsène Brouard. Imprenta I. Escalante, S. A. México.

BOULY DE LESDAIN, M. 1929. Lichens du Mexique. Deuxième Supplément. Lichens recueillis par le Frère Amable St. Pierre. Annales de Cryptogamie Exotique 2: 217-254.

BOULY DE LESDAIN, M. 1933. Lichens du Mexique. Troisième Supplément. Annales de Cryptogamie Exotique 6: 99-130.

BRODO, I. M. & D L. HAWKSWORTH. 1977. Alectoria and allied genera in North America. Opera Botaqnica 42:1-164

CLERC, P. 1984a. Contribution à la révision de la systématique des usnées (Ascomycotina, Usnea) d'Europe. I -Usnea florida (L) Wigg. emend. Clerc. Cryptogamie: Bryologie et Lichénologie 5: 333-360

CLERC, P. 1984b Usnea wirthii -A new species of lichen from Europe and North Africa. Saussurea 15 33-36.

CLERC, P. 1987a. Systematics of the Usnea fragilescens aggregate and its distribution in Scandinavia. Nordic Journal of Botany 7: 479-495.

CLERC, P. 1987b. On the morphology of soralia in the genus Usnea, pp. 99-102. In E. Peveling (ed.), Progress and Problems in Lichenology in the Eighties. Bibliotheca Lichenologica Vol. 25. Berlin-Stuttgart.

CLERC, P. 1991 Usnea madeirensis Motyka (ascomycète lichénisé): une espèce méconnue de l'Europe et de l'Amèrique du Nord. Candollea 46: 427-438.

CLERC, P. 1992. Some new or interesting species of the genus Usnea (lichenised Ascomycetes) in the British Isles. Candollea 47 513-526.

CLERC, P. 1994. Comment Usnea mutabilis Stirton, une espèce nord-américaine, se cache en Europe sous le nom d' Usnea marocana Motyka. Une contribution à la systématique du genre Usnea (ascomycètes lichénisés). Bulletin de la Société Linnéenne Provence 45: 309-316.

CLERC, P. 1997. Notes on the Genus Usnea Dill. ex Adanson. Lichenologist. 29 (3): 209-215.

CLERC, P. & P. DIEDERICH. 1991. Usnea wirthii Clerc new to North America and the British Isles. Lichenologist 23: 405-407.

CLERC, P. & M.A. HERRERA-CAMPOS. 1997. Saxicolous species of the genus Usnea in North America. The Bryologist 100 281-301.

COUTIÑO, B. & A. MOJICA. 1982. Estudio de líquenes cortícolas de bosque mesófilo de montaña y de coníferas del estado de Hidalgo. Boletín de la Sociedad Mexicana de Micología 17. 166-180

COUTIÑO, B. & A. MOJICA. 1985. Líquenes de la región del Cofre de Perote-Xalapa. Revista Mexicana de Micología 1: 379-399.

CULBERSON, C. & K. AMMANN. 1979. Standardmethode zur Dunnschichtchromatographie von Flechtensubstanzen. Herzogia 5: 1-24 .

CULBERSON, C. & A. JOHNSON. 1982. Substitution of methyl tert-butyl ether for diethyl ether in standardized thin-layer chromatographic method for lichen products. Journal of Chromatography 238: 438-487 .

CULBERSON, W., C. CULBERSON & S FISCUS. 1983 A new lecanoric acid-producing Usnea from Mexico. The Bryologist 86. 254-256 .

CULBERSON, C , W. CULBERSON & A. JOHNSON. 1988 Gene flow in lichens. American Journal of Botany 75 : 1135-1139.

DELGADILLO, C. 1993. Diversity in the Mexican Bryoflora, pp. 365-377. In Ramamooerthy, T. P , R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press Oxford.

DODGE, C. W. 1956. Some lichens of tropical Africa. II Usnea. Annals of the Missouri Botanical Garden 43· 381-396.

DODGE, C. W 1956. Some lichens of tropical Africa. II. Usnea (continued). Annals of the Missouri Botanical Garden 44: 1-76.

Du RIETZ, G. E. 1924. Die Soredien und Isidien der Flechten. Svensk Botanisk Tidskrift. 18: 371-396.

DUVIGNEAUD, P. 1952. Les usnèes barbues et le Crossopterygo-Usnetum des savanes du Bas-Congo. Bulletin de la Société Royale de Botanique de Belgique 85· 99-114.

FINK, B. 1971. The Lichen Flora of the United States. The University of Michigan Press, Ann Arbor.

GALLOWAY, D. J. 1991. Biogeographical relationships of Pacific tropical lichen floras. In: D.J. Galloway (ed.) Tropical Lichens· Their Systematics, Conservation, and Ecology, pp. 1-6. Systematics Association Special Volume No. 43, Clarendon Press, Oxford.

GALLOWAY, D. J. 1996. Lichen biogeography, pp 199-216. In T. H. Nash (ed.), Lichen Biology. Cambridge University Press, New York.

GILBERT, A. 1935. Líquenes del Valle de México. Tesis de Maestría. Facultad de Ciencias, UNAM. México.

GOMEZ-PERALTA, M. 1992. Contribución al conocimiento de los líquenes del campo geotérmico Los Azufres, Michoacán, México. Acta Botánica Mexicana 18: 31-53.

GONZÁLEZ DE LA ROSA, M. E. & G. GUZMÁN. 1976. Estudios sobre los Líquenes de México, III. Observaciones sobre especies no consideradas anteriormente Boletín de la Sociedad Mexicana de Micología 10: 27-64.

GUZMÁN, G & GONZÁLEZ DE LA ROSA, M. E. 1976. Estudios sobre los Líquenes de México, IV. Especies de Usnea citadas por Motyka en 1936-1938 de México. Boletín de la Sociedad Mexicana de Micología 10: 65-70.

HALE, M., Jr. 1979. How to Know the Lichens. 2nd Edition. Wm. C. Brown Co. Dubuque, Iowa.

HALONEN, P., P. CLERC, T. GOWARD, I M. BRODO & K. WULFF 1998. Synopsis of the genus Usnea (Lichenized Ascomycetes) in British Columbia, Canada. The Bryologist 101 (1) in press.
HAWKSWORTH, D. L. 1972. Regional studies in Alectoria (Lichenes) II. The British species. Lichenologist 5: 181-261.
HAWKSWORTH, D. L. 1984. The lichen-forming fungi. Blackie. Glasgow and London.
HERRE, W. C. T. 1960. Notes on Chilean Usneas with description of one new species. Rev. Bryologie et Lichenologie 29: 274-276.
IMSHAUG, H. 1956. Catalogue of Mexican Lichens. Rev. Bryologie et Lichenologie 25: 321-385 .
JAMES, P., P. CLERC, & W. PURVIS 1992. Usnea , pp. 620-629. In O. W. Purvis, B. J. Coopins, D. L. Hawksworth, P W. James, & D. M. Moore (eds), The L:ichen Flora of Great Britain and Ireland. Edinburgh.
LÓPEZ, F.M. 1986. Censo de macrolíquenes venezolanos de los estados Falcón, Lara, Mérida, Tachira y Trujillo. Universidad de Los Andes. Facultad de Farmacia. Venezuela.
MATTSSON, J. & H. LUMBSCH (1989). The use of the species pair concept in lichen taxonomy. Taxon 38: 238-241.
MOTYKA, J 1936-1938 Lichenum Generis Usnea. Studium Monographicum, Pars Systematica. 1937. Leopoli.
POELT, J 1970. Das Konzept der Artenpaare bei den Flechten. Deutsche Botanische Gesellschaft. Neue Folge 4: 187-198.
POELT, J. 1972. Die taxonomische Behandlung von Artenpaaren bei den Flechten. Botanika Notiser 125: 77-81.
RZEDOWSKI, J. 1981. La Vegetación de México. Ed. Limusa. México.
RZEDOWSKI, J. 1993. Diversity, and Origins of the Phanerogamic Flora of Mexico, pp. 129-143. In T. P. Ramamoorthy, R. Bye, A. Lot & J. Fa (eds.) Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.
ROGERS, R. & G. STEVENS. 1988. The Usnea baileyi complex (Parmeliaceae, lichenised ascomycetes) in Australia. Australian Systematic Botany 1. 355-361.
SCHINDLER, H. 1983. Ueber den Nachweis der Diffractassäre in der Flechte Usnea ceratina aus dem Schwarzwald. Andrias 2: 5-8.
SHARP, A. J. 1939. Taxonomical and ecological studies of eastern Tennessee bryophytes American Midland Naturalist 21: 267-354.
STEVENS, G. 1990. Usnea himantodes Stirton and its synonyms. Lichenologist 22: 409-412.

STEVENS, G. 1991. The tropical Pacific species of Usnea and Ramalina, and their relationship to species in other parts of the world, pp 47-67. In D J. Galloway (ed.), Tropical Lichens· Their Systematics, Conservation, and Ecology. Systematics Association Special Volume No. 43. Clarendon Press, Oxford.

STEVENS, G. 1992. Variation in thallus morphology in response to climatic, and geographical distribution in an Usnea complex Lichenologist, 24: 229-248.

SWINSCOW, T & H. KROG. 1975. The Usnea undulata aggregate in East Africa Lichenologist 7: 121-138

SWINSCOW, T. & H. KROG. 1976 The Usnea articulata aggregate in East Africa. Norwegian Journal of Botany 23: 261-268.

SWINSCOW, T. & H KROG. 1976 The Usnea bornmuelleri aggregate in East Africa. Norwegian Journal of Botany 23· 23-31.

SWINSCOW, T. & H KROG. 1978. Pendulous species of Usnea in East Africa. Norwegian Journal of Botany 25: 221-241.

SWINSCOW, T. & H. KROG. 1979. The fruticose species of Usnea subgenus Usnea in East Africa. Lichenologist 11: 207-252.

THOMSON, J. W. 1984. American Arctic Lichens. 1. The Macrolichens. Columbia University Press. New York.

VAINIO, E. A. 1926. Lichenes Mexicani a F. M. LIEBMANN A. 1841-43 collecti, in Museo Hauniensi asservati. Dansk Botanisk Arkiv 4: 1-25.

WEBER, W. A. 1993. The Lichen flora of Guadalupe Island, Mexico, pp. 65-71 In F. J. Hochberg (ed.), Recent Advances on the California Islands. Santa Barbara Museum of Natural History. Santa Barbara.

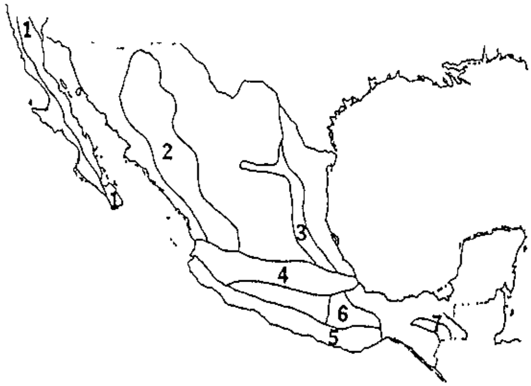


FIGURE 1. Pertinent physiographic provinces. 1. Sistema Montañoso de Baja California. 2. Sierra Madre Occidental. 3. Sierra Madre Oriental. 4 Eje Neovolcánico Transversal. 5. Sierra Madre del Sur. 6. Sistema Montañoso del Norte de Oaxaca. 7. Macizo Central de Chiapas. (Modified from Rzedowski 1981).

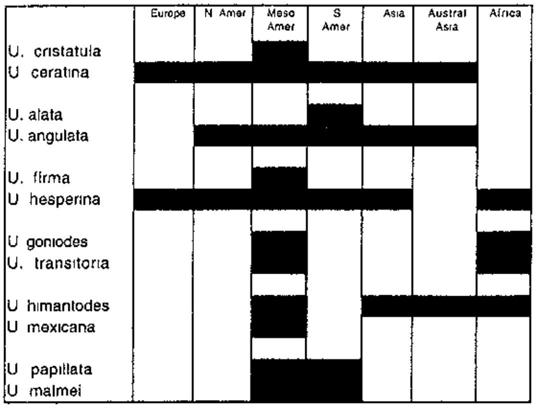


FIGURE 2. Comparison of known world distribution of some primary and secondary species of *Usnea*. North America: Canada and United States. Mesoamerica· Mexico and Central America. Primary species are mentioned first in each pair.

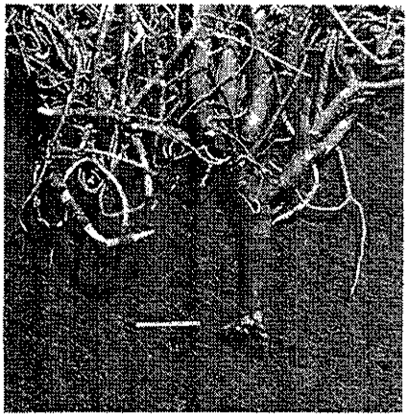


FIGURE 3. Trunk of *Usnea subscabrosa*, *Herrera-Campos 1588* (MEXU). Scale 1 cm.

TABLE 1. Cortex, medulla, and axis (CMA) percentages of the pendulous species of *Usnea* in Mexico* * Percentages relative to the total width of the branch Mean, standard deviation values, and extreme values are given, *n* = total of individual thalli measured.

Species	Cortex	Medulla	Axis	*n*
U. angulata	[(4 5)–6–8.5%–11–(15)]	[(2)–8–14%–20–(28.5)]	[(31)–41–53%–65–(83)]	35
U. cavernosa	[(2.5)–4–6%–8–(10 5)]	[(10.5)–19–25%–31–(40 5)]	[(7.5)–27 5–38%–48 5–(62 5)]	39
U. ceratina	[(3)–6 5–9%–11 5–(18)]	[(12.5)–19–24%–29–(38 5)]	[(9)–26–34.5%–42 5–(57)]	123
U. cristatula	[(6)–8.5–11 5%–14 5–(16 5)]	[(12)–17–21 5%–26–(33)]	[(21 5)–27–34%–41–(48 5)]	27
U. filipendula	[(6.5)–7.5–9 5%–11.5–(13)]	[(11)–17–22%–27–(30.5)]	[(21 5)–26.5–36 5%–46 5–(58)]	35
U. firma	[(7)–8–10 5%–13–(13.5)]	[(11)–12–14 5%–17–(19)]	[(43 5)–46 5–50%–53 5–(55)]	12
U. goniodes	[(1.5)–5.5–8.5%–11 5–(15)]	[(1.5)–4–9%–14.5–(26)]	[(18 5)–49 5–64 5%–79 5–(94)]	30
U. hesperina	[(3.5)–8.5–11.5%–14 5–(20.5)]	[(6.5)–10.5–14 5%–18.5–(23)]	[(27)–37–47 5%–58–(80)]	53
U. malmei	[(6.5)–8–13%–18–(18)]	[(9.5)–9–14 5%–20–(24 5)]	[(32.5)–35–45%–55–(60)]	5
U. merrillii	[(6)–10–13%–16–(21)]	[(7 5)–14–18%–22–(28.5)]	[(25)–32–38.5%–45–(53)]	60
U. mexicana	[(2)–3–6.5%–10–(15)]	[(12)–16–20%–24.5–(26)]	[(30)–36 5–48%–59.5–(71.5)]	10
U. papillata	13%	14 5%	45%	1
U. sanctaeritae	[(8)–10–13%–16–(17)]	[(12)–14–17%–20–(22.5)]	[(30)–33–39 5%–46–(53)]	20
U. scabrata	[(5)–6–9%–13–(19)]	[(21)–25–30.5%–36–(41.5)]	[(12)–20–29.5%–39–(49)]	20
U. subscabrosa	[(9)–11.5–15%–18 5–(24 5)]	[(4.5)–7–9 5%–12–(15)]	[(21.5)–33–40 5%–48–(55)]	72
U. transitoria	[(2 5)–4–8%–12(20)]	[(2.5)–6–11%–16–(29 5)]	[(27.5)–48 5–62%–75–(88)]	32
U. vitrea	[(7)–9–14%–19–(21)	[(13.5)–14 5–16%–17.5–(18)]	[(30)–31–40%–49–(53)]	8

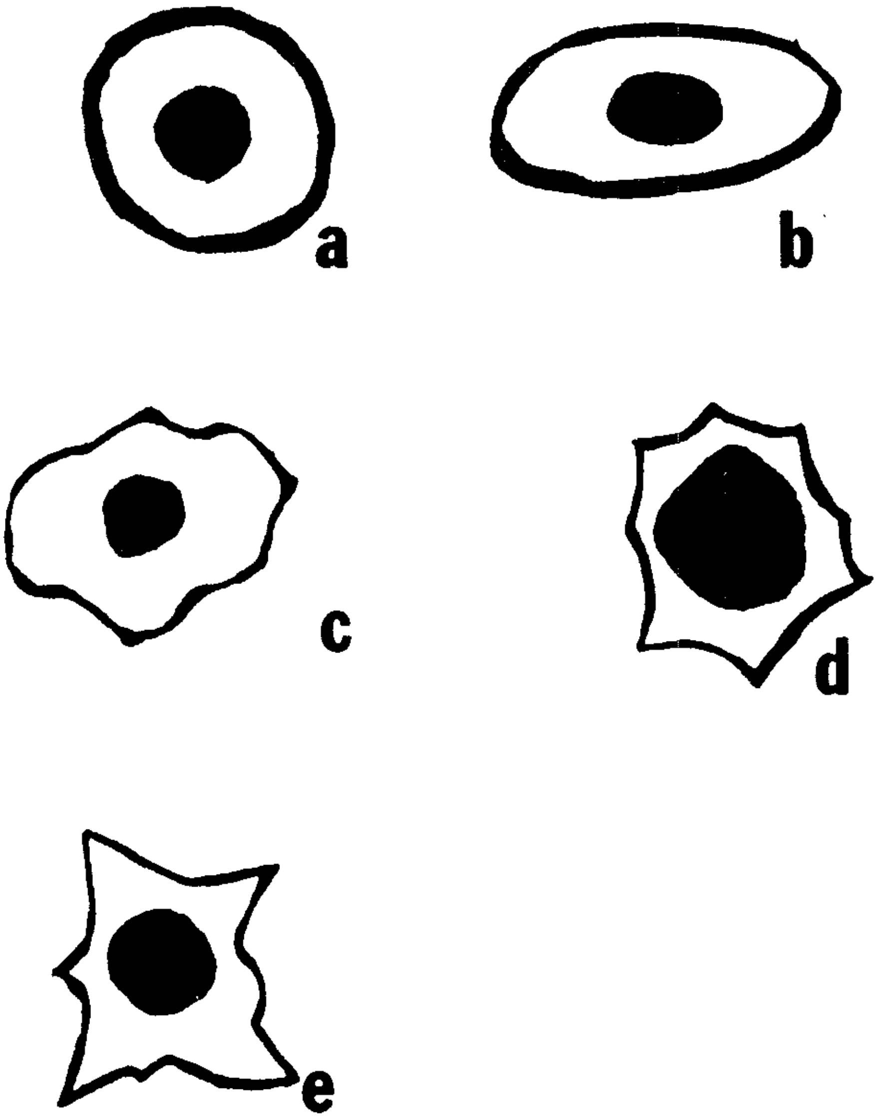


FIGURE 4. Shape of branch segments in transverse section. — a. Terete (*U. hesperina*) — b. Flattened. — c. Irregular, foveolate or furrowed with deformed segments (*U. cavernosa*). — d. Ridged i.e., deforming the segments (*U. transitoria*). — e. Alate (*U. angulata*).

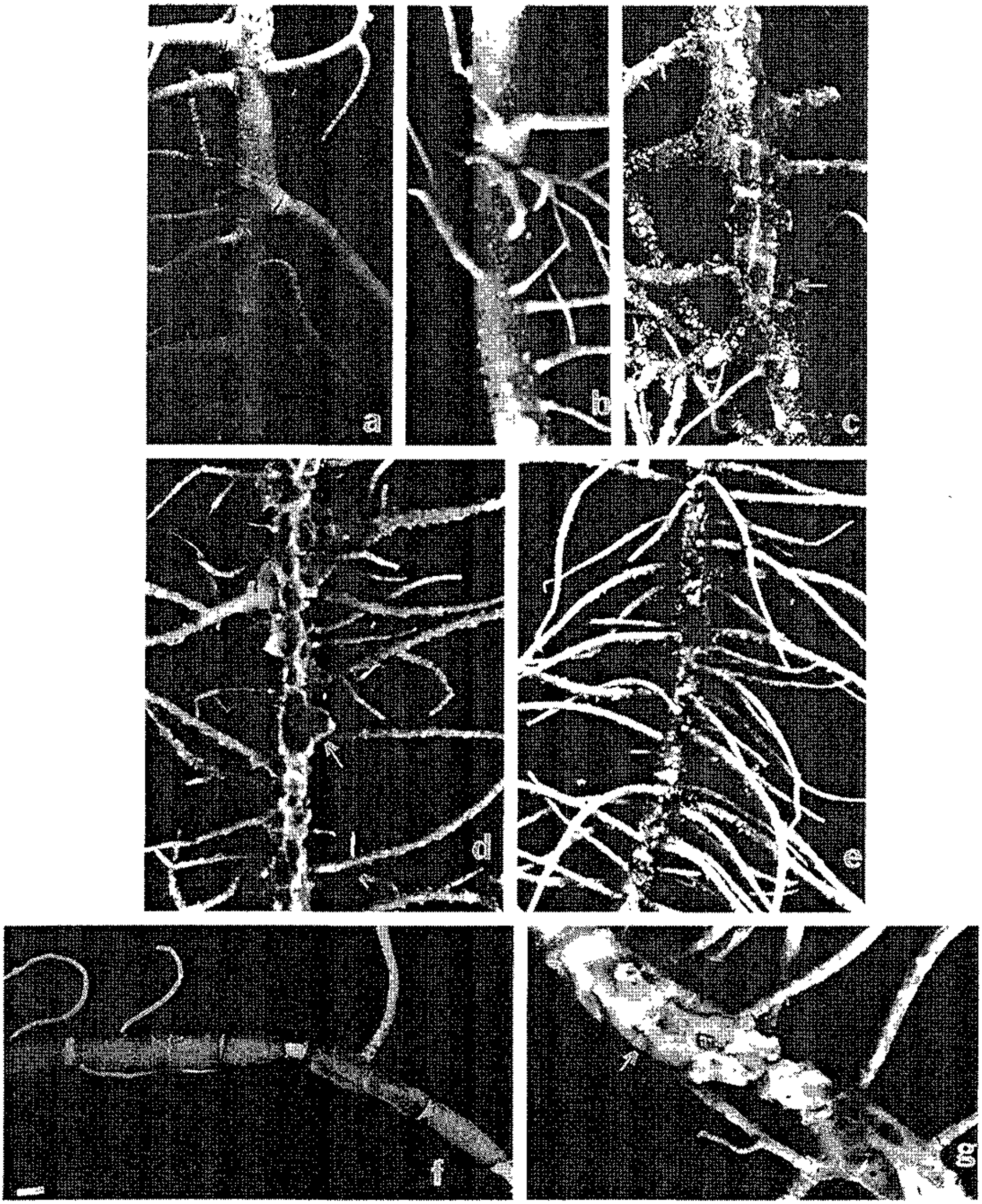


FIGURE 5. Shape of branch segments in longitudinal section. — a. Main branch of *U. hesperina* with longitudinally cylindric segments, *Herrera-Campos 269* (MEXU). — b. Main branch of *U. subscabrosa* with longitudinally cylindric segments, note the numerous papillae, *Herrera-Campos 2623* (MEXU). — c. Main branch *U. transitoria* with ridged segments. Arrow pointing at ridge, *Herrera-Campos 4669* (MEXU). — d Main branch of *U. angulata* with trapezoidal segments. Arrow pointing at wing, note the fish-bone arrangement of the fibrils, *Zambrano*, November 29, 1992, (MEXU). — e. Main branch of *U. filipendula* with longitudinally cylindric segments *scabrata* with slightly "sausage-like" segments, *Ruiz-Oronoz*, November 10, 1957 (MEXU). g. Main branch of *U. cavernosa* with segments deformed by depressions and foveolae in the cortex (arrow), *Nash 14656* (COLO).

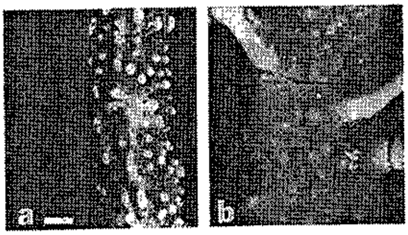


Figure 6 Main branches — a *Usnea transitoria* with tubercles, *Herrera-Campos 5461* (MEXU) — b *U subscabrosa* with papillae, *Herrera-Campos 2623* (MEXU). Scale 0 25 mm

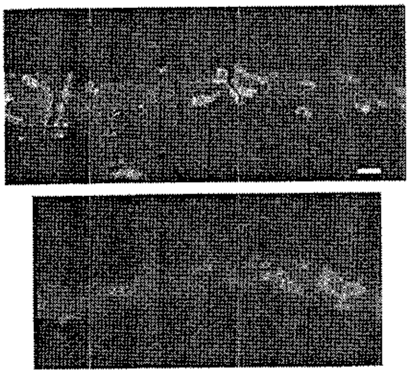


Figure 7. Pseudocyphellae of *U malmei* on secondary branches, *Herrera-Campos 2743* (MEXU) Scale. 0.3 mm

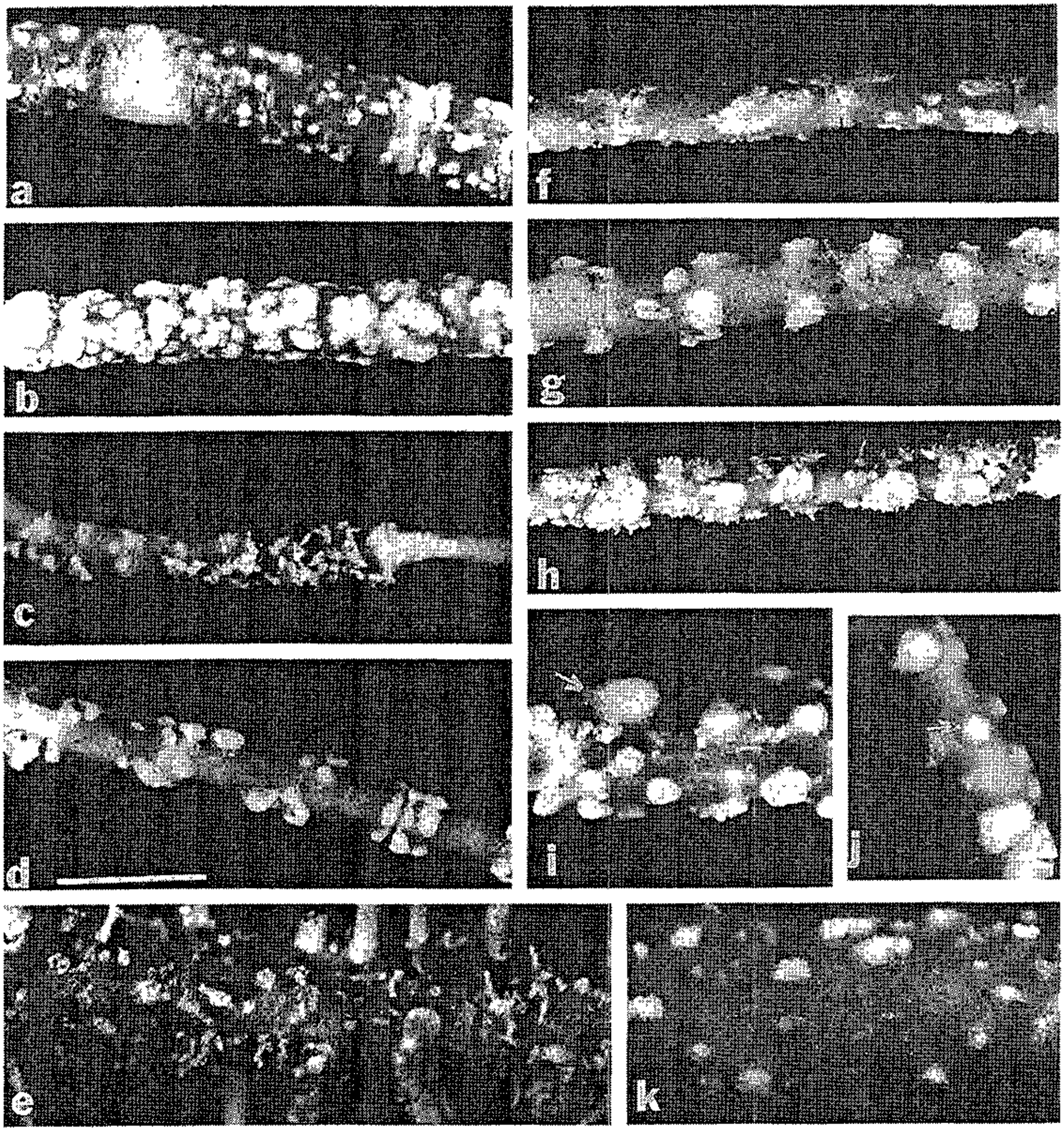


FIGURE 8 Types of soralia in pendulous species of *Usnea*. — a. Tips of *U. hesperina* with punctiform, superficial, or slightly raised soralia, some of them immature appearing as pseudocyphellae. — b. Tips of *U. hesperina* with plane to convex, confluent enlarged soralia, *Zambrano*, November 29, 1992 (MEXU). — c. Tips of branches of *U. merrillii* showing isidiomorphs on soralia, *Gimate 264* (ENCB). — d. Tips of branches of *U. merrillii* with small, circular, slightly tuberculate, and convex soralia, *Herrera-Campos 2746* (MEXU). — e. Secondary branch of *U. filipendula* with soralia arising from fibercles, with conspicuous isidiomorphs mostly on young soralia, *Herrera-Campos 4879* (MEXU). — f. Terminal branches of *U. subscabrosa* showing punctiform and confluent soralia, enlarging to transversely or longitudinally oblong, arising from the cortex, *Zambrano*, November 29, 1992. — g. Terminal branches of *U. subscabrosa* with soralia on top of papillae or tubercles. The soralia show a plane or convex surface, *Herrera-Campos 229* (MEXU). — h. Terminal branches of *U. subscabrosa* with isidiomorphs on young and mature soralia, *Herrera-Campos 2739* (MEXU). — i–j. Fibrils of *U. angulata* showing soralia that are punctiform to larger than half of the width of the branch, circular, slightly to distinctly tuberculate, with a conspicuous cortical margin when mature (arrow), *Herrera-Campos 2750* (MEXU). — k. Lateral branch of *U. ceratina* with punctiform to circular, not confluent soralia, with margin, and arising from the cortex or on tubercles, *Herrera-Campos 4344*. Scale, 0.5 mm.

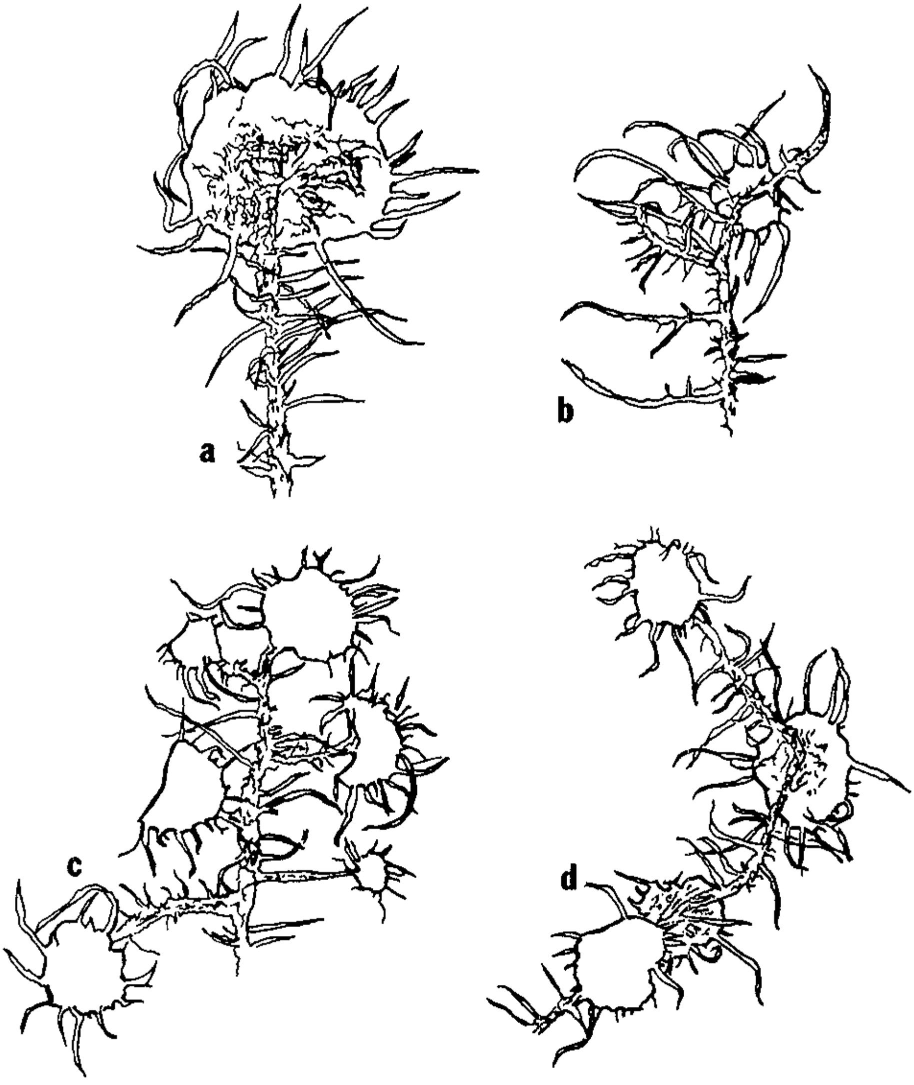


FIGURE 9. Apothecia. — a. Terminal — b Subterminal. — c. Lateral. — d. Serial.

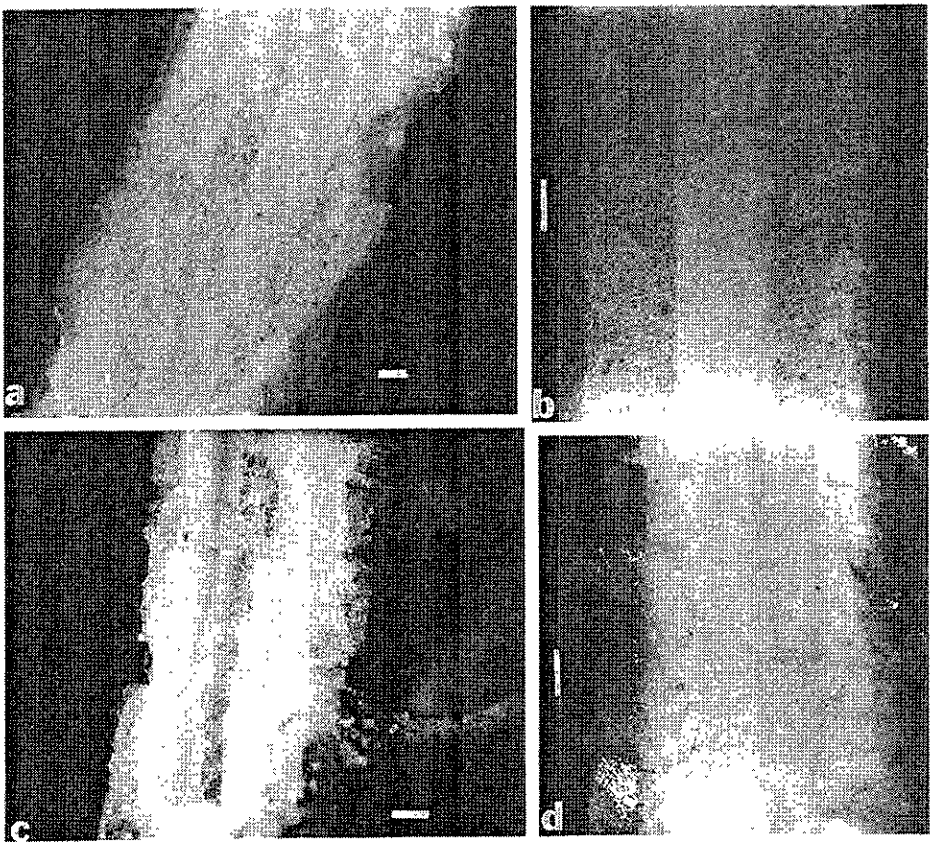


FIGURE 10 Cortex, medulla, and axis shown in longitudinal section of the branch. — a. Main branch of *U. cavernosa* with thin and shiny cortex, dense medulla, and thin axis, *Nash 14656* (COLO). — b. Main branch of *U. scabrata* with thin cortex, loose medulla, and thin axis *Ruiz-Oronoz*, November 10, 1957 (MEXU). — c. Main branch of *U. transitoria* with thick cortex, inconspicuous medulla, and very thick fistulose axis, *Herrera-Campos 4669* (MEXU). — d. Main branch of *U. subscabrosa* with thick and vitreous cortex, compact medulla, and thick axis, *Herrera-Campos 4530* (MEXU). Scale: 0.15 mm

Table 2 Main (+) and accessory (±) secondary chemical compounds of the species. U = usnic acid, Df = diffractaic acid, B = barbatic acid, St = stictic acid, Cst = constictic acid, N = norstictic acid, S = salazinic acid, Sq = squamatic acid, P = protocetraric acid, FP = fumarprotocetraric acid, HP = hypoprotocetraric acid, Ca = caperatic acid, U1 and U2 = unknown substances Rf 1 and 2

Species	U	Df	B	St	Cst	N	S	Sq	P	FP	HP	Ca	U1	U2
U. angulata	+	—	—	—	—	+	—	—	—	—	—	—	—	—
U. cavernosa	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. ceratina	+	+	±	—	—	—	—	±	—	—	—	—	—	—
U. cristatula	+	+	±	—	—	—	—	±	—	—	—	—	—	—
U. filipendula	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. firma	+	—	—	—	—	—	—	—	+	—	—	—	—	—
U. gonoides	+	—	—	—	—	—	±	—	—	—	—	±	—	—
U. hesperina	+	—	—	—	—	—	—	—	+	—	—	—	—	—
U. malmei	+	—	—	±	—	—	—	—	—	—	—	—	+	+
U. merrillii	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. mexicana	+	±	—	—	±	—	±	—	±	—	—	—	—	—
U. papillata	+	—	—	±	—	—	—	—	—	—	—	—	+	+
U. santaritae	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. scabrata	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. sp. 1	+	—	—	—	—	—	+	—	—	—	—	—	—	—
U. subscabrosa	+	—	—	—	—	—	—	—	+	±	±	—	—	—
U. transitoria	+	—	—	—	—	—	±	—	—	—	—	±	—	—
U. vitrea	+	—	—	—	—	—	—	—	+	±	±	—	—	—

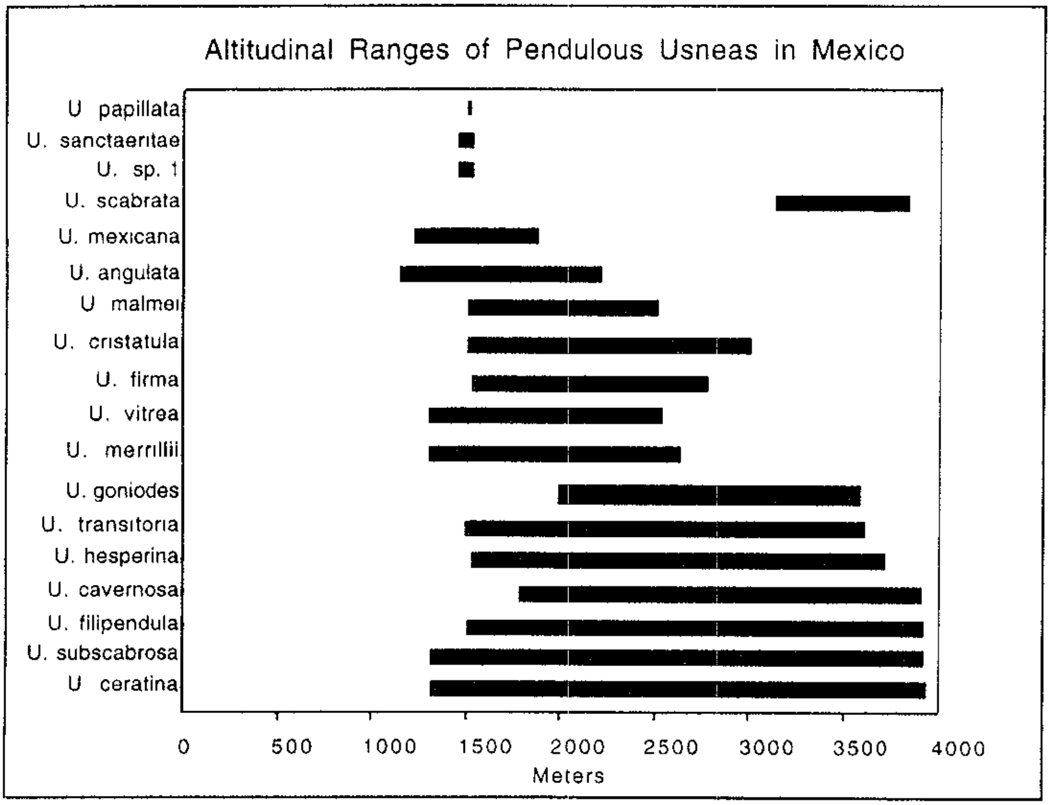


FIGURE 11. Elevational ranges of pendulous *Usnea* species in Mexico.

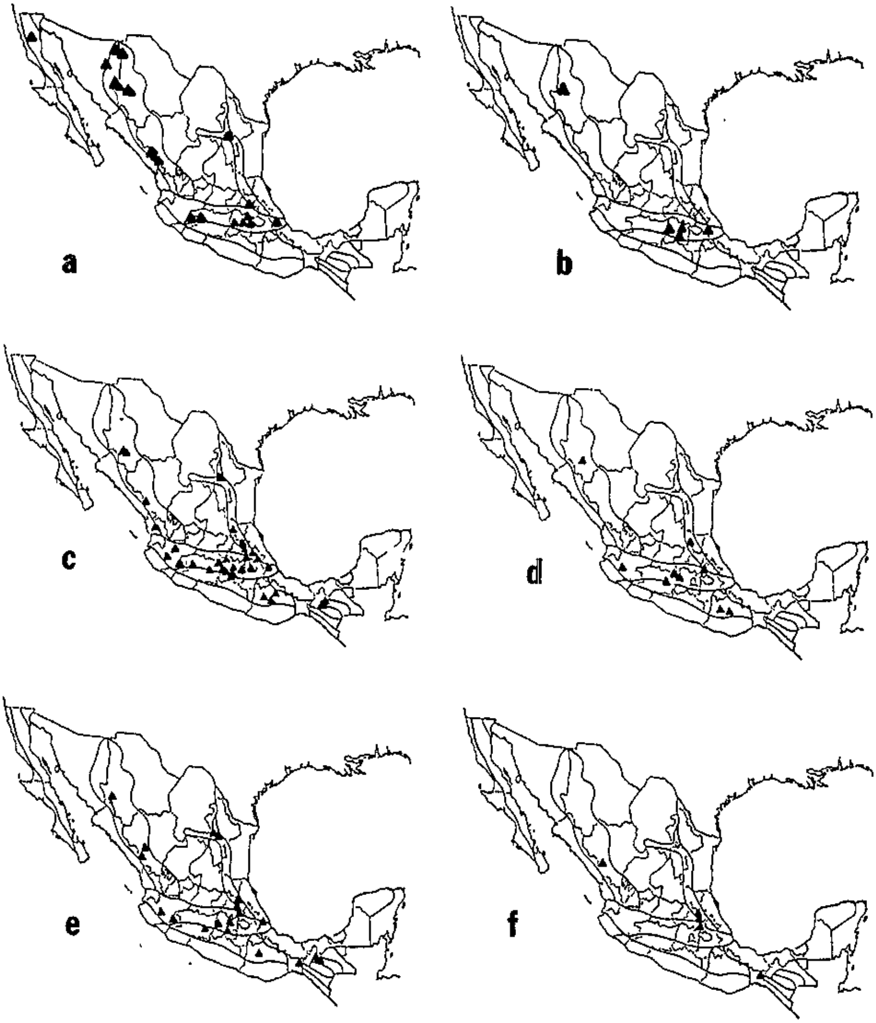


FIGURE 12. Distribution of *Usnea* species in Mexico. — a. *U. cavernosa.* — b. *U. scabrata.* — c. *U. ceratina.* — d. *U. cristatula.* — e. *U. subscabrosa.* — f. *U. vitrea.* — g. *U. hesperina.* — h. *U. firma.* — i. *U. filipendula.* — j. *U. angulata.* — k. *U. mexicana.* — l. *U. transitoria.* — m. *U. goniodes.* — n. *U. merrillii.* — o. *U. sanctaeritae.* — p. *U. malmei.* — q. *U. papillata.*

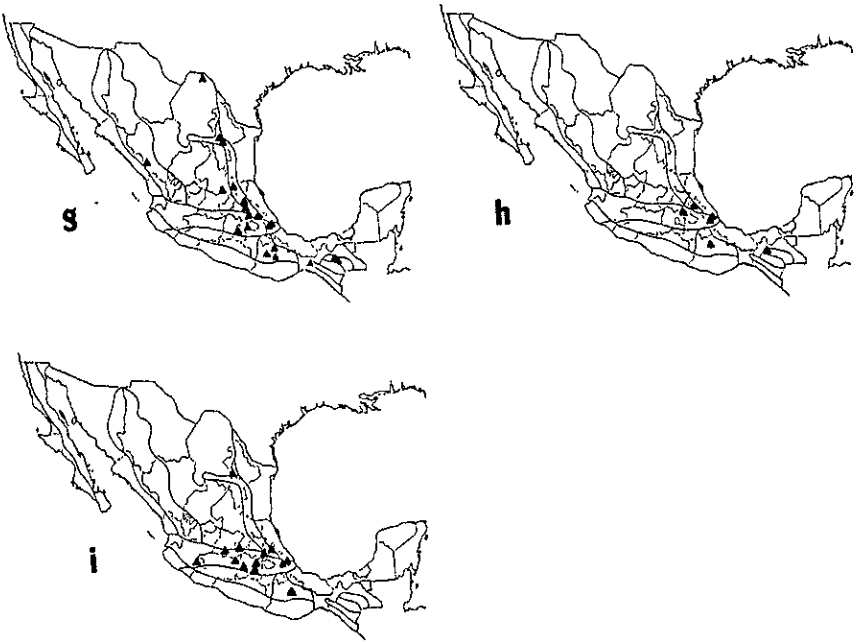


FIGURE 12. Continued.

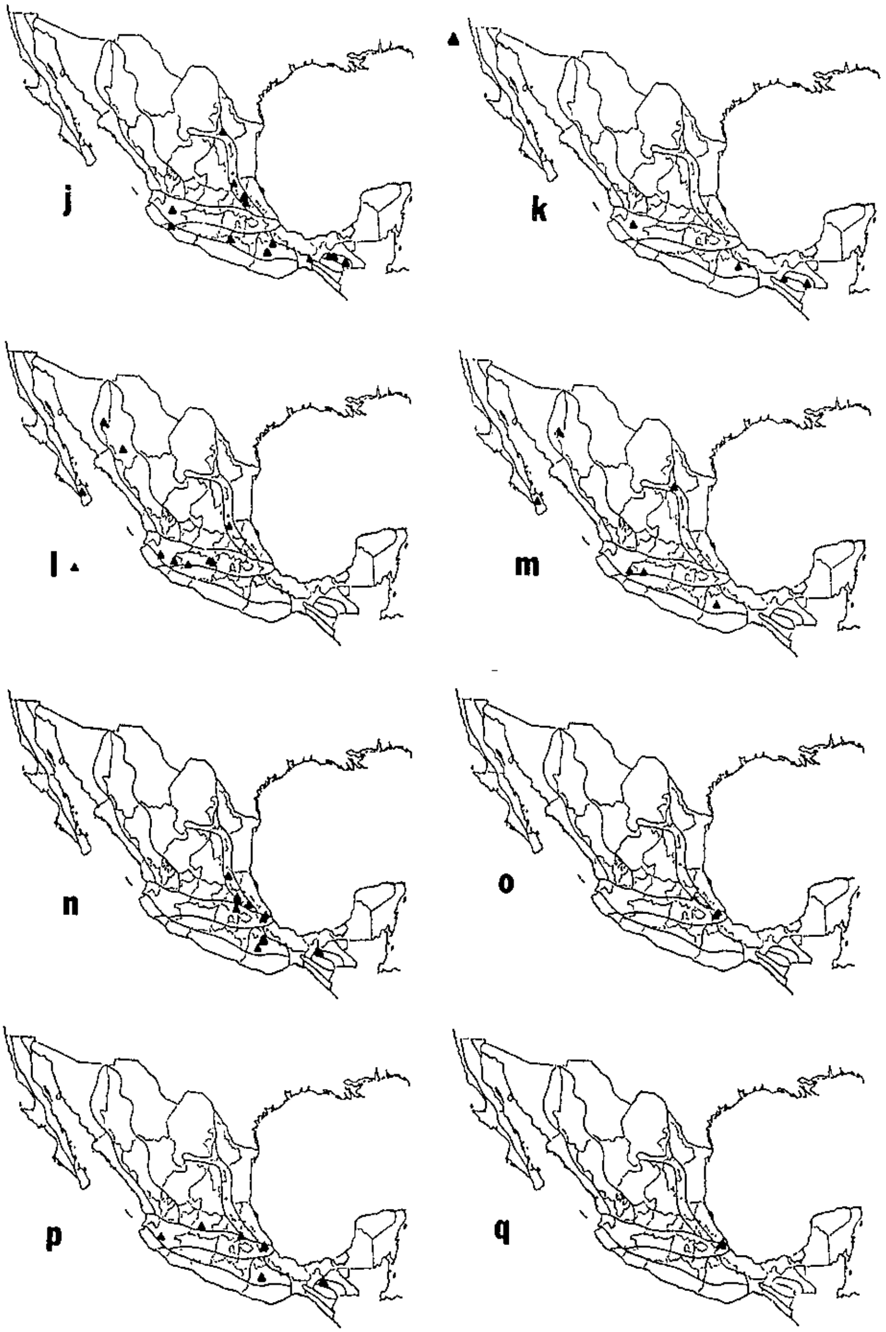


Figure 12. Continued.

Clerc, P. y Herrera-Campos, M A. 1997 Saxicolous species of Usnea subgenus Usnea (Lichenized Ascomyecetes) in North America. The Bryologist 100: 281-301

Especies saxícolas de Usnea subgénero Usnea (Ascomiceto Liquenizado) de Norteamérica

RESUMEN

Se estudian doce especies. Cuatro son principalmente saxícolas Usnea amblyoclada (Mull Arg.) Zahlbr., U. ammannii P. Clerc y Herrera-Campos sp nov., U halei P Clerc sp. nov. , U. nashii Clerc y Herrera-Campos sp. nov., para las que se presentan descripciones detalladas y mapas de distribución, así como también para U. dasaea Stirt , la cual es principalmente cortícola. U. amblyoclada es un registro nuevo para Norteamérica y U. dasaea para Norteamérica, Sudamérica, África y Asia. U. ammannii P Clerc y Herrera-Campos sp. nov., y U. nashii Clerc y Herrera-Campos sp. nov son sólo conocidas para México.

Las especies restantes son fundamentalmente cortícolas y para ellas se presentan únicamente descripciones más generales. Éstas son: U ceratina Ach., U cornuta Koerb, U. hesperina Mot., U. mutabilis Stirt , U. rubicunda Stirt., U. subscabrosa Mot. y U. wirthii P. Clerc.

Se proponen las siguientes sinonimias: U. dasaea (Syn. nov. U dolosa Mot., U. galbinifera Asah., U spinigera Asah., U. spinulifera (Vain.) Mot., U undulata Stirt.) y U. amblyoclada (Müll. Arg) Zahlbr (Syn. nov. U. globularis Mot.).

El término fibérculo se propone para designar las protuberancias que quedan una vez que las fibrillas se desprenden.

Se incluye una clave para las especies estudiadas.

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

Philippe Clerc
Conservatoire et Jardins Botaniques, Case Postale 60, CH-1292 Chambézy, Switzerland

María Angeles Herrera-Campos
Department of Botany, Arizona State University, Tempe, AZ 85287-1601, U.S.A.

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 amblyoclada (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 wirthii 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 amblyoclada 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, fibercles, 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. subfusca 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. amblyoclada (Müll. Arg.) Sahlbr. 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, FH, G, 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).

Thickness 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 X50 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 mm^2.

In addition to the types of the European species, the original material of most of the some 140 Usnea species reported by Motyka (1936-38) 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 radically symmetrical branches. The thallus is shrubby (Figs 1c, 2a) i.e., short thallus with strongly divergent branches; subpendent (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) filamentosic-dichotomous where type a occurs in the basal part of the thallus, and type b predominate 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. ceratina.

Fibercles (Fig. 2e, 8c). -We propose to introduce this term for structures what 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. amblyoclada (Fig. 2e). In Usnea nashii (Fig. 8c) they produce up to three short thin fibrils at their apex. It is important to differentiate tubercles form fibercles as some species produce only tubercles (U. ceratina) while other species produce only fibercles (U. amblyoclada 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 spinulous (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, fibercles 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 (1978b). Furthermore, it is essential to observe on which structures soralia begin their development: on the plain cortex, at the top of a tubercle, on fibercles, 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 mm) 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, isidiomorphs 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. amblyoclada 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 hyphae more or less loosely arranged with large empty spaces between them; dense (Fig. 6e) with more or less densely disposed hyphae, with space between them but still visible individually; and compact with hyphae arranged so densely that they form a compact mycelial mass. Sometimes, the medulla is heterogeneous 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 hyphae 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 b-orcinol depsidones, including stictic acid, norstictic, galbinic, and protocetraric acids, b-orcinol paradepsides including barbatic and diffractaic acids, a b-orcinol metadepside, thamnolic acid, and diverse fatty acids e g., 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 acids, whereas U. halei (n=62), U. 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. fragilescens var. fragilescens is found exclusively on stone, but it is rather uncommon (Clerc 1987a). However, observations 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. fragilescens 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. diplotypus, 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 serofilo) 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 balds, heath balds, 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
1. Cortex without red pigment or if spot-like red pigment present, then lateral branches distinctly narrowed at attachment point.. 2

 2. Medulla C+ yellow, CK+ deep yellow orange, with pink pigment in the medulla; diffractaic acid present.......................... .. .. 5. U. ceratina
 2. Medulla C-, CK-, and K- or CK+, and K+ orange red, without a pink pigment; diffractaic acid absent 3

3 Medulla with wine red pigment; soralia punctiform, with numerous isidiomorphs, papillae present or absent, fatty acids of the murolic group absent; medulla usually K-, PD-....... .. . .9 U. mutabilis

3 Medulla without wine red pigment, soralia punctiform or large, with or without isidiomorphs, papillae present or absent, fatty acids of the murolic group absent, medulla usually K+ or PD+ (rarely both reactions negative, but see chemotype 5 of U. cornuta s. l.) 4

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

4. Medulla without yellow pigment, lateral branches narrowed or not at point of attachment; cortex glossy or mat; both norstictic or psoromic acids present but not restricted acids to the soralia.... 5

5. Medulla K- and Pd+ red orange; protocetraric acid as main substance 6

5. Medulla K+ and Pd+ yellow to red orange; never protocetraric acid as main substance 9

6. Large fibercles with white summits present (Fig. 8c); short isidiomorph-like fibrils occurring on fibercles; soralia absent .. ..4. U. nashii

6 Large fibercles, and isidiomorph-like fibrils absent; soralia mostly present 7

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

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

8. Cortex distinctly glossy to vitreous, main branches not conspicuously annihilated .... 11. U. subscabrosa

8. Cortex mat, main branches distinctly annihilated, 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, or 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 mat; soralia ± tuberculous and convex with mature, usually reaching 1/2 branch diameter or more (Figs. 6c, d), with numerous and clustered isidiomorphs (Fig. 6d), fibercles absent ... ... 3. U. halei

10. Cortex glossy to vitreous, soralia ± level to cortex, punctiform (Fig. 2e), rarely enlarged (see, however, U. dasaea), occurring on fibercles or not, isidiomorphs present or absent, clustered or single, fibercles absent to numerous 11

11. Isidiomorphs thick, usually not clustered but often sitting alone on soralium, black-tipped (Fig. 2d), always present; soralia punctiform, never enlarged, ± tuberculous, numerous, densely disposed (Figs. 2b, e), occurring on fibercles .... 1. U. amblyoclada

11. Isidiomorphs thin, clustered, never black-tipped or absent; soralia punctiform or more or less enlarged, especially on terminal branches, ± level with the cortex, occurring on cortex ad initio or on fibercles 12

12. Fibrils short and spinulose, densely but ± irregularly covering restricted parts (rarely the entire length) of branches (Figs. 9a, 10a, b); soralia enlarged to 1/2 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.

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

Usnea barbata var. amblyoclada Müll. Arg., Flora 72, 509. 1889. TYPE: ARGENTINIEN [Argentinia]. Felsen am Fuss der Sierra Ventana, 1881, Lorentz (G!, holotype). %C/%M/%A. 8.5/25.5/32 (thallus a), 7/16.5/53 (thallus b). Chemistry· usnic, salazinic, and norstictic acids (both specimens).

Usnea globulàris Motyka, Lich. Gen. Usnea Stud. Monogr., Pars Syst. 2· 310. 1938. TYPE: MEXICO. Morelia, San Juanico, 1926. Amable (LBL!, holotype). %C/%M/%A: 6/16.5/54 Chemistry; usnic, salazinic, norstictic, and galbinic acids.

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 was 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 subpendent, (Fig 1b), 2-10 cm long, grayish green; branching isotomic-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), cylindric 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; fibercles low, numerous, mostly sorediate; fibrils short (1-3 mm), often spinulous (Fig. 2c), mostly present in oldest part of thallus, breaking away early in youngest branches leaving conspicuous scars (fibercles); soralia punctiform, smaller than half the diameter of branches (Fig. 2e), densely disposed (16-) 29-40-51 (-70) soralia/0.5mm^2 (n=22), slightly tuberculate, arising on fibercles; 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.

Chemistry. -1. Usnic, norstictic, galbinic, and salazinic acids, sometimes with trances of protocetraric acid (n = 78) 2. usnic acid, norstictic, and salazinic acids (n = 3)

Variation. -Usnea amblyoclada is quite a variable species in appearance depending on its exposure on rock. For instance, the shape of the branches may vary from nearly cylindric (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 diaspores, 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. amblyoclada 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. amblyoclada in detail. She indicated that galbinic acid occurs in two collections from South America. The identity of the of the specimen with salazinic, protocetraric, and fumarprotocetraric acid, mentioned by Walker (1985) needs confirmation. The Usnea bornmuelleri aggr. as discussed by Swinscow and Krog (1976) needs a world revision. Usnea bornmuelleri Steiner has large soralia with isidiomorphs, 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. amblyoclada. 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 labeled U. pulvinata is morphologically, anatomically, and chemically different from U. amblyoclada.

Usnea amblyoclada 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 spinulous 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 amblyoclada 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 (1936038) and Walker (1985) recorded U. amblyoclada from South America where the original material was collected. Ongoing investigations on South American species of Usnea (Velisek-Grundlehner & Clerc, unpublished) will shed new light on the distribution of this species on this continent.

Exsiccatae. -Hale, Lich. Amer. Exs 32, sub U. subfusca (DUKE) Weber, Lich. Exs 61, sub U. diplotypus (CUW, G). Weber, Lich. Exs 62, sub U diplotypus (CUW). Weber, Lich. Exs 407, sub U herrei (DUKE, G).

Selected specimens examined. -Saxicolous specimens: MEXICO. BAJA CALIFORNIA SUR. W of San Ignacio, Clerc 89/415 (G). CHIHUAHUA. 80 km, W of la Junta, Nash 13692 (ASU); Valle de Tomochic, Herrera-Campos 2418 (MEXU). DURANGO. 8 km N of Durango, Nash 13859 (ASU); Sierra Madre Occidental; 47 km W of Durango, Herrera-Campos 2667 (MEXU). HIDALGO. Paso de Leon, Herrera-Campos 1050 (MEXU). SONORA. 4 km E of Santa Rose, Nash 10952 (ASU). U.S.A. ALABAMA. TALLADEGA CO., Horn Mt , Dey 8107 (DUKE). ARIZONA. SANTA CRUZ CO., Sycamore Canyon, Nash 13062 (ASU). ARKANSAS. YELL CO , Mt. Nebo, Demaree 42032 (US). KANSAS. GREENWOOD CO., Fall River, Hale 4776 (US). MISSOURI. VERNON CO , Halley Bluffs, 30.9 1938, Shoop (US). NEW MEXICO. COLFAX CO., Ute Park, Standley 13595 (US). NORTH CAROLINA, ORANGE CO., Duke Forest, Clerc 89/286 (G). OKLAHOMA. CARTER CO., Ardmore, Hale 4852 (US). TENNESSEE. MONROE CO., Citico Creek, Dey 7879 (DUKE). TEXAS. BREWSTER CO., Big Bend Nat. Pk., Wetmore 40874 (ASU) Corticolous specimens: ARIZONA. SANTA CRUZ CO., Madera Canyon, Clerc 88/284 (G). NORTH CAROLINA. TRANSYLVANIA CO , Pisgah Nat. Forest, Clerc 89/622 (G) Oklahoma. LE FLORE CO., near Ludlow, Hale 5046a (US).

2 USNEA AMMANNII P. CLERC & M. HERRERA-CAMPOS sp. nov.

(Fig. 4, 5)

Fungi saxicola. Thallus 1 5-3.0 cm altus, erectus. Rami principales teres. Rami terminales crassi, non nihil ramosi. Spinulae sparsae. Papillae verrucosae, sparsae. Soralia isidiosa, plana vel ex cortice leviter excavato ad initio, aut ex papillis superne erosiis, magna cum matura. Cortex nitens. Apothecia rara. Acidum usnicum et acidum salazinicum continens.

Etymology. -This species is dedicated to Klaus Ammann, Director of the Botanical Garde, 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 anisotomic-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; fibercles absent; fibrils short spinulous, 1-2(-3) mm long, irregularly distributed on whole thallus; soralia superficial to slightly tuberculate, 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 ad 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. fragilescens 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 1,950 m and 2,800 m. So far U. ammannii is endemic to Mexico (Fig. 5), but more collections are needed to understand its distribution pattern

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, ASU, G, isotypes). %C/%M/%A. 5.5/26.5/35 Chemistry usnic and salazinic acids.

Additional specimens examined. -**MEXICO**. CHIHUAHUA. Cascada de Basaseachic, Herrera-Campos 2455, 2501 (MEXU); Sierra Tarahumara, E of San Rafael, Herrera-Campos. 3296 (MEXU). DURANGO. La Michilia, Cerro Blanco, 5 12. 1992, Zambrano (MEXU) -all Paratypes.

3. USNEA HALEI P. Clerc, sp. nov. (Fig. 6, 7)

Fungi saxicola et corticola. Thallus 2-15 cm altus, erectus vel subpendulus; ad basim saepius fulvus, sulcis conspicuis annularibus ornatus. Rami teretes, not or leviter tumidi et contracti Fibrillae sparsae. Papillae verrucosae, sparsae. Soralia isidiosa punctiformia usque nagna, parum tuberculata ex papilis erosis orta ad thalli basem atque ad apicem cum excrescentiis erosis. Cortex opacus. Apothecia desunt. Acidum usnicum, acidum sallazinicum et acidum norstiticum continens.

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 subpendent (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; fibercles absent; fibrils 24 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 mm^2 (n = 25), arising on low tubercles in lower part of thallus, and on cortex ad 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).

Variations. -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. 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. 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. amblyoclada 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 anisotomic-dichotomous ramification type, a thinner and shiny cortex, and occurs principally on bark. The most closely related species seems to be the European U. flammea (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. amblyoclada. 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

TYPE: U S A NORTH CAROLINA. TRANSYLVANIA CO., Horsepasture River Gorge, between Drift & Robinson falls, 850 m., on boulder, June 23, 1964, Moore 1707 (DUKE, holotype; G, isotype). %C/%M/%A: 8/31.5/21. CHEMISTRY: usnic, salazinic, norstictic, and ± protocetraric acids.

Selected specimens examined. -Saxicolous. - MEXICO. CHIHUAHUA. Sierra Tarahumara, E of San Rafael, Herrera-Campos 3294, 3295 (MEXU), El Creel, Herrera-Campos 3204 (MEXU). DURANGO La Michilia. Cerro Blanco, 5.12.1992, Zambrano (MEXU); Sierra Madre Occidental, 2 km W from the border with Sinaloa, Herrera-Campos 2898 (MEXU). U.S.A. ARIZONA. SANTA CRUZ CO., Santa Rita Mts., Nash 2994 (ASU). GEORGIA. RABUN CO., Black Rock Mt., Culberson 7388 (DUKE). NORTH CAROLINA. JACKSON CO., Nantahala Nat. Forest, Clerc 89/780 (G). TENNESSEE CARTER CO., Roan Mt., Dey 2214 (DUKE). VIRGINIA. PAGE CO., Shenandoah Nat. Park, Hermann 15847 (US). Corticolous. -U.S.A. NORTH CAROLINA. AVERY CO., Linville Falls Trir Lodge, Clerc 88/252; TRANSYLVANIA CO , Horsepasture River, Clerc 89/793a (G); YANCEY CO., Mt Mitchell, Clerc 89/567 (G) - All Paratypes

4. USNEA NASHII P. Clerc & M Herrera-Campos, sp. nov. (FIG. 8, 5)

Fungi saxicola. Thallus 2-12 cm altus, erectus. Rami principales terees, distinct segmentati, inter segmenta medulla valde erumpitur. Tubercula copiosa, magna conspicua, orinuntur ex cicatricibus fibrillorum delapsarum; at medulla erupta apicalis observatur. Fibrillae juveniles brevissimae isidiiformes, oriuntur summo tuberculo, quandoque fasciculatae. Soralia adsunt. Cortex plus minusvenitens, distincte, fissuratus per longum atque transversaliter, medulla conspicue erupta ex fissuris. Acidum usnicum, acidum protocetraricum continens.

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 anisotomic-dichotomous; trunk short (1-3 mm), variously pigmented but never jet black, sometimes barely developed, often rugose to ± decorticated (Fig. 8d); branches usually tapering, conspicuously 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, axils nearly 90°; foveoles absent; transverse furrows sometimes present, papillae minute, hardly distinct; tubercles absent; fibercles large (7-10 x 10-20 mm), conspicuous and numerous on whole thallus (Fig. 8c); fibrils of mature length rather rare and only present near basal part, short (0.5 mm) isidiomorph-like fibrils produced (sometimes in bundles) on top of fibercles (Fig. 8c); soralia absent; isidiomorphs absent; cortex ± glossy, distinct 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)]; 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).

Variations. -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 fibercles producing short isidiomorph-like fibrils at their summit.

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

TYPE. MEXICO CHIHUAHUA. Municipio Ocampo Parque Nacional Cascada de Basaseachic, 28°12'N, 108°14'W, Bosque de coniferas y Acer, 1950m, 22.05.1992, Herrera-Campos 2495 (MEXU, holotype, ASU, G, isotype) %C/%M/%A: 6/34/21 (holotype). Chemistry usnic and protocetraric acids

Additional specimens examined. -MEXICO. CHIHUAHUA. Cascada de Basaseachic, Herrera-Campos 2454 (MEXU); El Creel, Herrera-Campos 3203 (MEXU). DURANGO La Michilia, Cerro Blanco, 5.12 1992, Zambrano (MEXU) - all paratypes.

PRIMARILY CORTICOLOUS SPECIES,
RARELY COLLECTED ON ROCKS

5. USNEA CERATINA Ach., Lich, Univ. 610 1810.

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 orangish. It is rarely found growing on rocks The specimens 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).

Saxicolous specimen examined. -U S A. CALIFORNIA MARIN CO. Pt. Reyes, Ryan 22020 (herb. Ryan).

6. USNEA CORNUTA Koerber, Parerga Lichenol. 2. 1959., 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 and ± 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. fragilescens 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 & Hübner, 19 09 1989, (G) (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 558 (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).

7 USNEA DASAEA Stirt., Scott Naturalist. 6: 104. 1881 (FIGS 9, 10, 11)

TYPE. MADEIRA. Funchal, Payne (BM!, holotype). %C/%M/%A. 9.5/26 5/28. Chemistry: usnic, norstictic, galbinic, and salazinic acids.

Usnea dolosa Motyka, Lich. Gen. Usnea Stud. Monogr , Pars Syst. 2. 494. 1937. TYPE: ROMANIA. TRANSSILVANIA. in monte Rusca, in Fago, 1872, Lojka (w! lectotype). Chemistry: usnic, norstictic, galbinic, and salazinic acids.

Usnea galbinifera Asahina, J. Jap. Bot. 38. 257. 1963. TYPE. INDIA. DARJEELING. en route from Phalut to Sandakphu, 10.5.1960. Togashi (TNS!, holotype). %C/%M/%A: 5/31/28 Chemistry usnic, norstictic, galbinic, and salazinic acids.

Usnea spinigera Asahina, Lichens of Japan, vol 3. Genus Usnea: 85. 1956. TYPE. JAPAN. ITINOMIYA. Kazusa, May 1952, Asahina 52330 (TNS! holotype) %C/%M/%A. 5.5/27 5/34 Chemistry. usnic, norstitctic, and salazinic acids.

Usnea spinigera fo. subnuda Asahina, Lichens of Japan, vol. 3. Genus Usnea· 86 1956 TYPE. JAPAN. INIOMIYA. Kazusa, May 1952, Asahina 52330b (TNS!, holotype) %C/%M/%A: 6 5/29.5/29. Chemistry: usnic, norstictic, and salazinic acids.

Usnea spinulifera (Vain.) Motyka, Lich Gen. Usnea Stud. Monogr., Pars Syst 2: 518. 1937. TYPE BRASILIA MINAS GERAES, Lafayette, 1885, Vainio (TUR!, holotype). %C/%M/%A. 5 5/31/28 Chemistry· usnic, norstictic, galbinic, and salazinic acids

Usnea undulata Stirt. Scott. Naturalist. 6: 104 1881 TYPE· MADEIRA Funchal, Payne (BM!, holotype) %C/%M/%A· 9.5/26.5/28. Chemistry: usnic, norstictic, galbinic, and salazinic acids

Morphology. -Thallus shrubby (Figs. 9b, c) to subpendent (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 thing; 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, spinulous (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 spinulous 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)], glossy, not conspicuously cracked; medulla large [(13-)21-26 5%-32(-37.5) (n = 77)], compact to dense, periaxially 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 spinulous 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. fragilescens agg.

More than 100 specimens form 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 aggregates' in East Africa was discussed by Swinscow and Krog (1975) The emphasized the difficulty in delimiting species in this group. Especially difficult was the separation of U. leprosa Motyka from U. undulata Stirt. and they illustrated this by showing a table (Swinscow & Krog 1975, Table 2) where 'transitional and mixed forms of a single population' were listed. However the characters chosen by Swinscow 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 synonym 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 Swinscow and Krog (1975) in light of the characters mentioned above seems to be necessary. Examination of the holotype of U. undulata shows that there are no essential differences from U. dasaea, and therefore U. undulata is here considered synonymous 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 spinulous 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 spinulous fibrils, which are the main morphological character segregating U. dasaea from other species in the U. fragilescens agg. Due to its large variability, this species has been described many types, and U. chilensis Motyka, U. feeana Motyka, U. filimentosa Motyka, U. furfurosula (Hahlbr.) Motyka, U spilotoides 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 discuss 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 are 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 for North America, South America, Africa, and Asia. Australia 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-Campos 3283 (MEXU). U.S.A. GEORGIA. DADE CO., Lookout Mountain, Clerc 88/259 (G) NORTH CAROLINA. BUNCOMBE CO., vicinity of Montreat, Standley & Bollman 10146 (US). Corticolous: MEXICO. BAJA CALIFORNIA NORTE Cerro Kenton, Clerc 89/315 (G) CHIAPAS. Tzentontwitz-Chalam, Herrera-Campos 3399 (MEXU) DURANGO, Sierra Madre Occidental, 2 km W from the border with Sinaloa, Herrera-Campos 2899 (MEXU) HIDALGO Zacualtipan, Herrera-Campos 1372, 1373 (MEXU). JALISCO: Sierra de Manantlan, Herrera-Campos 4029 (MEXU). NAYARIT. Volcan Zanganguey, Herrera-Campos 4030 (MEXU). NUEVO LEON. Cumbres de Monterrey El Manzano, 1992, Zambrano (MEXU) OAXACA. Puerta del Sol Macuiltianguis, Herrera-Campos 3050 (MEXU). SAN LUIS POTOSI. Sierra Madre Oriental, El Potos, 1992, Zambrano (MEXU). SONORA Santa Ana, Nash 11050 (ASU). U.S A. CALIFORNIA. SANTA BARBARA CO., Santa Barbara, Cole 1290 (US). FLORIDA. CHARLOTTE CO., Englewood, Moore 1352a (DUKE). KENTUCKY. KNOX CO , Jarvis Store, Hubricht 306d (US). LOUISIANA. Bayou Millieu, 1896, Langlois (US). NORTH CAROLINA. AVERY CO., Pisgah Nat. Forest, Clerc 89/939 (G). MAINE, KENNEBECK CO., Manchester, Sargent (US). MASSACHUSETTS. HAMPSHIRE CO., Amherst, 1856. Tuckermann (DUKE). MISSOURI. ST. LOUIS CO., St. Louis 1841 (US). VIRGINIA. GILES CO., Mountain Lake, Clerc 11394a (G). TEXAS COMAL CO., New Braunfels, Lindheimer 429 (US).

8. USNEA HESPERINA Motyka, Lich. Gen. Usnea Stud. Monogr., Pars Syst. 2: 383. 1936-1938.

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 protocetraric acid in the medulla The distribution of U. hesperina in Mexico is treated by Herrera-Campos and Clerc (in press).

Saxicolous specimen 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 Mountains, Egan 12431 (MIN); SWAIN CO, Blue Ridge Parkway, Clerc 89/715 (G).

9. USNEA MUTABILIS Stirt. Scott. Naturalist 6: 107 1881

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 is much rarer in the western part of the country. Usnea mutabilis is rarely found on sandstone.

Saxicolous specimens examined. -U.S.A. ARKANSAS MONTGOMERY CO., Ouachita Nat Forest, Demaree 43338 (US). IOWA. BOONE CO, Ledges State Park, Wetmore 13140 (MIN); CLAYTON CO Giard School, 16 July 1930, Shimek (MIN).

10. USNEA RUBICUNDA Stirt., Scott. Naturalist 6: 102. 1881.

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

Saxicolous specimens examined. -MEXICO BAJA CALIFORNIA. Cerro Kenton. Moberg 8683 (UPS). U S.A MINNESOTA. HOUSTON CO , Crooked Creek Valley, April 1977 Trana (MIN). NORTH CAROLINA. BUNCOMBE CO., vicinity of Montreat, Standley & Bollman 10/146 (US) TENNESSEE. Calkins (MIN)

11 USNEA SUBSCABROSA Motyka, Lich. Gen. Usnea Stud. Monogr., Pars Syst. 2: 313, 1936-1938

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).

12. USNEA WIRTHII P Clerc, Saussurea 15: 34. 1984.

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., Ryan 31090 (hb. B. Ryan).

EXCLUDED SPECIES

USNEA DIPLOTYPUS Vainio, Medd. Soc. Fauna Fl. Fenn. 48: 172 1924.

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 diplotypus 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 diplotypus 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. diplotypus. This species has a trunk which is often black pigmented; minute soralia with numerous isidiomorphs; verrucous to cylindric papillae; and salazinic, ± barbatic acids, or alectorialic acid in the medulla. In North America, U diplotypus 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. diplotypus has been found to occur on trees in British Columbia in Canada (Halonen et al , in press). All collections cited Wetmore (1976) as U diplotypus are most probably U. amblyoclada with galbinic acid, and not stictic acid as mentioned here Specimens cited by Dey (1978) under U. diplotypus are U cornuta and U. halei.

USNEA HERREI Hale nom illeg. How to Know the Lichens Second Edition. Wm. C. Brown Company, Dubuque: 219 (1979), nom illeg. (Code, Art. 32)

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

USNEA SUBFUSCA Stirt., Scott. Naturalist 6: 108. 1881

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).

ACKNOWLEDGMENTS

Our sincerest thanks to Thomas Nash III for his support and great interest in the Mexican lichen flora. We are much indebted to the curators and owners of the herbaria listed in the text for loan of specimens. We are grateful to Maryse Kolakowski (Geneva) for photographic assistance to Hèléne Geser (Geneva) for technical assistance with TLC. We want to thank Bernardi (Geneva) for his invaluable help with Latin diagnosis. We also thank Saskia Pernin-Winström (Geneva) for constructing the distribution maps. Field studies of the senior author were made possible by a postdoctoral grant from the Swiss National Foundation. M. A. Herrera-Campos deeply acknowledges the support received from Departamento de Botánica, Instituto de Biología, UNAM through Patricia Dávila Aranda; the grants 190/92/PADEP/68 from UNAM, and BSSR-920-1111 from NSF, as well as CoNaCyT financial support. Special thanks to S. Kirchheimer and K. Pigg for their invaluable assistance

LITERATURE CITED

ASAHINA, Y. 1956. Lichens of Japan Vol. III. Genus Usnea. Research Institute for Natural Resources Shinjuku, Tokyo.

CLERC, P. 1984a Contribution à la revision de la systématique des usnées (Ascomycotina, Usnea) d'Europe. I. -Usnea florida (L.) Wig. emend. Clerc. Cryptogamie, Bryologie et Lichénologie 5: 333-360.

___. 1984b. Usnea wirthii -- a new species of lichen from Europe and North Africa. Saussurea 15: 33-36.

___. 1987a. Systematics of the Usnea fragilescens aggregate, and its distribution in Scandinavia. Nordic Journal of Botany 7 479-495.

___. 1987b. On the morphology of soralia in the genus Usnea, pp. 99-102. In E. Peeling (ed.), Progress and Problems in Lichenology in the Eighties. Biblioteca Lichenologica, Vol 25 Berlin-Stuttgart.

___ 1991. Usnea madeirensis Motyka (Ascomycète lichènisè). une espèce méconnue de l'Europe et de l'Amérique de Nord. Candollea 46: 427-438.

___. 1992. Some new or interesting species of the genus Usnea (lichenized Ascomycetes) in the British Isles. Candollea 47: 513-526

___. 1994. Comment Usnea mutabilis Stirt. une espéce nord-amèricaine, se cache en Europe sous le nom d'Usnea marocana Motyka. Une contribution ~a la systématique du genre Usnea (ascomycètes lichénisés). Bulletin de la Société Linnéenne de Provence 45: 309-316.

___. 1997. Notes on the genus Usnea Dill. ex Adanson Lichenologist 29· 209-215.

CLERC, P. & DIEDERICH. 1991. Usnea wirthii Clerc new to North America and the British Isles. Lichenologist 23: 405-407.

CULBERSON, C. F & K. AMMANN. 1979. Standardmethode zur Dünnschichtchromatographie von Flechtensubstanzen. Herzogia 5: 1-24

CULBRSON, C. F. & A. JOHNSON. 1982. Substitution of methyl tert-butyl ether for diethyl ether in the standardized thin-layer chromatographic method for lichen products. Journal of Chromatography 238: 483-487.

DEY, J. P. 1978. Fruticose and foliose lichens of the high-mountain areas of the southern Appalachians. THE BRYOLOGIST 81: 1-93

___. 1979. Notes on the fruticose and foliose lichen flora of North Carolina and adjacent mountainous areas. Veroffentlichungen des Geobotanischen Institutes der ETH Stiftung Rübel, Zürich 68: 185-205.

FICUS, S. 1972. A survey of the chemistry of the Usnea florida group in North America. THE BRYOLOGIST 75: 299-304.

HALE, M. E. 1956 A note on Lichenes Americani Exsiccati fascicle II. THE BRYOLOGIST 59· 284-285.

___ 1958. The status of Usnea diplotypus in North America. THE BRYOLOGIST 61 247-248

___. 1962. The chemical strains of Usnea strigosa. THE BRYOLOGIST 65: 291-294

___. 1979. How to Know the Lichens W. C Brown Co. Dubuque, Iowa

HALONEN, P. & A. PUOLASMAA. 1995. The lichen genus Usnea in eastern Fennoscandia. I. Usnea hirta. Annales Botanici Fennici 32 127-135.

___, P. CLERC, T. GOWARD, I. M. BRODO & K. WULFF. Synopsis of the genus Usnea (Lichenized Ascomycetes) in British Columbia. THE BRYOLOGIST. In press.

HAWKSWORTH, D. L. 1972 Regional studies in Alectoria (Lichens) II. The British species. Lichenologist 5. 181-261

____, P. W. JAMES & B. J. COPPINS. 1980. Checklist of British lichen-forming lichenicolous, and allied fungi. Lichenologist 12: 1-115.

HERRERA-CAMPOS, M. A & P. CLERC. Pendulous species of Usnea from the temperate forests in Mexico. THE BRYOLOGIST. In press.

JAMES, P. W. 1979. Noes on Usnea rubiginea and U rubicunda. Lichenologist 11: 322-323.

____, CLERC, P. & W PURVIS. 1992 Usnea, pp 620-629 In W. PURVIS B. J. Coppins, D. L. Hawksworth, P. W. James & D. M. Moore (eds.), The Lichen Flora of Great Britain and Ireland. Edinburgh.

MOTYKA, J. 1936-1938. Lichenum Generis Usnea Studium Monographicum Pars Systematica. Leopoli.

RZEDOWSKI, J. 1986. Vegetación de México. Lumusa. Mexico.

SWINSCOW, T. D. V. & H. KROG. 1975. The Usnea undulata aggregate in East Africa. Lichenologist . 121-138

____ 1976. The Usnea bornmuelleri aggregate in East Africa. Norwegian Journal of Botany 23: 23-31.

____ 1979. The fruticose species of Usnea subgenus Usnea in East Africa. Lichenologist 11. 207-252.

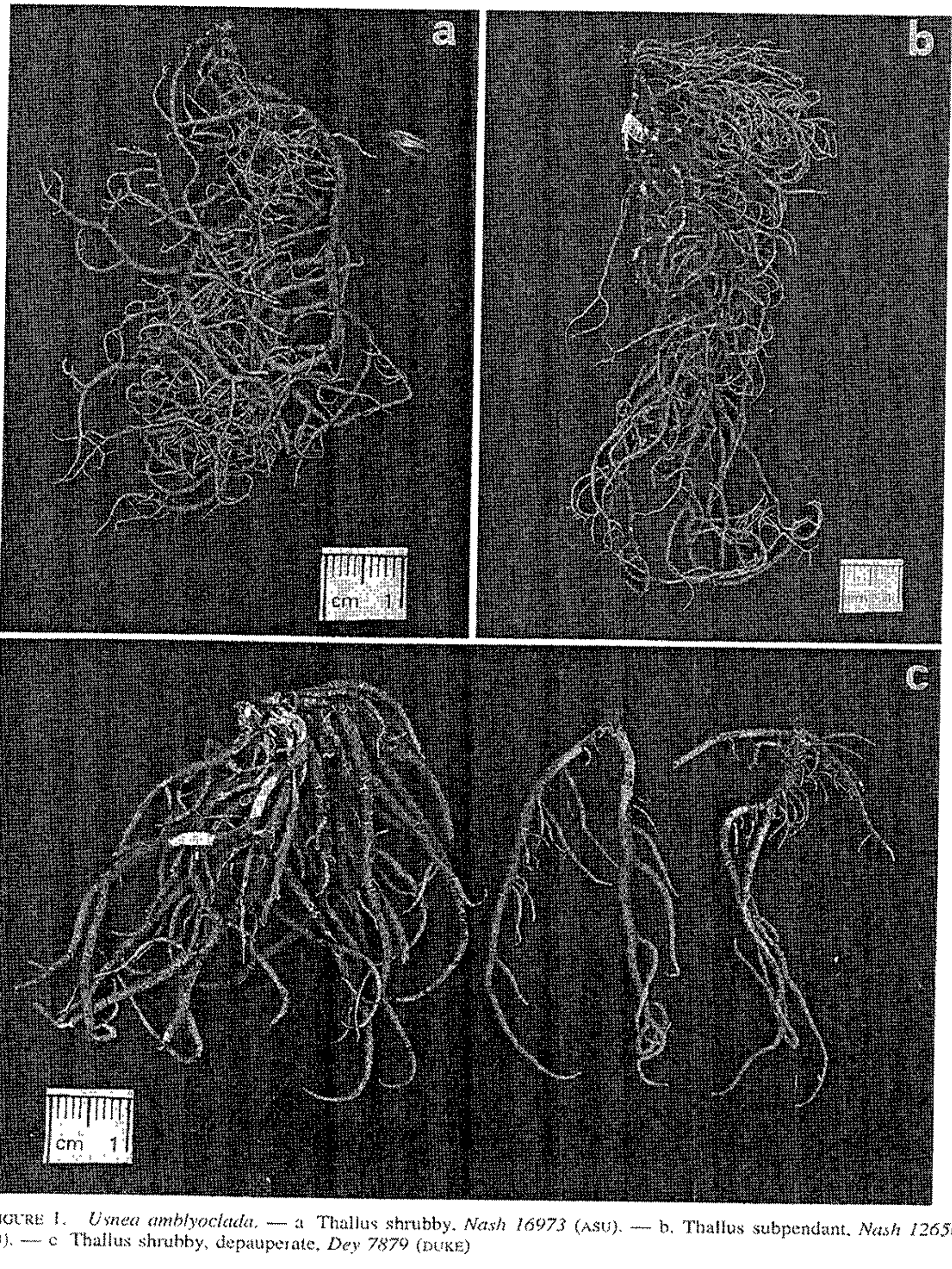
TAYLOR, C. J. 1968. The lichens of Ohio - part II. Fruticose and cladoniform lichens. The Ohio Biological Survey Biological Notes 4· 153-227

THOMSON, J. W. 1956. Usnea diplotypus Vainio in North America. THE BRYOLOGIST 59: 221-222.

VANKAT, J. L. 1979. The Natural Vegetation of North America. Wiley & Sons, New York.

WALKER, F. J. 1985 The lichen genus Usnea subgenus Neuropogon Bulletin of the British Museum (Natural history). Botany 13 1-130.

WETMORE, C. M 1976 Macrolichens of Big Bend National Park, Texas. THE BRYOLOGIST 79 296-313



IGURE 1. *Usnea amblyoclada.* — a Thallus shrubby. *Nash 16973* (ASU). — b. Thallus subpendant. *Nash 12650*). — c Thallus shrubby, depauperate. *Dey 7879* (DUKE)

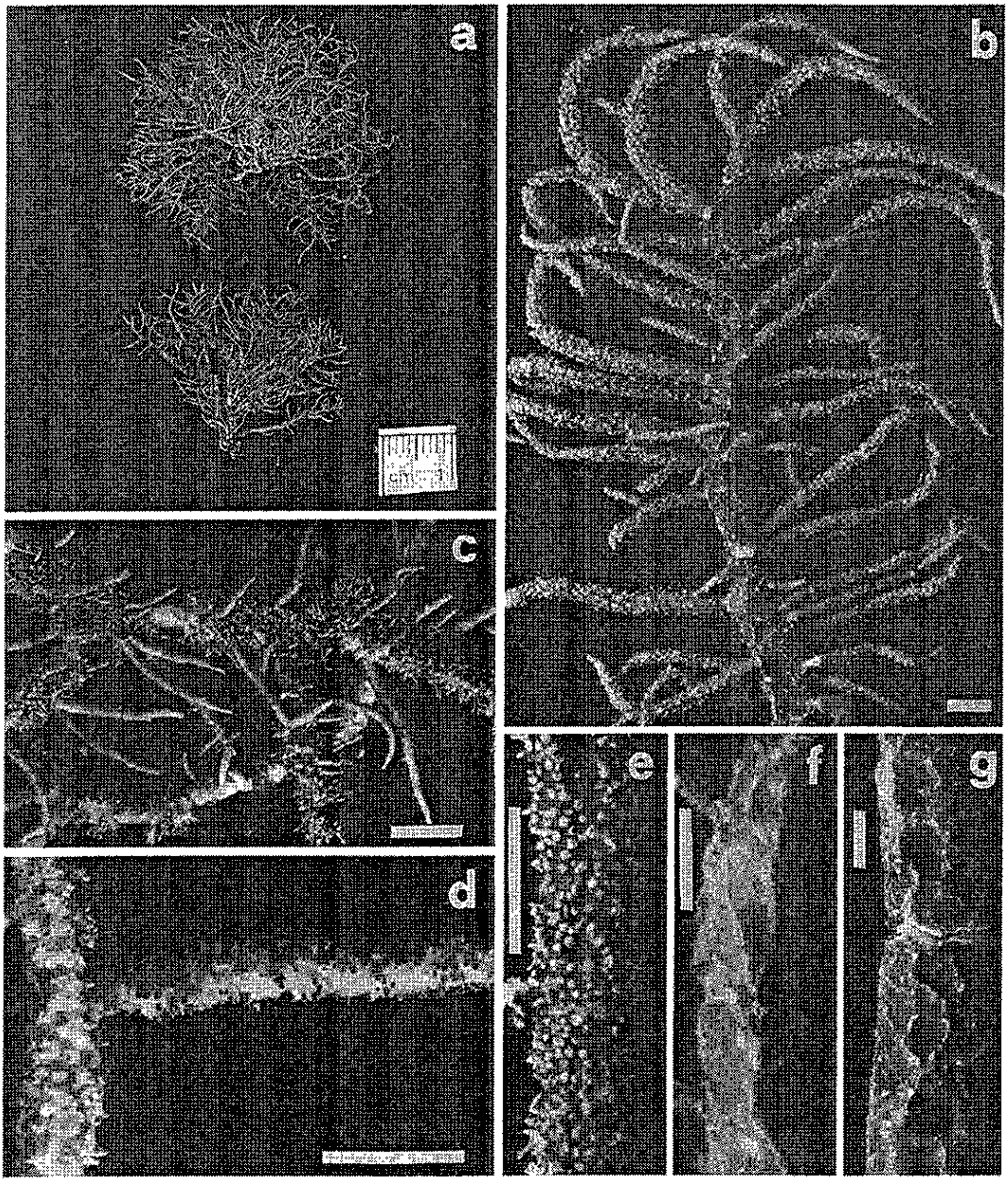


FIGURE 2. *Usnea amblyoclada*. — a. Thallus shrubby, compact-pulvinate, *Nash 13859* (ASU) — b. Terminal branches with minute soralia. *Herrera-Campos 1405* (MEXU). — c. Spinulous isidiomorph-like fibrils, *Nash 15088* (ASU). — d. Lateral branch constricted at attachment point. Black tipped isidiomorphs clearly visible, *Nash 16973* (ASU). — e. Branch with punctiform soralia on fibercles, May 22, 1992, *Herrera-Campos* (MEXU). — f. Branch with ridges, *Dey 7879* (DUKE). — g. Branch with foveoles, *Dey 7877* (DUKE). Scale bars Fig. b–g = 1 mm.

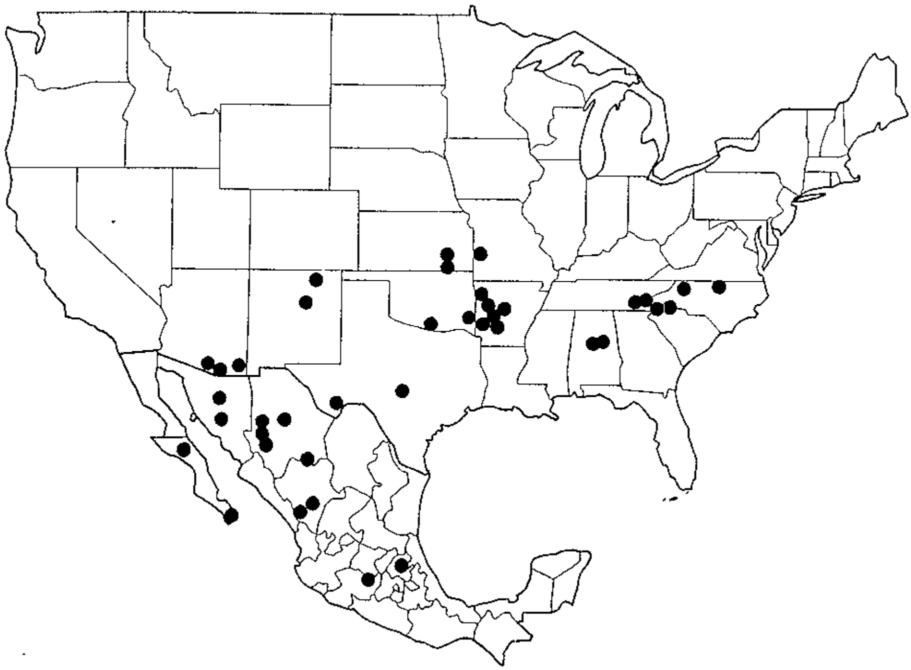


FIGURE 3 Known distribution of *Usnea amblyoclada* in North America

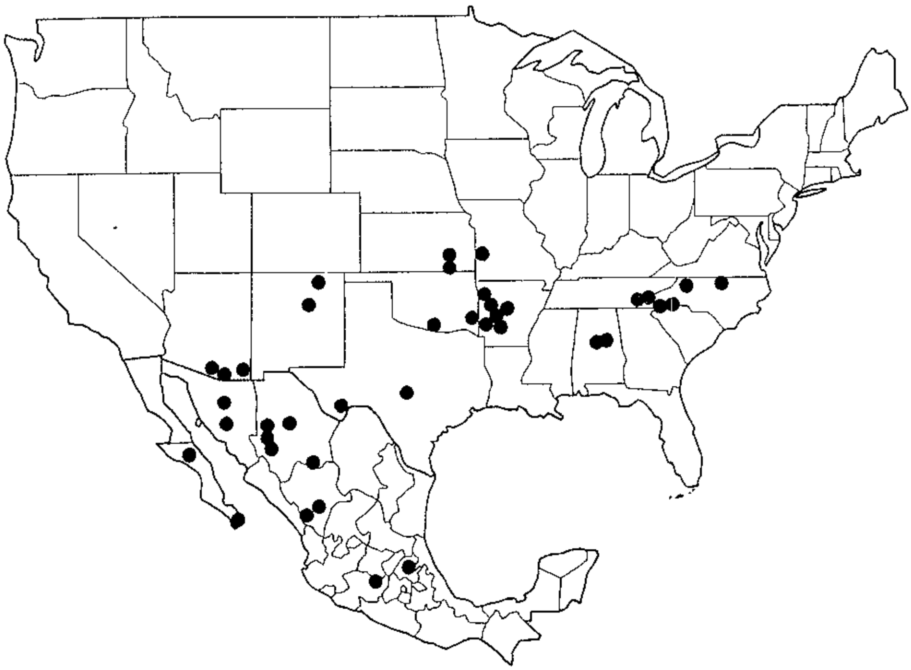


FIGURE 3 Known distribution of *Usnea amblyoclada* in North America

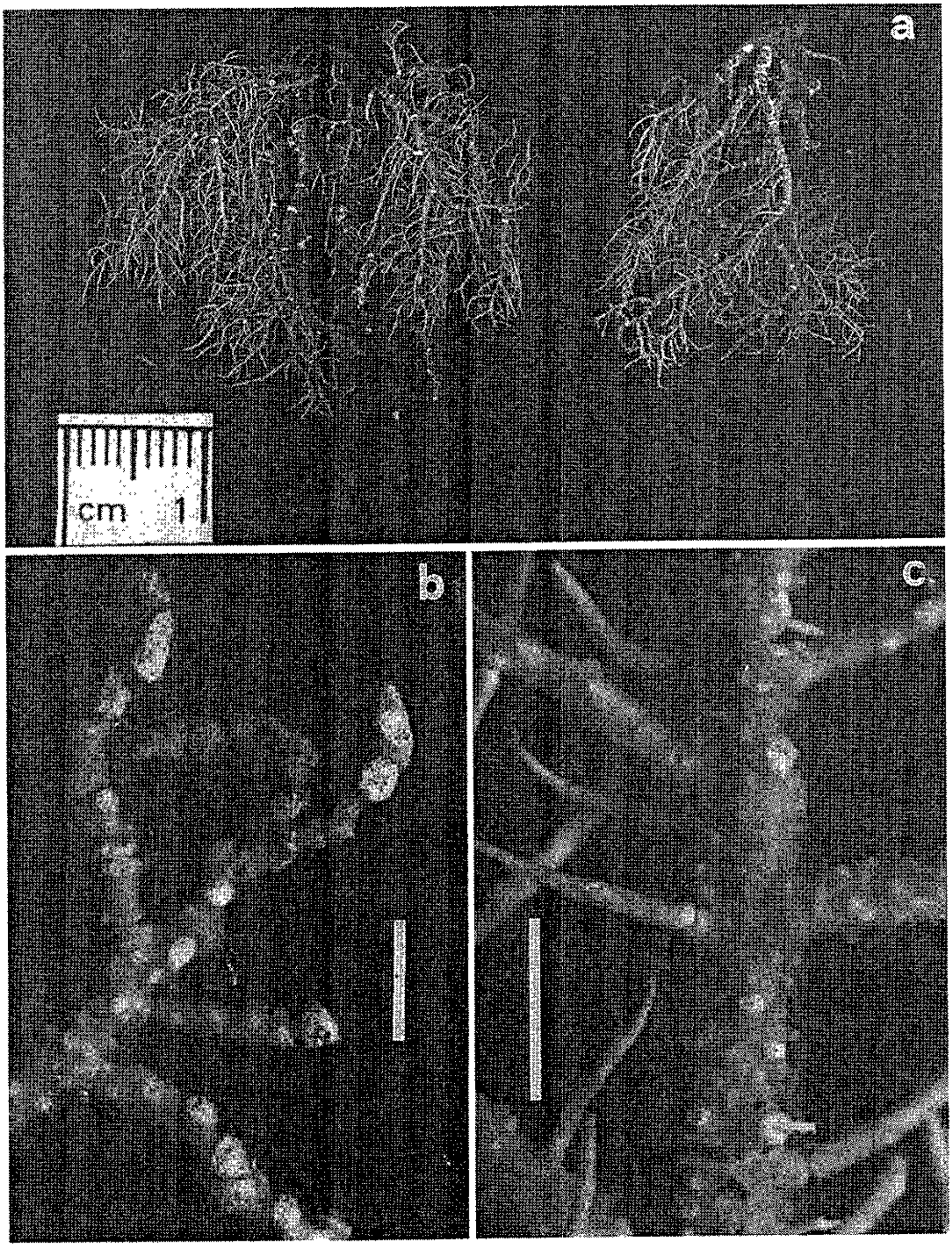


FIGURE 4. *Usnea ammannii.* — a. Thallus small, shrubby, holotype. — b. Terminal branch with soralia, holotype. — c. Branch with verrucous papillae and fibrils, May 22, 1992, *Herrera-Campos* (MEXU). Scale bars: Fig. b–c = 1 mm

FIGURE 5. Known distribution of *Usnea ammannii* and *U. nashii* (both species have the same generalized distribution).

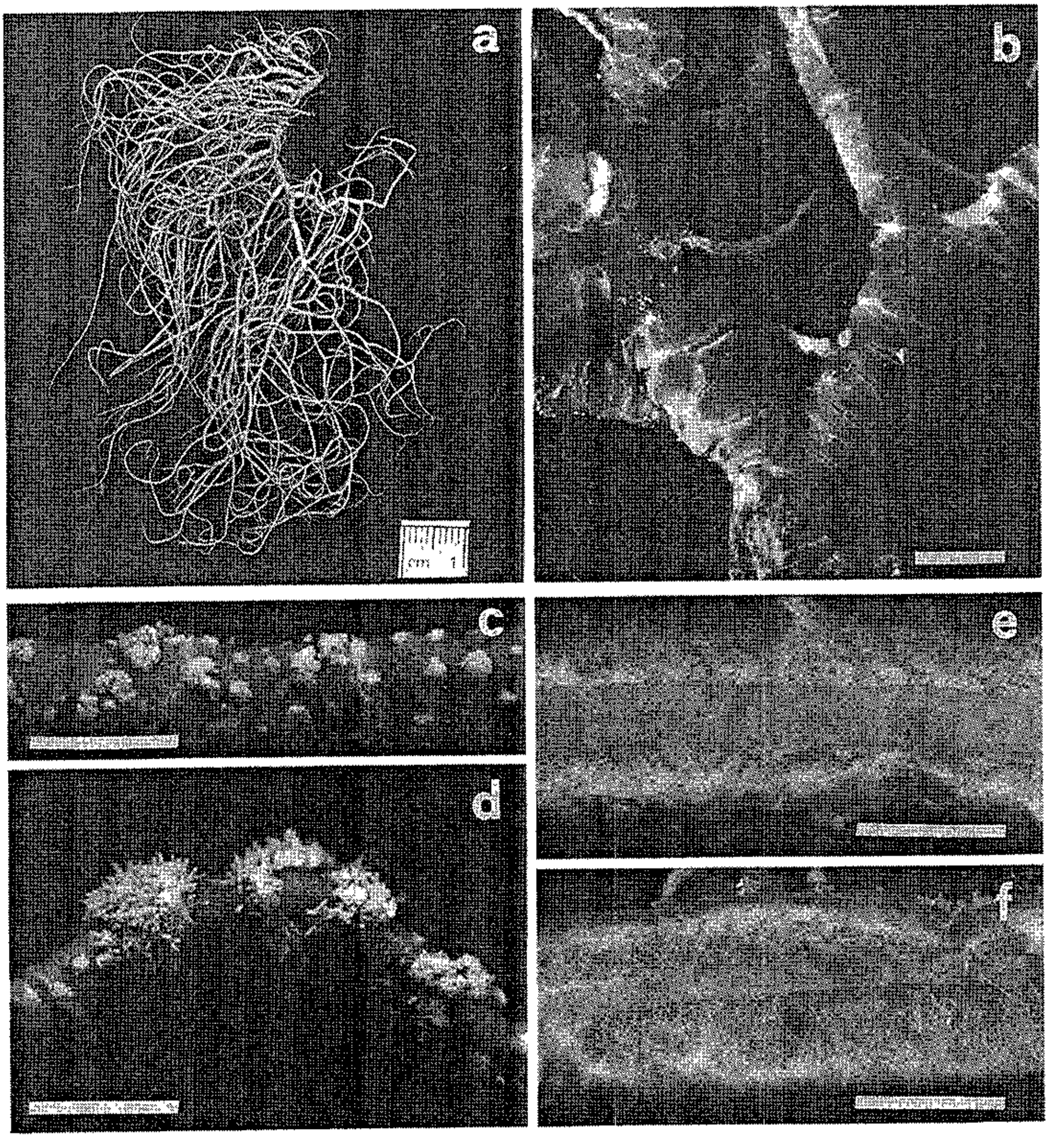


FIGURE 6. *Usnea halei* — a. Thallus subpendent, *Clerc 89/818* (G). — b. Basal part with annular cracks, *Dey 7834*, hb. Dey) — c. Branch with punctiform soralia, *Dey 568* (hb. Dey) — d. Branches with capitate soralia and isidiomorphs, *Dey 2266* (DUKE). — e. Longitudinal section of branch, central axis thick, medulla dense, *Moore 1841* (DUKE). — f Longitudinal section of branch, central axis thin, medulla lax, *Dey 568* (hb. Dey). Scale bars: Fig. b–f = 1 mm.

FIGURE 7 Known distribution of *Usnea halei*.

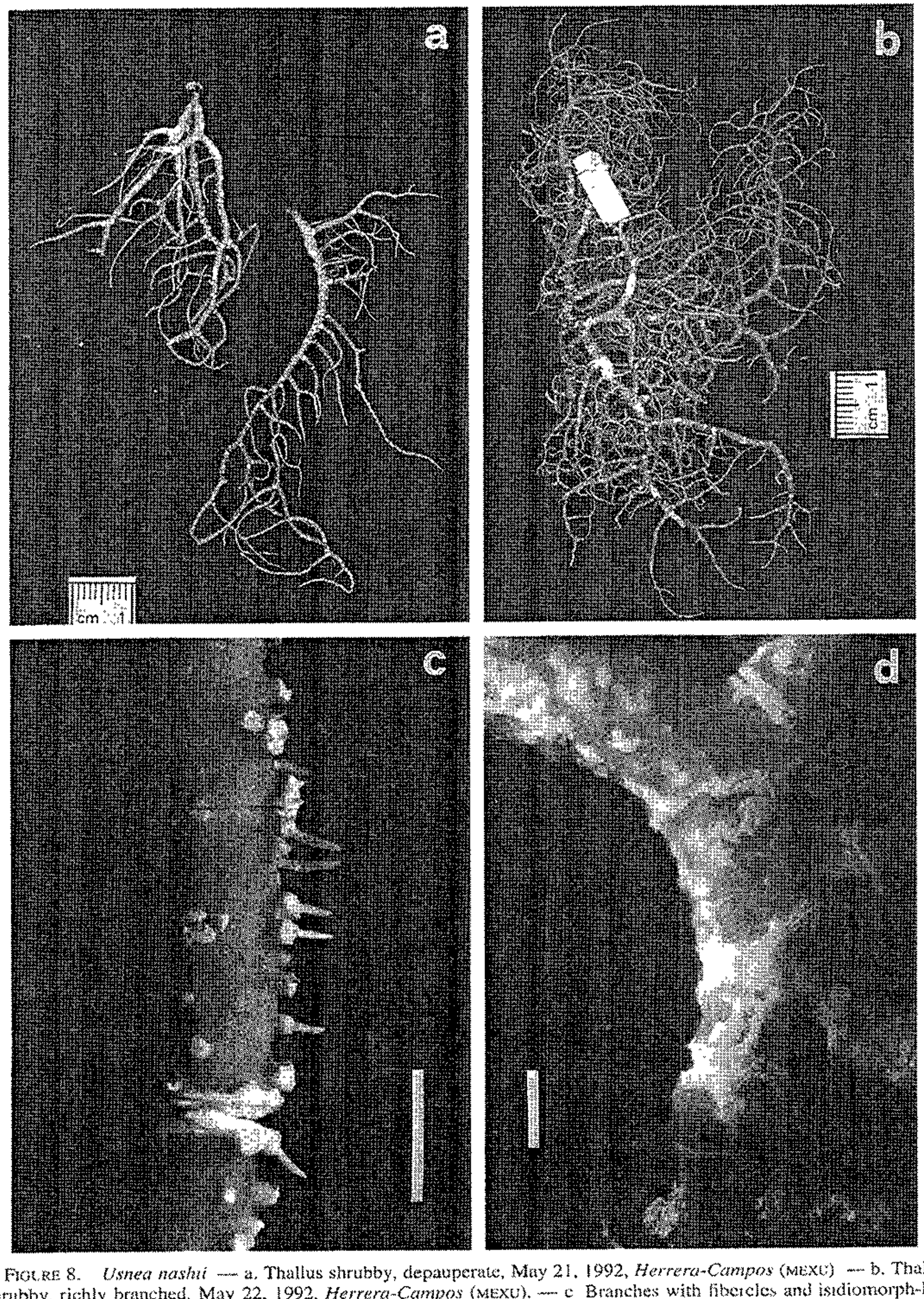


FIGURE 8. *Usnea nashii* — a. Thallus shrubby, depauperate, May 21, 1992, *Herrera-Campos* (MEXU) — b. Thallus shrubby, richly branched, May 22, 1992, *Herrera-Campos* (MEXU). — c Branches with fibercles and isidiomorph-like fibrils, holotype (MEXU). — d. Basal part with cracks and everted medulla, holotype, (MEXU). Scale bars. Fig. c-d = 1 mm.

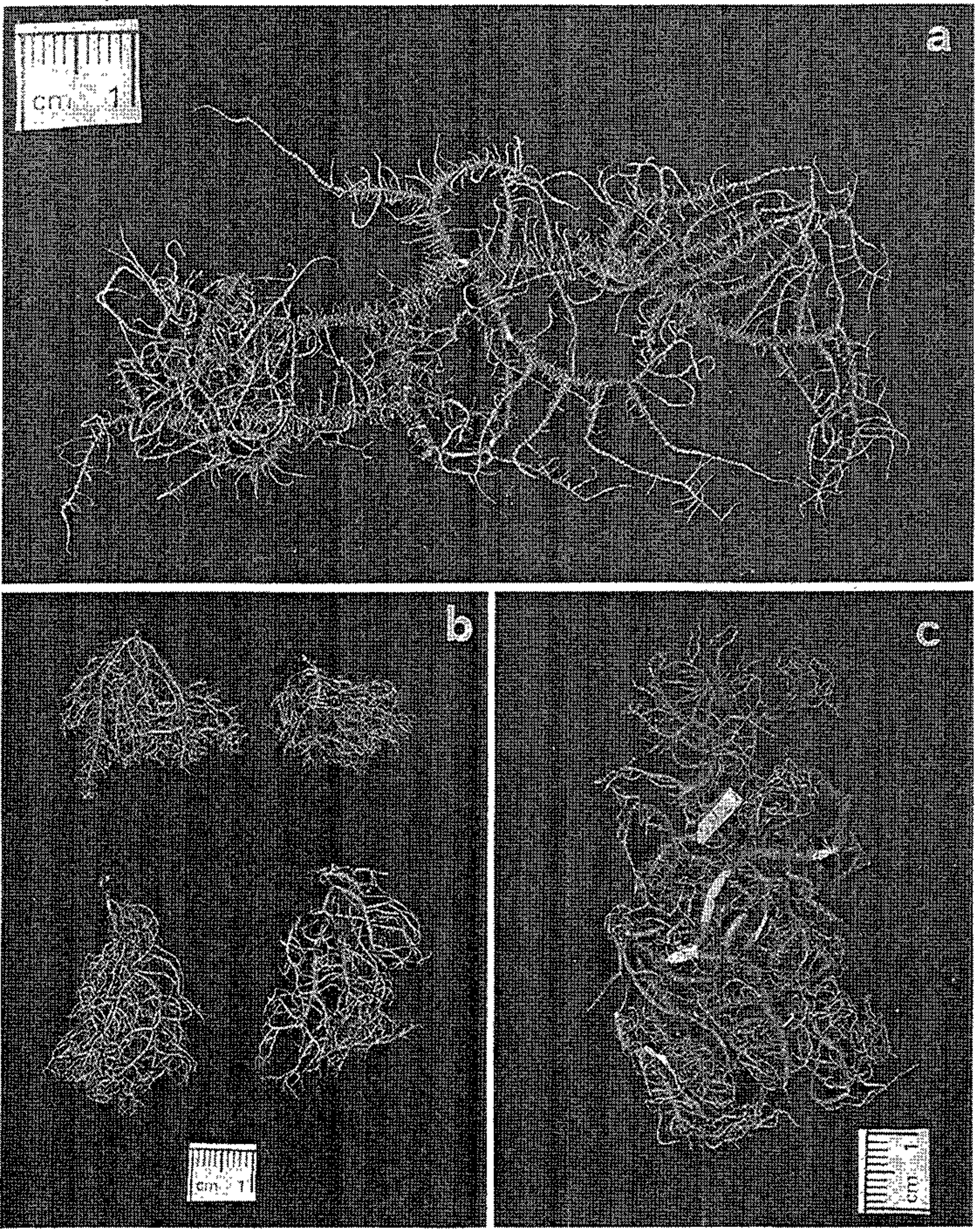


FIGURE 9. *Usnea dasaea*. — a. Thallus subpendant, with numerous fibrils, *Moore 799* (DUKE). — b. Thallus small ubby, compact, *Clerc 89/315* (G). — c. Thallus shrubby, with thick main branches, *Clerc 88/29* (G)

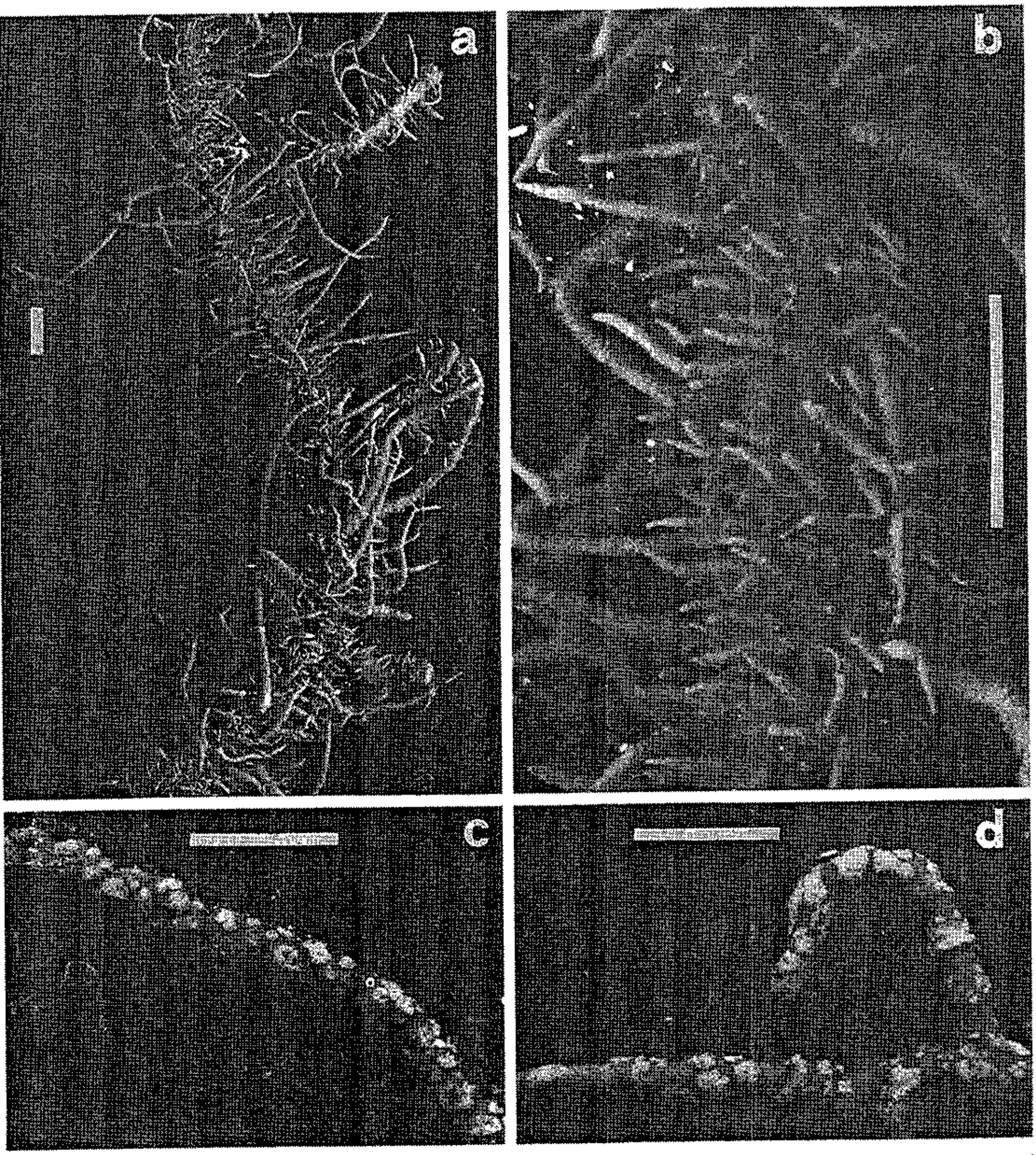


FIGURE 10. *Usnea dasaea*. — a. Branch with spinulous fibrils, *Culberson 6152* (DUKE). — b. Close up of spinulous rils and isidiomorph-like fibrils, *Culberson 6152* (DUKE). — c. Branch with more or less minute soralia, *lberson 4865* (DUKE). — d. Branches with large soralia, *Culberson 4865* (DUKE). Scale bars = 1 mm.

TABLE 1. Main secondary metabolites in North American saxicolous *Usnea*. Ch., chemotype; +, present in all pecimens examined; ±, not always present (accessory); –, not present. Bar, barbatic acid, Dif, diffractaic acid; Tha, hamnolic acid; Pro, protocetraric acid; Nor, norstictic acid; Gal, galbinic acid; Sti, stictic acid, Sal, salazinic acid; Pso, soromic acid; Fat, fatty acid(s).

Taxon		Bar	Dif	Tha	Pro	Nor	Gal	Sti	Sal	Pso	Fat
U. amblyoclada	Ch. 1	–	–	–	–	+	+	–	+	–	–
	Ch. 2	–	–	–	–	+	–	–	+	–	–
U. ammannii		–	–	–	–	–	–	–	+	–	–
U. ceratina		+	+	–	–	–	–	–	–	–	–
U. cornuta	Ch. 1	–	–	–	±	–	–	–	+	–	–
	Ch. 2	–	–	–	+	–	–	–	±	–	–
	Ch. 3	–	–	–	+	–	–	–	–	±	–
	Ch. 4	–	–	–	–	+	–	–	–	–	–
	Ch. 5	–	–	+	+	–	–	–	–	–	–
	Ch. 6	–	–	–	–	–	–	–	–	–	+
U. dasaea	Ch. 1	–	–	–	–	+	+	–	+	–	–
	Ch. 2	–	–	–	–	+	–	–	+	–	–
U. halei		–	–	–	±	+	–	–	+	–	–
U. mutabilis		–	–	–	–	–	–	–	–	–	+
U. nashii		–	–	–	+	–	–	–	–	–	–
U. rubicunda	Ch. 1	–	–	–	–	+	–	+	–	–	–
	Ch. 2	–	–	–	–	+	–	–	+	–	–
U. subscabrosa		–	–	–	+	–	–	–	–	–	–
U. wirthii	Ch. 1	–	–	–	–	+	–	–	–	–	–
	Ch. 2	–	–	–	–	–	–	–	–	+	–

Herrera-Campos, M.A., P. Clerc, T H Nash III y A. Zambrano.

El complejo U fragilescens en México.

RESUMEN

Este es el primer estudio encaminado a la revisión del complejo Usnea fragilescens en México Se describen, para nueve especies, los caracteres morfológicos, anatómicos y químicos, así como la distribución geográfica. Asímismo, se presenta la distribución actualizada de U dasaea.

Se practicó un análisis discriminante a los datos anatómicos de CMA para demostrar la utilidad de la relación entre los caracteres anatómicos y químicos en la separación de las especies.

U. brasiliensis (Zahlbr.) Mot., U. esperantiana Clerc, U. fragilescens Lynge var. mollis (Vainio) Clerc, U. jamicensis Ach , U. ramillosa Mot., and U wirthii Clerc son nuevos registros para Mexico.

Se incluye la clave para el complejo U. fragilescens en México.

Usnea fragilescens aggregate in Mexico.

MARIA ANGELES HERRERA-CAMPOS*

PHILIPPE CLERC**

THOMAS H. NASH III*Y ANGEL ZAMBRANO*

*Plant Biology Department, Arizona State University, Tempe, AZ 8528, USA.

**Conservatoire et Jardin Botaniques, Case postale 60, 1292 Chambèsy, Switzerland

ABSTRACT. This study is the first step towards the revision of the Usnea fragilescens complex in Mexico. Morphological, anatomical, and chemical characters, as well as their distribution are described for nine species. The updated distribution of U. dasaea Stirt.corticolous in Mexico is provided.

A discriminant analysis of the CMA of the best represented species is used to demonstrate the reliability of anatomical features and chemistry in their separation, also related to soralia shape and distributional trends.

U. brasiliensis (Zahlbr.) Mot., U. cornuta Koerb s. lat., U. esperantiana Clerc, U. fragilescens Lynge var mollis (Vainio) Clerc, U. jamaicensis Mot ,
U. ramillosa Mot. s. str and U. wirthii Clerc represent new records for Mexico

A key for the U. fragilescens group in Mexico is provided.

The lichens described in this paper belong to the U. fragilescens aggregate as defined by Clerc (1987a). The species of this aggregate are characterized by their shrubby and erect habit, branches of irregular diameter along their length with swollen and/or deformed segments, thin cortices (8-15% of the branch diameter), loose to dense medullae (60-76% of the branch diameter), often heterogeneous (i.e. with a denser zone just below the cortex), and thin axis (15-23% of the branch diameter). They are mainly corticolous although some saxicolous specimens have been reported (Clerc & Herrera-Campos, 1997). Among the species treated in this paper, the only one recently reported from Mexico is U cirrosa Mot (Coutiño y Mojica 1985).

The species of this aggregate studied for Mexico are U. cornuta Koerb. s lat., U brasiliensis (Zahlbr) Mot., U. esperantiana Clerc, U fragilescens var mollis (Vain.) Clerc, U. glabrata (Ach.) Vain., U. jamiacensis Mot., U. wirthii Clerc, U ramillosa Mot. s str., U. cirrosa Mot., and U. dasaea Stirt The latter species is described in detail by Clerc and Herrera-Campos (1997) therefore just a distribution for corticolous specimens is given herein.

Most of the species in the aggregate can be readily recognized by a combination of characters (discussed below) utilizing the species concept employed previously (e.g. Herrera-Campos et al. 1998). However, one group of species centered in U brasiliensis, U. cirrosa, U. cornuta s. lat., U. glabrata, and U. ramillosa s. str. exhibit a range of morphological, anatomical, and chemical variation that make them particularly difficult fo separate. Therefore, we have employed multivariate analyses to examine the degree to which these five taxa may be distinguished.

This paper is part of a more comprehensive study on the genus Usnea in Mexico. It follows the general approach mentioned by Herrera-Campos et al. (1998). Its main purpose is to initiate a discussion of the fruticose species included in the Usnea fragilescens aggregate, collected mainly in coniferous (Abies or Pinus dominated), mixed forests (Pinus-Quercus) and cloud forests.

MATERIALS AND METHODS

Most of the specimens examined are primarily the senior author's personal collections from temperate forests of the montane areas of Mexico as referred by Herrera-Campos et al. (1998). Collections deposited in the following herbaria are also included: ASU, BERN, COLO, DUKE, ENCB, FH, H, G, IBUG, LAM, LE, LUB, MEXU, MIN, NY, O, S, TUR, UPS, VT, and W.

The collections were initially grouped according to the presence of soralia and/or isidiomorphs, apothecia, and pigmentation. The specimens were morphologically, anatomically, and chemically analyzed following the methodology of previous studies (Clerc 1984a, Clerc and Herrera-Campos 1997, Herrera-Campos et al. 1998) Finally, among the species for which enough material had been collected, a statistical analysis was done to the CMA (cortex, medulla, axis) data to examine relationships of these anatomical features, soralia, segment shape, and the chemistry of the thalli. The CMA values are expressed as percentage of the total width of the branch, measured in the thickest part of the thickest branch. In the species descriptions the maximum, mininum, mean and standard error values are given for each one of these characters.

The percentage size of the cortex, medulla, and axis relative to the branch diameter were separately compared by one-way ANOVA among five species: U. brasiliensis (n=60), U. cirrosa (n=66), U. cornuta s. lat. (n=49), U. glabrata (n=45), and U. ramillosa s. str.(n=38). A logarithmic and a square transformations for the cortex and axis data, respectively, were necessary to achieve normality. The Tukey's HSD was used to compare the species means after ANOVA. The analysis were performed with the GLM procedure in SAS (1990).

Statistical Analyses

As appropiate standard errors for means were calculated, graphed, and added to tables. The discriminant analysis of the CMA data for the five best represented species of the U. fragilescens aggregate, was inducted using the DISCRIM and CANDISC procedures in SAS (1990) The analysis employed 68 specimens of U. cornuta s. lat., 60 of U. brasiliensis, 66 of U. cirrosa, 38 of U. ramillosa s. str., and 44 of U. glabrata.

Multiple-group discriminant analysis (MDA) was used to explore the similarities and differences among the five species mentioned above based on the size of predetermined groups of objects by maximizing the between groups to within groups sum of squares ratio (Sharma 1996), and it has been successfully applied to taxonomic problems (e g. Hess and Stoynoff 1998). for such purpose, and because the relative size of the cortex, medulla, and axis as typically expressed in the so-called CMA ratio (Clerc 1984a, 1987a, 1991, Clerc and Herrera-Campos 1997, Halonen et al. 1998; Herrera-Campos et al. 1998) is not suitable for this type of analysis, we used the actual values of these variables, though a log 10 transformation was necessary to achieve normality. In addition, because the assumption of equality of the covariance matrices was rejected (Bartlett's test), we use a quadratic rather than a linear discriminant function as the classification rule.

Calculations were performed with a program using the DISCRIM and CANDISE procedures in SAS (1990) According to the min {G-1, p} rule, where G is the number of groups, and p is the number of variables, respectively, 5 and 3 in our data set, we assessed three discriminant functions.

SPECIES CONCEPT

The species in the Usnea fragilescens group are defined by the combination of different morphological, anatomical and chemical characters, in which at least two independent ones (e.a. soralia morphology and chemistry, or chemistry and anatomy, etc.) are correlated (Herrera-Campos et al. 1998). It is also important to consider whether the geographical distribution patterns are consistent with the definition of the species. However, the delimitation of the species is considerably complicated by the variety of chemotypes and morphotypes that are found, as well as for the numerous intermediate morphs that seem to draw a continuum without end between closely related species Different chemotypes of identical morphology are not given any taxonomic rank.

In Usnea, the intergradation of the morphology among species that grow together, which seems to be more a rule than an exception, makes it harder to separate and delimit combinations of characters defining them (Stevens 1992; Swinscow and Krog 1979). Particularly puzzling are the intermediate morphs, specimens with mixed characters between two different species morphologically, anatomically, and chemically distinguishable, as in the case of U. subfloridana and U. wasmuthii (Clerc 1992), U fragilescens and U. cornuta (Tavares 1997), and U. fulvoreagens and U. glabrescens (Halonen et al 1998). Such specimens have been considered as possible "vegetative hybrids" (Brodo 1978; Clerc 1992; Fahselt 1996, Halonen et al. 1998) although lichen hybridization is not well understood.

MORPHOLOGY

The diagnostic characters of the species in this genus have been explained and defined before (Clerc 1984a, 1987, Clerc and Herrera-Campos 1997, Halonen et al. 1998; Herrera-Campos et al. 1998; Swinscow and Krog 1979), therefore they will only be briefly as they apply to the U. fragilescens aggregate.

Thallus

All the species described have mostly erect, shrubby thalli from 2-8 cm high, usually with one well developed attachment point or holdfast. The color of the thalli varies from pale yellow to dark olive green, but it is not considered a diagnostic character because it appears to reflect phenotypic variation related to different levels of illumination.

Ramification

Specimens may vary fom weakly to densely ramified. The ramification pattern of these shrubby species is isotomic dichotomous or anisotomic dichotomous, with divergent branches.

Trunk

The trunk is 3-5 mm long and varies from attenuated to straight, indistinct, or continuous with the main branch (Fig 1). Unlike some pendulous species from Mexico (Herrera-Campos et al. 1998), the color of the basal part of the trunk in the U. fragilescens aggregate is not diagnostic.

Branches

The branches are very distinctive in this group. They can be frequently constricted at the base, cylindrical to irregular, sometimes fusiform, deforming depressions on the cortex are frequently present. The segments are swollen ("sausage-like") or deformed, and they vary from slender to coarse, and from slightly or not deformed to deeply deformed as in U. brasiliensis (Fig. 2)

Papillae and tubercles

The distinction between these structures was established by Swinscow and Krog (1979). Papillae are just bumps of cortical material, whereas tubercles have both cortex and medulla. The species studied here may have one or both types of structures, however the only characteristically tuberculate one is U. jamaicensis (Fig. 3)

Fibrils

Fibrils are mainly short up to 5 mm, sometimes very crowded on the branches as with the typical spinules of U. dasaea (see Clerc and Herrera-Campos 1997) and U cirrosa. They can also be scattered and irregularly distributed along the thallus as in U cornuta s. lat. and U. brasiliensis (Figs. 4, 5). U. jamiacensis has the longest (15 mm) and somewhat more characteristic fibrils of the species treated herein (Fig. 7)

Fibercles

The fibercles, defined as the scars or gaps with protuding medulla left when the fibrils brake away (Clerc & Herrera-Campos 1997), are irregularly present on U. cornuta s. lat , but so far, they have not prove to be diagnostic character for any species within this aggregate .

Pseudocyphellae

To the extent of our knowledge, these structures are absent in this complex.

Soralia

The soralia produce farinose or granular soredia, and frequently originate from the cortex, tubercles, papillae, or around cracks. Although soralia are highly variable, certain tendencies can be found. For example, U. cornuta s str typically has plain, small, confluent soralia (Clerc 1987 a, b. Fig. 7. However, U. cornuta s. lat. shows greater variability (Figs. Fig. 8) For example U. brasiliensis has more tuberculate and separate soralia (Fig. 9); U fragilescens soralia, typically separate and delimited with a cortical margin (Fig 10); U glabrata deeply excavate soralia (Fig. 11); and U. esperantiana, slightly or not excate soralia (see Clerc 1992).

Isidiomorphs

These structures occur with variable density, from absent or scarce to abundant and crowded, deforming the tips of the branches, a characteristic that has been considered typical of U. cornuta (James et al. 1992). However, it can also be found in other species of this aggregate and even in extreme forms of U. ceratina from air-polluted locations.

Apothecia

As previously interpreted by Clerc (1987 a), the species of this complex include only soredio-isidiate species in which the apothecia are rare or have not been found. In this study few fertile species are included because they exhibit the characteristic features previously mentioned for the group, i. e. habitus, branch segments, and anatomy.

Fertile species of the U. fragilescens group may be actually several small aggregates of species, and U. ramillosa s. lat. is one of them. It includes species with shrubby thalli, 2-4 to 8-10 cm long, straight to attenuate trunks, sometimes bifurcate, short to well developed, concolorous with the main branch, reddish, brown or partially black; branches constricted at the base; branch segments terete in cross section and swollen in longitudinal section; crowded spinules or long disperse fibrils; cortex thin, shiny or vitreous; medulla mainly loose and thin axis. The secondary compounds found in this complex of fertile species are usnic, salazinic, protocetratic, norstictic, stictic and galbinic acids. Besides U cirrosa and U. ramillosa s str., this aggregate may include, among others, the central and South American species U steinerii Zahlbr., U andina Mot., U. subelegans (Vain.) Mot. and a morphotype of U. cirrosa recently reported for southwestern U.S. by Tavares and Sanders (1998).

U. ramillosa s str. is defined here as containing protocetratic acid and lacking pigments or pycnidia. However it is recognized that a more comprehensive study on the apotheciate species of the genus is needed.

ANATOMY

In Usnea, anatomical characters, particularly CMA, have been interpreted in different ways by several authors. Motyka (1936-1938) and Asahina (1956) use the dimensions of the cortex, medulla and axis in their species descriptions. The relative widths of these features have proven to be reliable in several instances (Clerc 1984a, 1987 a; Clerc and Herrera-Campos 1997; Herrera-Campos et al 1998, Walker 1985). However Swinscow and Krog (1979) find that using the thickness of the cortex was too imprecise, although CMA was helpful in the determination of U. picta (Steiner) Mot.

The same anatomical features studied for the pendulous Usnea for Mexico (Herrera-Campos et al. 1998) were studied. This aggregate is characterized by the thin cortices, thick medullas and thin to moderately thick axes, all referred as the relative percentage of the total width of the branch.

Cortex

The cortices in these species vary from shiny to vitreous. Cortical average thickness ranges from 8% in U. ramillosa s. str. to 14% U. glabrata (Fig. 12, 13).

According to the significant differences found in the thickness of the cortices, two contrasting groups can be identified: a) species with thinner cortex: U. ramillosa s. str., U. brasiliensis and U cirrosa and b) species with thicker cortex: U. glabrata and U cornuta s lat. The cortex is significantly different between these two groups but not among the individual species in each group (Fig. 14).

Medulla

In the U. fragilescens aggregate the medulla is typically heterogeneous, with a denser area below the cortex, dense to loose or very loose towards the axis. It ranges from 62% in U. cornuta s. lat. and U. glabrata to 76% in U. brasiliensis and U. ramillosa s str. (Figs. 12, 13).

Three groups can be separated among which significant differences in the thickness of the medulla were observed: a) U. ramillosa s. str and U. brasiliensis, b) U. cornuta s. lat. and U. glabrata, and c) U. cirrosa (Fig. 14). U. ramillosa s. str and U. brasiliensis have the thickest and loosest medulla. U. cornuta s lat. and U glabrata exhibit more variability in medullary thickness than the previous two species Their medullary density varies in U. cornuta s. lat from loose to dense and in U. glabrata from very loose to loose. Lastly U. cirrosa has medullary widths that are intermediate between the first two groups, and its medullary density also varies from very loose to loose as in the last species mentioned.

Axis

The axis is mostly thin, solid and straight and varies from 15% to 24% of the branch diameter in U. brasiliensis and U. glabrata, respectively (Figs. 12, 13).

The variation of the axis thickness parallels that of the cortex. The same separation can be observed according to the significant differences in this parameter U ramillosa s str and U. brasiliensis have thinner axes, while U. glabrata, U. cornuta s lat., and U cirrosa have thicker axes. Again, the variation of U. ramillosa s. str and U. brasiliensis is very similar, in contrast with the wider one of the other three species (Fig. 14).

CHEMISTRY

The utility of secondary metabolites in lichen taxonomy is unquestionable, because it assists in the delimitation of species, confirms the occurrence of species pairs, solves problems when morphological information is insufficient or unnoticed, and helps to understand the geographic distribution (Brodo 1986, Elix 1996; Hale 1983). However, the fact that some morphological species are differentiated into chemotypes correlated to differences in geography and ecology has caused controversial interpretations (Culberson 1969, 1970, 1986, Culberson and Culberson 1967, 1973, 1976, Egan 1986; Feige and Lumbsch 1995; Hawksworth 1976; Rogers 1989; Sheard 1978 a, b). Some guidelines, concepts, and alternatives have been proposed to solve them (Brodo 1986; Culberson et al. 1988; Hawksworth 1976).

Interpretation of lichen chemistry also varies among some studies of Usnea. Culberson et al. (1983) describe the new U. lecanorica W. Culb., C. Culb. and Fiscus on the basis of the occurrence of a secondary product not found previously in any other species of the genus, and distinguish U. lecanorica from U arizonica which has salazinic acid. In contrast, Stevens (1992) regroups the species of the Australian U. scabrida-U. molliuscula complex into two species with several subspecies according to differences in morphology related to distinct climatic regions and for which chemistry was considered of no importance because the secondary products found in all these species were closely related ß-orcinol depsidones Furthermore, for Swinscow and Krog (1979) the secondary substances found in the fruticose species in East Africa are of no taxonomical value unless they are treated in combination with morphology and/or pigmention. In more recent studies (Clerc and Herrera-Campos 1997; Herrera-Campos et al. 1998; Halonen et al 1998), chemical characters have been considered part of the combination of features that defines the species, without giving any taxonomical rank to the different chemotypes if they are morphologically indistinguishable.

In general, the medullary secondary substances found in the species of the U. fragilescens group in Mexico are the same as those found in the pendulous and saxicolous species: ß-orcinol depsidones salazinic, stictic, norstictic, galbinic, and protocetraric acids, ß-orcinol paradepsides barbatic, diffractaic acids, and bourgeonic acid, and an unknown fatty acid in U. cornuta s. lat. So far, orcinol secondary products such as evernic and lecanoric acids are unknown for this group (Table 1).

The species with the highest chemical variation is U. cornuta s lat. with four chemotypes. Among the saxicolous Usneae, this species is also the most chemically variable with six races (Clerc and Herrera-Campos 1997). However, after the analysis of the corticolous specimens, it is considered by the first author that the chemical race with protocetraric and psoromic acids corresponds to the South American species U. brasiliensis.

ECOLOGY AND DISTRIBUTION

The species studied are mainly corticolous, but some of them grow frequently or occasionally on rocks, i. e. U. dasaea, U. cornuta s. lat. and U. brasiliensis (Clerc and Herrera-Campos 1997), and very rarely U. glabrata. The main porophytes are Pinus, Quercus, and Abies, although they can also be found on Alnus, Burlegia, Juniperus, Acacia, Pyrus, and Prunus. No special preference for any species of tree was detected.

The altitude of the collection sites ranges primarily from 1240 m to 3650 m, and corresponded mainly to Abies forests and Pinus or Quercus dominated forests. Particularly interesting is an unusual stand Pinus-Quercus at 360 m, where only U cornuta s. lat. was collected.

U. cirrosa and U. dasaea are the most widely distributed species of this group. U. cirrosa reaches the highest elevation at 3650 m, followed by U. cornuta s lat. and U. dasaea. Although U. cirrosa is present in the dry coniferous forests of northern part of Sierra Madre Occidental in Chihuahua, it is not found in any locality in Baja California peninsula. U dasaea is the only one present in the arid lands of Baja California. It has the widest altitudinal amplitude of all Mexican species studied so far; from xerophilous sites between 30 and 200 m in elevation, to mesophilous montane cloud forests and temperate coniferous forests from 1550 m to 3000 m. This type of distribution in Mexico is only equal by the cosmopolitan U. rubicunda, which will be treated in detail in a future.

Other distributional trends include: 1) species (U. brasiliensis and U. cirrosa) that are particularly abundant in the Eje Neovolcánico Transversal in the center of the country. 2) other species (U. cornuta s. lat., U. dasaea, U. glabrata, and U. jamaicensis) that occur more commonly north and south of this volcanic chain. 3) two species (U ramillosa s. str. and U. fragilescens) that are more restricted to the south. 4) the rare species (U. esperantiana and U. wirthii) that occur too sporadically to fully chracterize (Fig. 15).

Key to the U. fragilescens aggregate in Mexico

1. Soralia and/or isidiomorphs present; apothecia absent or rare 2
1. Soralia and/or isidiomorphs absent, few to many apothecia present 8

2. Soralia small (less than half of the width of the bearing branch) mostly confluent 3
2. Soralia broad (more than half of the width of the bearing branch) mostly separate 6

3 Yellow pigment in the medulla (sometimes very faint) .... 10 U. wirthii
3 Pigment absent 4

4. Branches with abundant (rarely without) short triangular

spinules; galbinic acid major. . . . . 4. U. dasaea

4 Branches with (or without) slender short or long fibrils; salazinic or protocetraric acid major 5

5. Main branch segments conspicuously swollen and/or irregular in longitudinal section; thallus mostly rigid, never flaccid; cortex thin (x = 8.5%), medulla loose (x = 76%), axis thin (x = 15%), protocetraric acid major .... 1.U. brasilensis

5. Main branches segments not conspicuously swollen or irregular, mostly slender; thallus rigid to flaccid; cortex moderately thick (x =14%), medulla loose to dense (x = 63%), axis moderately thick (x = 23.5%); salazinic or stictic acid major ....3.U. cornuta s. lat.

6 Soralia circular, from slightly raised to tuberculate, mostly separate, slightly excavate or not; isidiomorphs present .... 6.U. fragilescens

6 Soralia irregular to circular, superficial, mostly confluent, slightly to deeply excavate, with or without margin; isidiomorphs absent...... 7

7 Soralia deeply excavate, frequently exposing the axis, stictic or protocetraric acid major .. .. 7.U. glabrata

7. Soralia not deeply excavate, never exposing the axis, bourgeonic acid major............................ .... 5 U esperantiana

8 Reddish pigment at the cortex edge of the apothecial disk.. U. cirrosa

8. Pigment absent 10

9 Branch segments conspicuously swollen, tubercles not conspicuous, protocetraric acid major .. .. 9 U. ramillosa s. str.

9 Branches mostly cylindrical, tubercles very conspicuous, cryptostictic or salazinic acids major .... 8 U. jamaicensis

TAXA

1 Usnea brasiliensis (Zahlbr.) Motyka, Lich. Gen. Usnea Stud. Monogr. Pars. Syst. 2: 504 1938

Thallus pale yellow green to olive green, erect, 4-9 (11 5) cm long, slender to coarse, flaccid to rigid, poorly to moderately branched, sympodial and divergent branches, a single point of attachment; trunk short 3 mm, continuous with the main branch, straight, constricted, bifurcate or attenuate at the base, sometimes annulated, concolorous, partially brown, black or yellow to orangish, occasionally pseudoroots may be present; branches thick (0.92)- 1.6± 0.55-(2 6) mm (n= 60), diameter somewhat uniform to irregular along their length, cylindrical or irregular due to depressions in the cortex, segments in cross section terete to irregular, rarely flattened, in longitudinal section swollen or sausage-like shape, sometimes fusiform, the axis may be exposed between the segments; apices commonly fine with diameter constant or decreasing slowly, also short and thick, curved or straight, ramified at 90°, rarely long and flexuose, papillae indistinct, scattered or abundant, sometimes absent; tubercles conspicuous, mainly on secondary and terminal branches, small, eroded at the summits; fibercles present; fibrils often absent, when present short (< 1-2 (4-5) mm) and spinulous, slightly or not constricted at the base, mainly on the terminal branches, regular or irregularly distributed, most remain attached to the thallus; pseudocyphellae absent, soralia originated from the cortex or from tubercles, more abundant on terminal branches and fibrils, some scattered on the secondary branches or rarely on the main ones, superficial, slightly raised to mostly tuberculate, plain, slightly convex to rarely capitate, minute to broad but less than half of the branch, punctiform or circular, with or without definite margin, separate, becoming totally or patially confluent, some with isidiomorphs; isidiomorphs mostly on soralia, few on cortex, from scarce to very abundant; cortex [(4.66) - 8 58 ± 0.33% - (15 92) n= 60], thin, mainly vitreous, sometimes shiny, generally not cracked, although some cracks may be present at the base of the thallus; calcium oxalate (?) sometimes present at the base of the trunk and secondary branches; medulla [(63.84) - 76.40 ± 0 71 % - (88 83) n= 60] thick, from very loose to loose, rarely dense, mainly fibrous; axis [(6.52) - 15.01 ± 0.56% - (27.76) n= 60] thin, solid and straight; apothecia absent or very rare, subterminal, 5 mm in diameter; chemistry usnic, protocetraric, and psoromic acids (60 specimens analyzed)

Variation.– U. brasiliensis is a polymorphic species whose variable features include the growth habit from erect to subpendant, the degree of ramification from poor to dense. The shape of the segments of the branches varies in cross section from terete to irregular, as well as in longitudinal section from cylindrical, sausage-like to fusiform. There is also variation in the abundance of tubercles, papillae, isidiomorphs, and fibrils. The shape of the trunk can be constricted, attenuate, straight, or bifurcate and the apices from normal and fine to coarse and thick, curved or not. Finally the soralia range from rarely superficial, slightly raised to tuberculate, minute to broad, separate to confluent, totally or remaining individual, plain to convex, sometimes capitate, rarely concave.

Distinctive features.– Usnea brasiliensis is a sorediate species mainly characterized by the vitreous and thin cortex, the loose or very loose medulla and the very thin axis. The soralia are mostly tuberculate or at least slightly raised. Protocetraric acid is the main secondary substance, sometimes with accesory psoromic acid.

Chemically Usnea brasiliensis is not as variable as U cornuta s. lat., since it has just two combinations: usnic and protrocetraric acids or usnic, protocetraric, and psoromic acids. In the statistical analysis of the CMA it was shown that there are significant differences between the specimens with salazinic-stictic acids group and those with protocetraric-psoromic acids.

Distribution and ecology.– Motyka reported this species from Costa Rica, Puerto Rico, Colombia, Bolivia, Peru, Venezuela, Brazil, and Argentina.

In Mexico, it has been collected from 1240 to 2990 m in the states of Durango, Durango-Sinaloa border, Estado de México, Jalisco, Nayarit, Michoacán, Morelos, Oaxaca, Veracruz, and Chiapas.

The distribution of U. brasiliensis and U. cornuta s. lat. in Mexico is very wide and they overlap in most of their range. U. brasiliensis has been collected in few more localities than U. cornuta s. lat., although no major differences in distribution between the two species is postulated The altitudinal range of U. brasiliensis is lower than that of U.

cornuta s. lat. and, so far, it is not known in Tlaxcala, where the latter species reaches its highest altitude. U. brasiliensis is not present either in the locality with the lowest elevation for U. cornuta s. lat., an unusual low altitude Pinus-Quercus forest in the vicinity of the tropical rain forest at the limits between Oaxaca and Chiapas. However, U. brasiliensis is more abundant in the forests of the central part of the country in the province of the Eje Neovolcánico Transversal, where the major Abies forests of the country are located. At the east side, on Sierra Madre Occidental, it is only U. cornuta s. lat. which reaches the mountains of Nuevo León, while both continue to the north on the west side of the country through different localities on the Sierra Madre Occidental, stopping at the border between Durango and Sinaloa.

Among the saxicolous chemotypes of U. cornuta s. lat. reported by Clerc and Herrera-Campos (1997), the specimens of the chemotype 6, containing protocetraric and psoromic acids, mentioned for Mexico, as well as recent corticolous collections from Washington (Rhoades 11/1/79), correspond well with our description of U. brasiliensis and represent an extension of its range that has not been reported before. Therefore it is the first time U. brasiliensis is recorded from North America (Fig. 15).

Mexico is a megacenter of diversity. Located between the holarctic and neotropical floristic realms, the region has been corridor and barrier to different kinds of species (Dávila and Herrera-MacBryde 1997; Delgadillo 1983, 1987, 1992, 1993, 1995; Graham 1993; Ramamoorthy et al. 1993, Rzdowski 1981, 1991, 1993; Toledo and Ordóñez 1993; Toledo et al. 1997) and we can assume this is also true of the lichens, as might be exemplified by U. brasiliensis. However, we need further studies on the South American material before making conclusive remarks about its geographic distribution and major taxonomical changes.

Selected specimens examined.– MEXICO. CHIAPAS. Camino a Tzontewitz-Chalam, Herrera-Campos 4781, 4838, 4834 (MEXU); DURANGO. Sierra Madre Occidental. Parque El Salto, 9 km WSW from El Salto and 110 km from Durango, Herrera-Campos 4777 (MEXU); 1 km from Barranca de Liebre and 2 km from the border with Sinaloa,Herrera-Campos 4839 (MEXU); HIDALGO. Parque Nacional "El Chico", Herrera-Campos 717, 4844 (MEXU); Zacualtipán, Herrera-Campos 1389 (MEXU); . JALISCO. Manantlán, rumbo a Las Joyas, Herrera-Campos 4773 (MEXU);

MICHOACAN. 38 km NE of Uruapan, Culberson & Culberson 18730 (DUKE); OAXACA. 17 km before the detour to Jialtianguis, Herrera-Campos 4829 (MEXU), VERACRUZ Zongolica, Cabrera 500B (ENCB).

2. *Usnea cirrosa* Mot., Lich. Gen. *Usnea* Stud. Monogr. Pars. Syst. 2: 526. 1938.

Thallus pale to dark olive green, erect, up to 6 cm long, rigid, moderately to densely branched, commonly "fan shaped", anisotomic or isotomic dichotomously ramified, one point of attachment; trunk indistinct or well defined, short 4 mm, straight to attenuate, or wide at the base, with pseudoroots, mainly concolorous, also paler or reddish, sometimes black at the segment in contact with the holdfast, branches thick (2.55) - 1.18 ± 0.06 - (2.77) mm (n= 65), mainly cylindrical, few times slightly irregular at the basis because of foveolae in the cortex, not frequently segmented 1 segment or a fraction of it per centimeter; segments in cross section terete, in longitudinal section long, swollen to fusiform, less frequently cylindrical; apices mostly short and thick, rarely somewhat fine, ramified at 90°, often foveolate, papillae absent or indistinct; tubercles and fibercles absent or scarce; fibrils very abundant, characteristically short (2 mm), spinulous, thick, often constricted at the base, remaining attached, mostly distributed along the whole length of the thallus, pseudocyphellae absent or inconspicuous, slightly ridged; soralia absent; isidiomorphs absent; cortex (4.00)- 10.41 ± 0.051% - (22 6) n= 66], thin, shiny, generally smooth, although some cracks of calcium oxalate (?) may be present at the base of the thallus and the secondary branches, medulla [(32.43) - 67 15± 1.54 % - (86.00)n= 66] thick, mostly from very loose to loose, rarely dense, fibrous, axis [(8.3) - 22 44 ± 1.2 % - (54.05) n= 66] thin; solid and straight; apothecia abundant, mostly terminal to subterminal, up tp 11 mm in diameter; frequently with a ring of wine red pigment around the inner part of the margin of the pruinous disk, with crowded fibrils at the edge and on the underside, these fibrils are often ramified giving a more caespitose appearance to the apothecium; spores colorless, 6-11 X 5-8 µm (average 9.19 X 6.29 µm, St dev. length 1.02, width 0.61, n= 363), pycnidia red, abundant, on terminal branches and spinules, sometimes deforming the apices; conidia hyaline, sublangeriform, up 11 µm long; chemistry usnic, norstictic and salazinic acids are the major secondary medullar

Selected specimens examined.– MEXICO. CHIHUAHUA. La Cieneguita, Herrera-Campos 5089 (MEXU); CHIHUAHUA. Barranca del Cobre, Herrera-Campos 5191 (MEXU), 20 km SE of Cascada de Cusárare, Nash 37400 b (ASU); DISTRITO FEDERAL. Parque nacional "Desierto de Los Leones", Balls B4065, (MEXU); DURANGO. Sierra Madre Occidental 47 km al W de Durango, Herrera-Campos 5086 (MEXU), ESTADO DE MEXICO. Carretera a Naucalpan, 1 km before Naucalpan, Herrera-Campos 975 (MEXU); MICHOACAN. Carindapaz, E of Ciudad Hidalgo, camino a Maravatio-Senguio, Varela 154; 38 km NE of Uruapan, Culberson & Culberson 18715 (DUKE), Pátzcuaro hills, C G. Pringle 119, (G), G Pringle 11-8-1890 (LAM); MORELOS, Volcán Tesoyo, 4.5 km N of Tres Marías, Acosta 113 (ENCB); PUEBLA-ESTADO DE MEXICO. Los Volcanes, vía Cholula. Paso de Cortés, Herrera-Campos 1952 (MEXU), SAN LUIS POTOSI. Parque Nacional "El Potosí". Cañada Grande, Zambrano 11-18-1992 (MEXU); SINALOA, 109 km E of Mazatlán W. L. Culberson 13417 (DUKE).

3. Usnea cornuta Körb, Parerga Lichenol 2. 1859, s. lat.

Thallus pale yellow green to olive green, shrubby, 3-5 (8.5) cm long; poorly to moderately ramified; anisotomic or isotomic dichotomous with divergent branches; with one point of attachment, trunk short to 3-4.5 mm long, concolorous with the branches, orangish to carbonaceous, wider at the basal part, straight or attenuated, sometimes annulate with calcium oxalate (?) excretions, pseudoroots may be present; branches [(0.55) - 1.02 ± 0.03% - (1.60) mm thick (n= 49)], tapering slowly, cylindrical to irregular, sometimes deformed by the presence of depressions, transverse furrows on the cortex, or rare foveolae, constricted at the base or not; segments weakly to visibly swollen, sometimes fusiform or cylindrical, terete or irregular in cross section; apices fine and normal or short and thick, at 90° and 60°; often curved; papillae absent or indistinct to verrucose, regularly or irregularly distributed on the thallus; tubercles absent to abundant, small; fibrils fine and short, spinule-type 1-5 mm long, few to numerous, irregularly distributed on the branches, commonly curved; pseudocyphellae absent; soralia mostly arising plain on the cortex, also at summit of papillae or tubercles on terminal branches and fibrils, mainly superficial few tuberculated, rarely slightly excavate or convex, plain, punctiform to enlarged, mostly totally confluent, some partially confluent i e. remaining individual, with or without a margin; isidiomorphs absent to abundant, on soralia, sometimes on the cortex; apothecia mostly absent, if present immature; cortex thick [(6.98) - 13.58 ± 0.51% - (26 67) n=68], shiny, rarely mat, generally smooth, sometimes cracked, occasionally with reddish spots; medulla [(37.78) - 62.52 ± 1.10% - (79.96) n=68], loose to dense, mainly cottony; axis solid, straight, and thin [(9.25) - 23.90 ± 0.77% - (40.48) n=68], sometimes pinkish to pale orange; chemistry usnic, salazinic acid, ± norstictic, ± stictic, ± consalazinic acids, ± unknown fatty acids C: 3,5,6, and few specimens with just an unknown fatty acid (68 specimens analyzed).

Variation – The variable features of *U. cornuta s. lat.* are the size of the thallus, the degree of swelling of the segments; the frequency of papillae, tubercles, and fibercles; the density of the fibrils from almost absent to numerous, and the color and shape of the base. Also included are the soralia which mostly are minute, superficial, without margin and totally confluent to slightly tuberculate, with a margin and not totally confluent, crowded or not, and the color of the axis, which sometimes may be pale pink.

Given the copious variability found in the *U. cornuta s. lat.*, it is likely that several already described species are represented under this name, such as *U. substerilis* Mot. reported for Mexico by Thomson (1984)

Distinctive features.– The distinctive features of *U. cornuta s str.* are the abundant small, punctiform, plane to slightly concave, and confluent soralia without conspicuous margin (Clerc 1987).

Distribution and ecology .– In Europe, *U. cornuta* is reported from Germany, Ireland, England, Belgium, Madeira, Portugal, France, Italy, Norway, Spain, and Switzerland (Motyka 1938, Purvis et al. 1992). In North America, Halonen et al. (1998) mention it from British Columbia and McCune and Geiser (1997) from the northwest of USA .

Recent collections in Mexico are from *Pinus* and *Pinus-Quecus* forests, *Liquidambar* dominated mixed cloud forests, and *Abies* forests, at an alititudinal range of (360 m) 1500-3400. From Durango and Durango-Sinaloa border, Jalisco, Tlaxcala, Nuevo León, Veracruz, Oaxaca, and Chiapas in the physiographic provinces of Sierra Madre Occidental, Sierra Madre Oriental, Eje Noevolcánico, Sistema Montañoso del Norte de Oaxaca, Macizo Central de Chiapas, and Sierra Madre de Chiapas.

U cornuta s. lat. is mainly corticolous on Pinus, Quercus, Abies, Juniperus, Alnus, Salix, Prunus, shrubs, and palms. It occasionally is saxicolous (Clerc and Herrera-Campos 1997) and, in this study it was found growing on rocks in an unusual Pinus-Quercus stand at very low elevation (360 m) in the environs of the rain forest in Oaxaca, close to the border with Chiapas, where U. brasilensis does not occur. In the country, the most northern site of its occurrence is in Nuevo León in the Sierra Madre Oriental province. It is the first record for Mexico.

Selected specimens examined.– MEXICO CHIAPAS. Road to Tzontewitz-Chalam, Herrera-Campos 4751 (MEXU); CHIAPAS-OAXACA. 16.5 km NE of Santiago Iztaltepec, road to Sta. María Chimalapa, Herrera-Campos 4694 (MEXU); DISTRITO FEDERAL. Delegación Tlalpan Volcán Ajusco. 2 km after the detour to Jalatlaco, Herrera-Campos 2391.1 (MEXU); DURANGO. Sierra Madre Occidental. Parque El Salto a 9 km al WSW of El Salto and 110 km of Durango, Herrera-Campos 4749 (MEXU); 1 km of Barranca de Liebre and 2 km from the border with Sinaloa, Herrera-Campos 4767 (MEXU); HIDALGO. Parque Nacional "El Chico", Herrera-Campos 670, 689, 705 (MEXU); Tlalchinol, La Virgen, Herrera-Campos 1205 (MEXU); Zacualtipán, Herrera-Campos 1380 (MEXU); JALISCO. Tapalpa, Romero 10-1-1983 (IBUG); NUEVO LEON Parque Nacional "Cumbres de Monterrey". El Tejocote, after Laguna de Sánchez, Zambrano 11-29-1992 (MEXU); OAXACA. 17 kmbefore the detour to Jialtianguis, Herrera-Campos 4678 (MEXU); Cerro del Veinte, Herrera-Campos 4681 (MEXU);TLAXCALA. Volcán La Malinche Axaltenco. Cerro Antonio. Agua Santa, Herrera-Campos 65 (MEXU); VERACRUZ. Cruz Blanca, Herrera-Campos 1921 (MEXU).

4. Usnea dasaea Stirt., Scott. Naturalist. 6: 104. 1881.

Usnea dasaea is a very variable species with saxicolous or corticolous habit. It is included in this study because some of its morphs may have similar characteristics to those in the U. fragilescens group, however it is not part of the aggregate. It is recognizable from the species of this group by the presence of abundant short spinules at least in part of the branches, by the branch segments which are mostly cylindrical or slightly ridged, by the small, raised or superficial soralia which enlarge at the apices of the terminal branches, and by the presence of galbinic acid as diagnostic secondary substance For a detailed description and general distribution in North America the reader is referred to Clerc and Herrera-Campos (1997)

In Mexico, its wide distribution includes both saxicolous and corticolous specimens. Also its altitudinal range is from 1500 to 2490 m. The localities where it has been found only growing on rocks are in Baja California Norte, Jalisco, Morelos, Nayarit, Oaxaca, San Luis Potosí, and Sonora; only on trees in Coahuila, Michoacán, Puebla, and Veracruz; on rock and on tress, in Chihuahua (although mainly on rocks), Chiapas, and Hidalgo.

U dasea is the widest distributed among the saxicolous species of this genus in Mexico. Towards the south it extends its range to the Pinus forests in Chiapas, and to the north it is present in Sierra Madre Oriental (Nuevo León, San Luis Potosí and Hidalgo). On rocks, it was collected not only in Pinus dominated communities of the west side of the country, but also on the east side, where more humid and warmer climatic conditions prevail. However when epiphytic, it is present in diverse types of vegetation, not only in more humid Pinus dominated forests, but also in places where Quercus prevails and in dense cloud forests characterized by the presence of the genus Liquidambar.

Although humidity seems to influence the distribution of this species, it is not clear how much the temperature may also be a limiting factor, but it has been noticed that, so far, U. dasea has been collected very rarely on rocks or on trees (only one corticolous specimen) in Abies forests, which have a similar humidity conditions that the cloud forests but develop at higher elevation and colder climate.

On the other hand, comparing the distribution of U. dasaea with those species of U. fragilescens aggregate in Mexico, U dasaea is the second best represented species, after U. cirrosa, and among the species treated herein, it is the only one growing in the arid areas in Baja California peninsula.

5. Usnea esperantiana Clerc, Candolea 47:514. 1992

Thallus pale green, 3.5 cm long, erect, with one point of attachment, densely ramified, isotomic dichotomous, branches divergent; trunk straight, up to 4 mm long, concolorous; branches 0.87 mm in diameter, cylindrical to slightly irregular, tappering very slowly; segments terete in cross section and in longitudinal section swollen; apices lax and short, frequently curved; ramified at 60°; papillae indistinct, scattered; tubercles and fibercles absent; fibrils short (4 mm), spinulous, fine; pseudocyphallae absent; soralia originated on the cortex, superficial, plain to slightly excavate, not larger than half the diameter of the branch, circular, with or without margin, partially to totally confluent, on fibrils and terminal branches; isidiomorphs absent; cortex 29% of the total width of the branch, shiny; medulla 29% of the total width of the branch, dense, fibrous; axis thick 42% of the total width of the branch, solid and straight; apothecia absent; chemistry usnic, constictic, and bourgeonic acids.

Variation.– We do not have enough material to document the variation of this species in Mexico. Although for the European specimens the size of the thallus, the density of the fibrils, and the soralia are characters that vary according to the habitat (Clerc 1992).

Distinctive features.– U.esperantiana is distinguishable from the other species in the U. fragilescens-group by the superficial and slightly excavate never isidiate soralia and the chemical combination of usnic, constictic and bourgeonic acids

Distribution and ecology.– U. esperantiana was first described from south and west of Europe (Clerc 1992), from one locality in British Columbia and in South America(Halonen et al 1998), also in this paper it is mentioned from California and South America. In Mexico, this species is extremely rare, just one specimen was found in Oaxaca It is the first record for Mexico.

Selected specimens examined.– MEXICO. OAXACA, Cerro del Veinte, Llano El Carrizalito, Herrera-Campos 1305 (MEXU)

6. Usnea fragilescens Lynge var. mollis (Vainio) clerc, Nord. J. Bot. 7: 492. 1987.

Thallus yellow green, erect, 5 cm long, somewhat rigid, poorly to moderately ramified; anisotomic dichotomous, branches divergent, thalli with one point of attachment; trunk continuous with main branch or distinctive up to 9 mm long, concolorous to black, straight or attenuate; branches [(1.62) - 1.10 ± 0.051- (0.78) mm n=16] cylindrical, tapering very slowly, rarely with small depressions in the cortex; segments terete in cross section and in longitudinal section fusiform to cylindrical; apices lax and long; ramified at 90°, papillae indistinct to verrucose, abundant or not; tubercles eroded surrounded by spinules, fibercles frequent; fibrils mainly short (1-2 mm) spinulous, distributed irregularly mostly on secondary branches, often more abundant towards the base, some remaining attached, frequently as clusters associated with tubercles or fibercles, pseudocyphellae absent; soralia originated on cortex and/or on small eroded papillae, or on nodules, superficial to slightly tuberculate, mostly plain but few slightly excavate, few convex to capitate, small, if broad always less than half of the branch; circular, few irregular; mostly with margin, separate and discrete, rarely confluent, isidiomorphs present on mature or young soralia; cortex [(5 42) - 13.05 ± 1.28% - (26.47) n= 16], thin, mainly shiny to vitreous, rarely mat (one specimen (R786); calcium oxalate absent; medulla [(44.11) - 64.67 ± 2.63% - (83.84) n= 16] thick, very loose to loose, rarely dense, fibrous; axis [(10.74) -22.28 ± 1.65% - (35) n= 16] thin; solid and straight, sometimes yellowish; apothecia absent; chemistry usnic, stictic, constictic and norstictic acids (16 specimens analyzed).

Variation.– The variable characters in this species are the size of the soralia, density and distribution of fibrils, papillae, tubercles, fibercles, the color of the axis, and the shape and color of the base.

Distinctive features.–The main distinctive character of this species are the discrete soralia and commonly fusiform branch segments, as well as the chemistry (Clerc 1987).

Distribution and ecology.– In Europe, *U. fragilescens* is reported from Norway, France and Great Britain (Mtyka 1938). *U. fragilescens* var. *fragilescens* and *U. fragilescens* var. *mollis* are reported from Scandinavia by Clerc 1987. Halonen et al. (1998) mention this variety for British Columbia as commonly growing at lower elevations on conifer and deciduous trees In Mexico *U. fragilescens* var. *mollis* it has been collected on bark, once on rock, in the center and south of the country· in Chiapas, Estado de México, Hidalgo, Oaxaca, and Veracruz in mixed forests of *Pinus-Quercus*, in mountain cloud forest, and in *Prunus* plantations, from 1900 m to 2805 m of elevation.

Selected specimens examined.– MEXICO. CHIAPAS. Grutas SE of San Cristóbal, Herrera-Campos 2717 (MEXU); HIDALGO Parque Nacional "El Chico", Herrera-Campos 2735 (MEXU); OAXACA. 17 km from the detour to Jialtianguis, Herrera-Campos 2713 (MEXU); km 104 of the Tuxtepec-Oaxaca Highway, Herrera-Campos 2710 (MEXU); Detour to San Juan Luvina, Herrera-Campos 2711 (MEXU);

VERACRUZ. Cruz Banca, Herrera-Campos 17 (MEXU);Highway 140, between Perote and San José Alchichica, Herrera-Campos 2707 (MEXU).

7. Usnea glabrata (Ach) Vain. Ann. Acad. Sci. Fenn. A 6(7)· 7 1915.

Thallus yellow to pale olive green, erect, 2-4 cm long, somewhat rigid, moderately to densely branched, anisotomic dichotomous, rarely isotomic, branches divergent, one point of attachment; trunk indistinct, continuous with main branch, or short 2.5 mm, concolorous or black, rarely whitish or orangish, attenuate; branches [(0 345) - 1.0 ± 0.06 - (2.6)] mm in diameter (n= 44), uniform; with circular depressions on the cortex, most of them constricted at the base; sometimes tapered, segments terete in cross section and in longitudinal section "swollen" or irregular; apices sometimes fine and acute, not capillary; ramified at 60° or 90°, papillae absent or indistinct, irregularly distributed on main and secondary branches; sometimes all over the thallus; tubercles absent, fibercles absent, fibrils absent or abundant; short (1-5 mm) spinulous; not constricted at the base; irregularly distributed on secondary and terminal branches; remaining attached; pseudocyphellae absent, soralia originated on the cortex; located mainly on terminal branches and fibrils, rarely on secondary branches or at union of the branches and/or fibrils, well excavated, exposing the axis, mostly concave some plain, broad, half or more of the diameter of the branch, from circular to irregular; with or without margin; totally confluent, although sometimes remaining individual; isidiomorphs absent; cortex smooth; shiny to vitreous, rarely mat; [(4 23) - 13 74 ± 0 89% - (30.00) n= 44], calcium oxalate? may be present between the segments of the branches, or at the base of secondary and tertiary branches; eventually some fine striations individually arranged may be present; rarely red spots present; medulla [(37.50) - 62.16 ± 2 01% - (93.66) n= 44] thick, mainly very lose or loose, sometimes dense; fibrous; axis [(2 11) - 24.10% ± 1.42 - (48 65) n= 44] thin; mostly thin; plain and straight; apothecia absent; chemistry usnic, stictic, constictic and norstictic acids (44 specimens analyzed)

Variation.— The base may vary from concolorous to black, rarely whitish or orangish and from indistinct, continuous with the branch to attenuate. Papillae are usually absent, but if present they are scattered and indistinct. The density of fibrils of the thallus is also variable from absent to abundant. The soralia are most frequently totally confluent, but in some cases soralia that remain individual can be observed. The medulla is regularly loose, but in a few specimens it was dense Occasionally small red spots are visible on the cortex.

Distinctive features.— Among the characters that distinguish U glabrata from the other species on the U fragilescens group are the broad excavate soralia that lack isidiomorphs. U. esperantiana is another species with more or less small thalli which may be distinguish from U glabrata by its soralia which are never as excavate and because of its chemistry with bourgeonic acid.

The rare red spots on the cortex of U. glabrata are similar to those of U. wirthii, however U. wirthii can be easily distinguished by the yellow pigment on the medulla and/or axis, its small soralia and its chemistry (usnic, psoromic acid, an unknown fatty acid and two more unknown substances) (Clerc 1984). Also U. cornuta s. str. occasionally has red spots on the cortex, but its soralia are superficial, small, and not deeply excavate.

Sometimes U. fragilescens may have slightly excavate soralia, but these never have torn margins and they are separate, almost never fusing together as U. glabrata. U lapponica Vain. is a species with very excavate soralia, that may resemble those of U. glabrata, however these two species differ in the size of the thallus, being regularly small in U. glabrata, in the shape of the branch segments which are swollen or deformed in U. glabrata and cylindrical in U. lapponica, which also has a different chemistry with usnic acid alone or salazinic acid as major secondary substance. Although Halonen et al. (1998) report additional chemical strains of U. glabrata, in Mexico one strain with usnic, stictic, constictic, and norstictic acids is by far the most commonly found. Only one specimen contained protocetraric acid and two with barbatic acid, none had salazinic, neither fatty acids

Distribution and ecology.— Motyka (1936-1938) reported this species from Ireland, France, Switzerland, Germany, Italy, Austria, Yugoslavia, Czechoslovakia, Rumania, Hungary, Poland, Sweden, Finland, Russia, Canada, USA, particularly in the Pacific Northwest (McCune & Geiser 1997) and Mexico. James et al. (1992) mention it also from Asia. In British Columbia it is reported as commonly intermontane and scattered in maritime areas by Halonen et al. (1998).

In Mexico it is corticolous in Veracruz, Hidalgo, Estado de México, Oaxaca, Chiapas, Chihuahua, Michoacán, and San Luis Potosí. Its altitudinal range is from 1500 m to 2825 m, mainly in mixed forests dominated by Quercus, with Pinus and/or Abies, occasionally with Alnus. The more frequent porophytes are Compositae shrubs, Burlegia, Pinus, Abies, and Prunus. Only one specimen was found growing on rock in a Quercus-Pinus stand in Oaxaca at 2070 m (Herrera-Campos 2722, MEXU).

Selected specimens examined – MEXICO CHIAPAS. aprox. 9 km S of San Cristóbal, Herrera-Campos 2724 (MEXU); PUEBLA, Zacatlán, Piedras Encimadas, Castorena 52 (ENCB); OAXACA km 90 of the Tuxtepec-Oaxaca Highway, Herrera-Campos 2718 (MEXU); SAN LUIS POTOSI, Parque Nacional "El Potosí", Cañada Grande Zambrano 11-28-1992 (MEXU); VERACRUZ, Cruz Blanca, Herrera-Campos 49, 51 (MEXU); Road to Las Minas, 2 km N of the detour to México 140 Highway, Johansen & Mojica 12-4-1982 (MEXU).

8. Usnea jamaicensis Ach Lich. Univ , 1810, p 619.

Thallus pale yellow, pruinose, erect, 8.5 cm long, anisotomic dichotomous, poorly or moderately branched; branches divergent, one point of attachment; trunk concolorous to black, 5 mm long, straight; branches (2.18)- 1.58 ± 0.12 - (0 92) mm n= 9] cylindrical, tapering very slowly, segments terete in cross section and in longitudinal section slightly fusiform to cylindric, sometimes not constricted; apices lax and long; ramified at 90°; papillae absent, tubercles abundant, very conspicuous all along the thallus, sometimes of irregular shape; fibercles; fibrils long up to 15 mm, slender, distribution irregular; pseudocyphallae large plain, circular to irregular; soralia absent, isidiomorphs absent; cortex [(5.93) - 11.22 ± 1.26 %- (18.33)
n= 9] thick, shiny, rarely mat; OxCa (?) sometimes present; medulla [(55) - 68.47 ± 3.05 %- (80.0) n= 9] thick, dense, cottony, axis [(11.63) - 20.30 ± 2.01 %- (27.42) n= 9] thin; solid and straight, sometimes slightly pink; apothecia lateral to terminal, 7 mm in diameter, disk pruinous, chemistry usnic, cryptostictic, and salazinic acids.

Variation.– It is a very uniform species, however some variation may be observed in the density of ramification of the thalli, the segment shape in longitudinal section vary from cylindrical to slightly swollen, and the chemistry also varies from salazinic acid to cryptostictic acid being the major secondary substance.

Distinctive features.–The most distinctive characters of this species are the pruinose appearance of the thallus, the large and abundant tubercles, and the long and slender fibrils Also this species is visibly yellower than the others.

Distribution and ecology.– Motyka (1936-1938) reported U jamaicensis Jamica, Bolivia, and Colombia. In Mexico, this corticolous species is not common, it has been collected only in few localities in Oaxaca, Chiapas, Hidalgo, and Durango.

Selected specimens.– MEXICO. CHIAPAS. Road to Tzontewitz-Chalam, Herrera-Campos 4939 (MEXU). DURANGO. 1km from Barranca de Liebre and 2 km from the border with Sinaloa, Herrera-Campos 4946 (MEXU); OAXACA km 88 of Tuxtepec-Oaxaca Highway, Herrera-Campos 4941 (MEXU); km 104 of Tuxtepec-Oaxaca Highway, Herrera-Campos 4938 (MEXU).

9. Usnea ramillosa Mot. s. str. Lich. Gen. Usnea. Stud. Monogr. Pars. Syst. 2: 526. 1938.

Thallus pale green, erect, up to 8 cm long, slightly to conspicuously coarse; somewhat rigid; poorly to moderately ramified; sympodial and divergent branches; a single point of attachment; trunk short 2 mm, straight or attenuate at the base, often continuous with the main branch, concolorous with the main branches, or from orange to dark brown, rarely partially black, sometimes with pseudoroots; branches (4.35) - 1.78 ± 0.12 - (0 29) mm in diameter (n=38), cylindrical, tapering slowly, mostly constricted at the base, with or without depressions or foveolae on the cortex, rarely with small and delicate ridges; segments more or less long 1-2/cm, in cross section terete; in longitudinal section swollen to fusiform, sometimes irregular, the axis may be exposed between the segments, apices commonly fine ramified at 90°; rarely long and flexuose; papillae inconspicuous to abundant, indistinct, conic (R-1042) or cylindrical, regularly or irregularly distributed on the thallus; tubercles and fibercles generally scarce, rarely abundant; fibrils scarce or abundant, short, (1-3 (4-5) mm) thin, irregularly distributed; pseudocyphellae absent or very rare; soralia absent; isidiomorphs absent; cortex [(2.12)- 8.24% ± 0.61 - (21.74) n= 38], thin, mainly vitreous; medulla [(50) - 76 37% ± 1.33 - (93.12) n= 38] thick, loose to dense; sometimes heterogeneous i.e. denser in contact with the cortex and loose towards the axis; axis [(4.76)- 15.39% ± 0.87 - (28.26) n= 38] thin; solid and straight; apothecia abundant, 11 mm diameter, mostly terminal, also subterminal, barely lateral, often densely fibrillate at the margins, disc pruinose, the underside of the apothecia somewhat foveolate; chemistry usnic and protocetratic acids.

Variation – The variable features of U. ramillosa s. str are the same as in U. brasiliensis, except for soralia. Among others, they include the type and density of ramification, the frequency of segmentation of the branches and the abundance and distribution of the fibrils and papillae.

Distinctive features.– U. ramillosa s. str is a species mainly characterized by its always erect habit, sympodial ramification, the swollen-fusiform segments of the branches, its vitreous and thin cortex, loose to dense medulla, thin axis, and the occurrence of protocetraric acid as main secondary medullary substance. We consider U. ramillosa s. str to be the primary species of U brasilensis

Distribution and ecology.– Motyka reported this species from Cuba on Acidocroton oligostemon, Jamaica, and from Texas on various shrubs. In Mexico, it has been recently collected growing on Quercus, Pinus, and Prunus in Chiapas, Durango, Jalisco, Oaxaca, and San Luis Potosí. Its distribution is more reduced than that of U. brasilensis. It has not been collected from the localities from Eje Volcánico Transversal, where U. brasilensis is abundant. On the other hand, U ramillosa s. str has been collected in more localities in Oaxaca and Chiapas, including at the border with Guatemala, and it is also found in San Luis Potosí where U. brasiliensis has not been collected.

It is a new record for Mexico.

Selected specimens examined.– MEXICO. CHIAPAS. 5 km NE de Las Ollas, Herrera-Campos 4893, 4898; Hacienda, E. Matuda January, 1938, (COLO); Central highlands, near San Cristóbal de Las Casas, on the old road to Chamula, Dillman 537 (ISU, RAY J. HERBARIUM); DURANGO. 12 km east of El Toro, Bell June, 1965 (DUKE); JALISCO. Manantlán, rumbo a Las Joyas, Herrera-Campos 4896, 4904; SAN LUIS POTOSI, Parque Nacional "El Potosí", Cañada Grande, Zambrano 11-28-1992; OAXACA. Cerro del Veinte, Herrera-Campos 4902, 4906; 18 km Nw of the junction of routes 131 NW 190, on 131 near Oaxaca state line, Culberson & Culberson 17236 (DUKE); 70 km NW of Oaxaca, Culberson & Culberson 16279 (DUKE).

10. Usnea wirthii Clerc, Saussurea 15 33-36, 1984

Thallus pale green, erect, 3cm long, isotomic dichotomous, moderately ramified; branches divergent, a single point of attachment point of attachment; trunk concolorous, short 2mm long, straight; branches [(0.906) - 0.776 ± 0 052 - (0.526) mm, n= 8] cylindric, tapering very slowly, segments terete, cylindric to slightly swollen; apices short, more or less fine; ramified at 60 or 90°; papillae verrucose, abundant or scarce, irregularly distributed, tubercles few; fibrils short (1-2 mm) spinulous, few or sometimes almost absent, distribution irregular mostly on main and secondary branches, pseudocyphallae absent; soralia on apices and fibrils, originated on cortex or from transverse cracks, superficial, slightly excavate; small, although in few specimens broad soralia, half or more the width of the branch were observed; circular, few irregular, with or without margin, separate and discrete to confluent, isidiomorphs absent or present, small, on young soralia, cortex [(9.37) - 16 32 ± 3.75% - (38.07)] thin, shiny, sometimes with superficial small red spots; medulla [(43.33) - 60.46 ± 3 90% - (71.8) n= 8] thick, very loose to dense, fibrous, yellow; axis [(15 23) - 23.21 ± 3 22% - (40) n= 8] thin; solid and straight, sometimes yellowish; apothecia absent; chemistry usnic, stictic, salazinic, norstictic, and/or psoromic acids (n=9)

Variation – U. wirthii seems to be a rare species in Mexico, as very few specimens were collected, and some of them not in optimal state. The variation recorded is difficult to interpret as normal variation of the species or modifications due to damage of the thalli. Sometimes the soralia were deeply excavate and broad.To the contrary, its soralia are minute and slightly excavate (Clerc 1984, Halonen et al. 1998). The papillae and/or small tubercles were variable in density, sometimes even absent. The same type of variation was observed for the fibrils. The yellow pigment of the medulla and of the axis was found in different concentration, from a strong yellow color to very faint. The red spots on the cortex were commonly observed, however compared to some specimens of U wirthii collected in California (i. e. Sanders 97629.1, dup. MEXU), the Mexican specimens have almost no pigmentation on the cortex, the spots are scattered and less numerous. The chemistry of this species was also variable usnic, ± psoromic and ± 2-dimethyl psoromic ±

constictic, ± salazinic, ± norstictic acids, being most frequent the strain with usnic and psoromic acid.

Distinctive features.– The most distinctive character of this species is the yellow pigment on the medulla and/or the axis and the red spots on the cortex.

Distribution and ecology.– It is reported from southern Europe, (Clerc 1984c), the Pacific Northwest in USA (McCune & Geiser 1997) and British Columbia (Halonen et al. 1998). In Mexico it has been collected very scantily only in two localities in Estado de México and Veracruz, in Pinus-Abies and Pinus-Alnus forests at 2800 m and 2450 m, respectively. U. wirthii is recorded for the first time from Mexico.

Selected specimens examined.– MEXICO. ESTADO DE MEXICO, Road to Sultepec, 2 km from the detour to La Guacamaya, Herrera-Campos 505 (MEXU) VERACRUZ. Cruz Blanca, Herrera-Campos 82, 83 (MEXU).

RESULTS AND DISCUSSION

Statistical analysis. U. brasiliensis and U. ramillosa s. str. are very similar on the basis of CMA measurements. Likewise U. cornuta s. lat. and U. glabrata are similar but different from the first pair Lastly U. cirrosa occupies an intermediate position. This interpretation was suppoted by univariate analysis (one way ANOVA, results not shown), but to determine the degree to which the taxa could be separated a discriminant analysis was run (Fig. 14). These results support recognizing three groups based on the original (i.e. not relativized) CMA measurements (Table 2). Although U. brasiliensis is not separated from U. ramillosa s. str., it is clearly distinct from U cornuta s lat., and therefore the synonimization is not sopported. Likewise U. cornuta s. lat. and U. glabrata are not separated, but U. cirrosa is distinct from all other species.

Although the discriminant analysis implies that only three groups are present, we support the interpretation that all five taxa should be recognized as separate species based on other criteria. U brasiliensis and U. ramillosa s. str. are judged to be a species pair, a concept widely used in lichenology (Awasthi, 1981; Bowler and Rundel 1975; Gowan and Ahti 1993; Inoue 1993; Kurokawa 1986; Llimona et al. 1976; Mattson and Lumbsch 1989; Nordnes 1982; Poelt 1970, 1972; Robinson 1975; Rundel and Bowler 1976). U. ramillosa s. str. is the fertile species with apothecia and U. brasiliensis is the predominantely asexual species with soralia. The fact that protocetraric acid is the dominant secondary product in both U. brasiliensis and U. ramillosa s. str. also supports treating them as a species pair. In the case of U. cornuta s. lat. and U. glabrata, they are separated on the basis of different soralia types (mainly small superficial, never deeply excavate in U cornuta s. lat. and broad deeply excavate in U glabrata). Finally U. cirrosa is a fertile species with red pycnidia and frequent red pigmentation at the edge of the apothecial disk.

EXCLUDED SPECIES

U. substerilis Mot was reported from Mexico by Thomson (1984) however we have not been able to confirm its occurrence in the country.

ACKNOWLEDGEMENTS

María Angeles Herrera-Campos deeply acknowledges the support received from Departamento de Botánica, Instituto de Biología, UNAM through Patricia Dávila Aranda, the grants 190/92/PADEP/68 from UNAM, and CoNaCyT financial support All the authors acknowledge the grant BSR-920-1111 from NSF.

We also are very grateful to the curators and owners of the herbaria listed in the text for loan of specimens, and to Dr. Isabel Tavares and Dr. William Sanders for their gift of specimens of U. cirrosa from Mexico and U wirthii from California, respectively.

Thanks to Dr.Milton Sommerfeld and Devon Ekenstam from Arizona State University for their support with photographic equipment, to C. Kazilek and Barb Backes, from the Visualization Laboratory at ASU, for assistance with the photographic work.

We also thank to Dr. Jana Fry, Brian Sherman, and Joaquín Marrufo from the GIS laboratory at ASU, for their help on the elaboration of the maps. Special thanks to Sara Kirchheimer and Beth Kantrud for their invaluable assistance in reviewing the text.

LITERATURE CITED

ASAHINA, Y. 1956. Lichens of Japan. Vol. III Genus Usnea. Research Insitute for Natural Resources, Shinjuku. Tokyo.

AWASTHI, D. 1981. The typification of Roccella montagnei. The Bryologist 84. 216-219.

BRODO, I. M. 1978. Changing concepts regarding chemical diversity in lichens. Lichenologist 10: 3-11.

BRODO, I. M. 1986 Interpreting chemical variation in lichens for systematic purposes. The Bryologist 89: 132-138.

BOWLER, P & P RUNDEL 1975 Reproductive strategies in lichens Botanical Journal of The Linnean Society (London) 70· 325-340 .

CLERC, P. 1984a. Contribution à la révision de la systématique des usnées (Ascomycotina, Usnea) d'Europe I.-Usnea florida (L) Wigg. emend Clerc. Cryptogamie, Bryologie et Lichénologie 5: 333-360.

CLERC, P. 1984b. Usnea wirthii -A new species of lichen from Europe and North Africa. Saussurea 15. 33-36.

CLERC, P. 1987a. Systematics of the Usnea fragilescens aggregate and its distribution in Scandinavia. Nordic Journal of Botany 7: 479-495

CLERC, P. 1987b. On the morphology of soralia in the genus Usnea, pp. 99-102. In E. Peveling (ed.), Progress and Problems in Lichenology in the Eighties. Bibliotheca Lichenologica Vol. 25 Berlin-Stuttgart.

CLERC, P. 1991. Usnea madeirensis Motyka (ascomycète lichénisé): une espèce méconnue de l'Europe et de l'Amèrique du Nord. Candollea 46. 427-438.

CLERC, P. 1992. Some new or interesting species of the genus Usnea (lichenised Ascomycetes) in the British Isles. Candollea 47: 513-526.

CLERC, P 1994. Comment Usnea mutabilis Stirton, une espèce nord-américaine, se cache en Europe sous le nom d' Usnea marocana Motyka. Une contribution à la systématique du genre Usnea (ascomycètes lichénisés). Bulletin de la Société Linnéenne Provence 45: 309-316

CLERC, P. 1997. Notes on the Genus Usnea Dill. ex Adanson Lichenologist. 29 (3)· 209-215.

CLERC, P. & P. DIEDERICH. 1991. Usnea wirthii Clerc new to North America and the British Isles. Lichenologist 23: 405-407

CLERC, P. & M.A. HERRERA-CAMPOS. 1997. Saxicolous species of the genus Usnea in North America. The Bryologist 100: 281-301.

COUTIÑO, B. & A. MOJICA. 1985 Líquenes de la región del Cofre de Perote-Xalapa. Revista Mexicana de Micología 1· 379-399.

CULBERSON, C. & W. CULBERSON. 1976 Chemosyndromic variation in lichens. Systematic Botany 1. 325-339.

CULBERSON, C., W CULBERSON & A. JOHNSON 1988. Gene flow in lichens American Journal of Botany 75 : 1135-1139

CULBERSON W 1969. The use of chemistry in the systematics of the lichens. Taxon 18: 152-166.

CULBERSON W. 1970. Chemosystematics and ecology of lichen-forming fungi. Annual Review of Ecology and Systematics 1: 153-170

CULBERSON W 1986. Chemistry and sibling speciation in the lichen-forming fungi: Ecological and biological considerations. The Bryologist 89: 123-131.

CULBERSON, W. & C. CULBERSON 1967. Habitat selection by chemically differentiated races of lichens. Science 158:1195-1197.

CULBERSON, W & C. CULBERSON. 1973. Parallel evolution in lichen-forming fungi. Science 180: 196-198

CULBERSON, W., C. CULBERSON & S FISCUS. 1983. A new lecanoric acid-producing Usnea from Mexico. The Bryologist 86: 254-256 .

DAVILA, P. Y O. HERRERA-MACBRYDE 1997. In Davis, S. D., V. H. Heywood, O Herrera-MacBryde, J. Villa-Lobos & A C. Hamilton (eds) Centres of Plant Diversity. A guide and strategy for their conservation The Wordl Wide Fund for Nature (WWF) and IUCN The World Conservtion Union.

DELGADILLO, C. 1983. Notas sobre la diversidad briológica de Mexico Revista de la S ociedad Mexicana de Historia Natural 44· 93-97

DELGADILLO, C. 1987. Moss distribution and the phytogeographical significance of the Neovolcanic Belt of Mexico. Journal of Biogeography 14· 69-78.

DELGADILLO, C. 1992. Moss interchange: Bryofloristic similarities between Mexico and Colombia and the phytogeographical role of the Central American bridge. The Bryologist 95· 261-265

DELGADILLO, C. 1993. Diversity in the Mexican Bryoflora, pp. 365-377. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

DELGADILLO, C. 1995. Neotropical moss floras: Species common to North and South America. Tropical Biology 10: 1-6

EGAN, R S. 1986. Correlations and non-correlations of chemical variation patterns with lichen morphology and geography. The Bryologist 89: 99-110.

ELIX, J. A. 1996. Biochemistry and secondary metabolites, pp. 154-180. In T H. Nash (ed.), Lichen Biology Cambridge University Press, New York.

FAHSELT, D. 1996 Individuals, populationns and population ecology, pp. 181-198. In T. H. Nash (ed), Lichen Biology. Cambridge University Press, New York.

FEIGE, G. B., & H. T LUMBSCH 1995. Some types of chemical variation in lichens. Cryptogamic Botany 5: 31-35.

GRAHAM, A. 1993. Historical factors and biological diversity in Mexico, pp 109-127. In Ramamoorthy, T. P., R. Bye, A. Lot & J Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

GOWAN, S & T. AHTI. 1993. Status of the lichen genus Porpidia in eastern Fennoscandia . Annales Botanici Fennici 30: 53-75.

HALE, M., Jr. 1979. How to Know the Lichens. 2nd Edition. Wm. C. Brown Co. Dubuque, Iowa.

HALE, M., Jr. 1983. The Biology of Lichens. London. Edward Arnold.

HALONEN, P., P. CLERC, T. GOWARD, I. M. BRODO & K. WULFF 1998. Synopsis of the genus Usnea (Lichenized Ascomycetes) in British Columbia, Canada. The Bryologist 101: 36-60.

HAWKSWORTH, D. L. 1976. Lichen chemotaxonomy, pp. 139-184 In D. H. BROWN, D. L. HAWKSWORTH & R. H. BAILEY (eds.) Lichenology: Progress and Problems, Academic Press. London.

HERRERA-CAMPOS, M. A., P CLERC & T. H. NASH III. Pendulous species of Usnea from temperate forests in Mexico. The Bryologist 101: 303-329.

HESS, W. J. & N. A. STOYNOFF. 1998. Taxonomic status of Quercus acerifolia (Fagaceae) and a morphological comparison of four members of the Quercus shumardii complex.

INOUE, M. 1993 Buellia subfrigida sp. nov. (Lichens, Buelliaceae) from Lutzow-Holm Bay area and Prince Olav Coast, East Antarctica- The asexual sorediate species forming a species pair with B. frigida Darb. Nankyoku Shiryo 37: 19-23

JAMES, P., P. CLERC, & W. PURVIS. 1992. Usnea, pp 620-629. In O. W Purvis, B J. Coopins, D. L. Hawksworth, P. W. James, & D. M. Moore (eds.). The Lichen Flora of Great Britain and Ireland. Edinburgh Natural History Museum and British Lichen Societey.

KUROKAWA, S 1986 Chemical variation in the Parmelia physcioides group (Lichenes) Journal of Japanese Botany 61: 257-268

LIMONA, X., R WERNER, R. LALLEMENT, J BOISSIÈRE. 1976 A propos du Buellia subcanescens R. G. Werner, espèce primaire du Buellia canescens (Dicks.) D.N Rev. Bryol. et Lichenol. , 42: 617-635 .

MCCUNE, B. & L. GEISER. 1997. Macrolichens of the Pacific Northwest Oregon State Universtiy, Corvallis

MATTSSON, J. & T. LUMBSCH. 1989. The use of the species pair concept in lichen taxonomy. Taxon 38: 238-241.

MOTYKA, J. 1936-1938. Lichenum Generis Usnea. Studium Monographicum, Pars Systematica. 1937. Leopoli.

NORDNES, J. 1982. Parmeliopsis esorediata comb nov. in South Norway. Nordic Journal of Botany 2. 381-382 .

POELT, J. 1970. Das Konzept der Artenpaare bei den Flechten Deutsche Botanische Gesellschaft. Neue Folge 4: 187-198.

POELT, J. 1972. Die taxonomische Behandlung von Artenpaaren bei den Flechten. Botanika Notiser 125· 77-81.

RAMAMOORTHY, T. P., R. BYE, A. LOT & J. FA. 1993. Introduction. In Ramamoorthy, T. P , R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

ROBINSON, H. 1975. Considerations on the evolution of lichens. Phytologia 32: 407-413.

ROGERS, R. W. 1989. Chemical variation and the species concept in lichenized ascomycetes. Botanical Journal of the Linnean Society 101: 229-239.

RUNDEL, P. & P. BOWLER. 1976. Ramalina leptocarpha and R. subleptocarpha: a fertile-sorediate species pair. The Bryologist 79: 364-369.

RZEDOWSKI, J. 1981. La Vegetación de México. Ed. Limusa. México.

RZEDOWSKI, J. 1991 El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar. Acta Botánica Mexicana 15: 47-64.

RZEDOWSKI, J. 1993 Diversity, and Origins of the Phanerogamic Flora of Mexico, pp 129-143. In Ramamoorthy, T. P., R Bye, A. Lot & J Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press Oxford.

SAS 1990. SAS/STAT User's Guide. Version G, 4 th ed. vol. I. SAS Institute, Cary, NC. USA.

SHARMA, S. 1996. Applied Multivariate Techniques. John Wiley & Sons. U. S. A.

SHEARD, J.W. 1978 a. The taxonomy of the Ramalina siliquosa species aggregate (lichenized Ascomycetes). Canadian Journal of Botany 56: 916-938.

SHEARD, J.W. 1978 b. The comparative ecology and distribution and within-species variation of the lichenized Ascomycetes Ramalina cuspida and R. siliquosa in the British Isles. Canadian Journal of Botany 56: 939-952.

STEVENS, G. 1992. Variation in thallus morphology in response to climatic, and geographical distribution in an Usnea complex. Lichenologist 24: 229-248

SWINSCOW, T & H KROG. 1979 The fruticose species of Usnea subgenus Usnea in East Africa. Lichenologist 11: 207-252.

TAVARES, I.1997. A preliminary key to Usnea in California. Bulletin of the California Lichen Society 4: 19-23.

TAVARES, I. & W. SANDERS. 1998. Preliminry report on the shor, apotheciate taxa of Usnea in the Soutywestern United States. In Lichenographia Thomsoniana. North American Lichenology in Honor of John W. Thomsons. M. G. Glenn, R. C. Harris, R. Dirig y M. S. Cole (eds.), pp 171-185. Mycotaxon LTD. New York.

THOMSON, J W. 1984.American Arctic Lichens. 1. The Macrolichens. Columbia University Press. New York.

TOLEDO, V & M. J. ORDONEZ. 1993. The biodiversity scenario of Mexico: A review of terrestrial habitats, pp. 757-777. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

TOLEDO. V., J. RZEDOWSKI & J VILLA-LOBOS 1997. Regional Overview: Middle America, pp 97-124. In Davis, S. D., V. H. Heywood, O Herrera-MacBryde, J. Villa-Lobos & A. C. Hamilton (eds.) Centres of Plant Diversity A guide and strategy for their conservation. The Wordl Wide Fund for Nature (WWF) and IUCN The World Conservation Union.

WALKER, F J. 1985. The lichen genus Usnea subgenus Neuropogon. Bulletin of the British Museum (Natural History). Botany 13: 1-130.

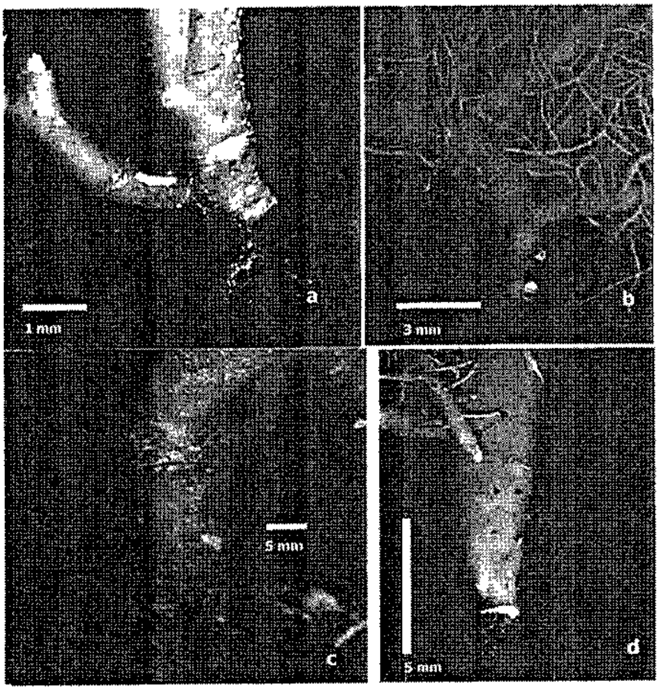


Figure 1. Shape of the basal part of the thallus. — a. Straight short base of U. cornuta s. lat., Herrera-Campos 20 (MEXU). — b. Base continuous with the main branch of U. jamaicensis Herrera-Campos 4941 (MEXU). — c Slightly attenuate base of U. brasiliensis, Herrera-Campos 4817 (MEXU). — d. Attenuate base of U. ramillosa, Herrera-Campos 4904 (MEXU).

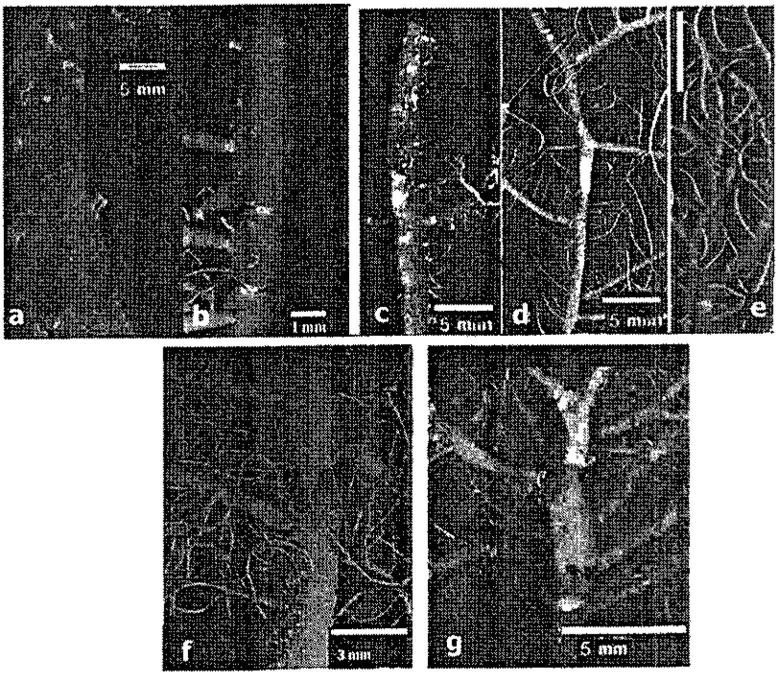


Figure 2. Longitudinal shape of the branch segments. — a. Irregular segments and b. Constricted or swollen segments of U. brasiliensis, Herrera-Campos 4817, 4816 (MEXU). — c. Cylindrical segments with small spinules, d & e. Constricted and slightly irregular segments of U. cornuta s. lat., Herrera-Campos 63, 4697, and 4679 (MEU). — f. Cylindrical segments of U. jamaicensis Herrera-Campos 4941 (MEXU). — g. Swollen segments of the main branch of U. cirrosa, note the numerous small spinules on the secondary branches, Herrera-Campos 4937 (MEXU).

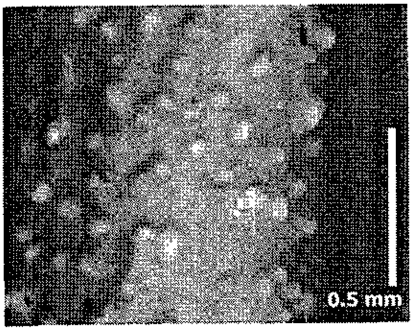


Figure 3. Tubercles of U. jamaicensis, Herrera-Campos 4941 (MEXU).

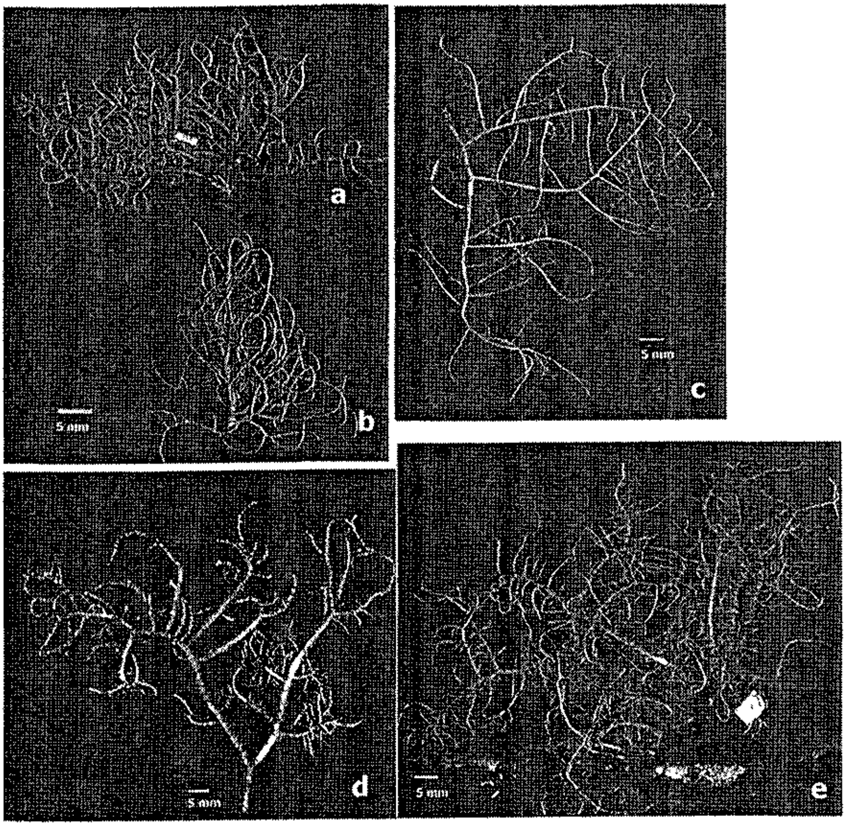


Figure 4. Thallus variation in U. cornuta s. lat. — a-c. Typical thalli of European morphs, small shrubby (a, b, Herrera-Campos 4679 (MEXU)) and subpendulous (c, Herrera-Campos 4697 (MEXU)), densely to moderately ramified, respectively. — d. Shrubby somewhat rigid, poorly ramified thallus with irregular distribution of short fibrils and curve apices, Herrera-Campos 63 (MEXU). — e. Shrubby, moderately ramified thallus with abundant fibrils and isidiomorphs, Herrera-Campos 1385 (MEXU)

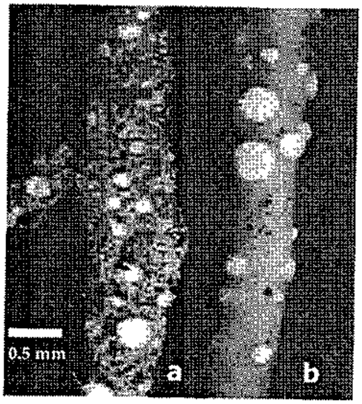


Figure 10. Soralia of U. fragilescens — a. Small, separate soralia with margin and abundant isidiomorphs. — Separate, tuberculate soralia, small to medium (no larger than half of the width of the branch), Herrera-Campos 2708 (MEXU).

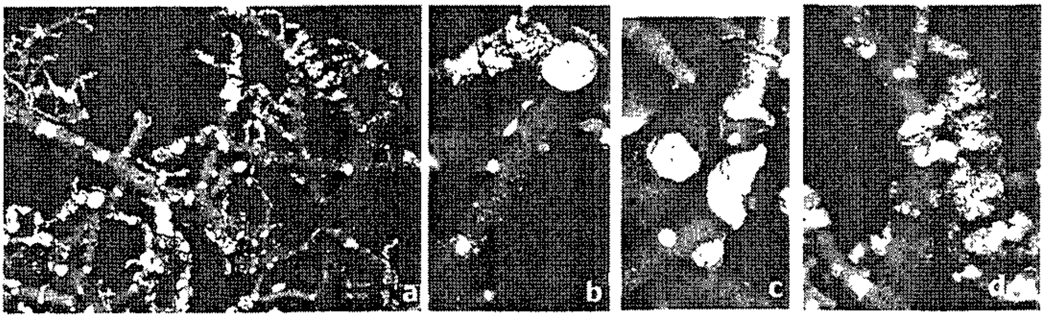


Figure 11. Deeply excavate soralia of U. glabrata, Herrera-Campos 2729 (MEXU).

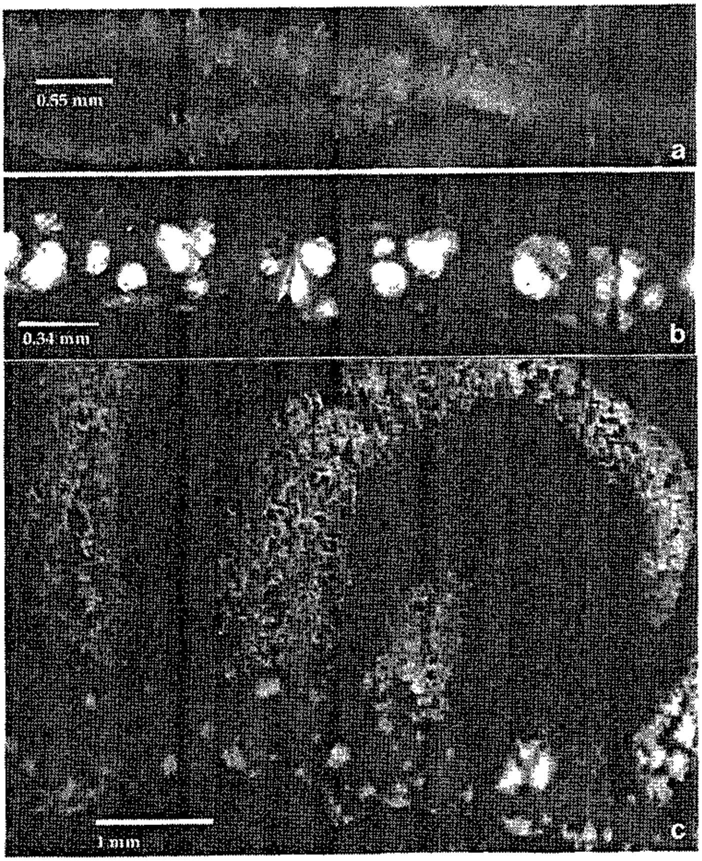


Figure 9. Variation of the soralia in U. brasiliensis . — a. Small superficial or slightly excavate soralia, with few small isidiomorphs, Herrera-Campos 4782 (MEXU). — b Broad, plain, tuberculate, separate soralia, with margin, Herrera-Campos 74 (MEXU).— c. Small and broad discrete soralia, with margin, crowded with isidiomorphs, curved tips, Herrera-Campos 4817 (MEXU).

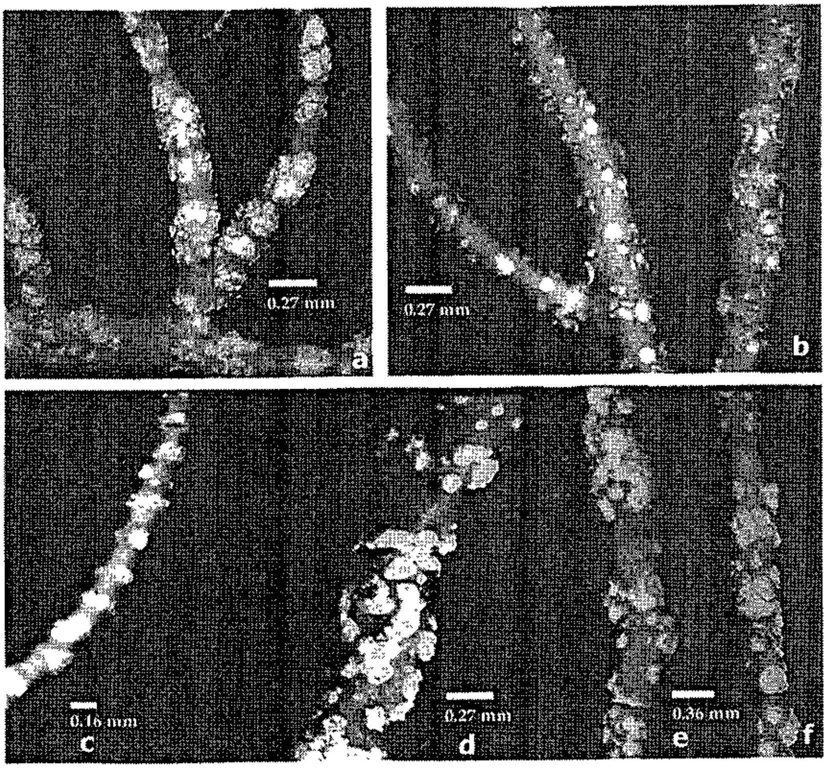


Figure 8. Variation of the soralia in U. cornuta s. lat. —. a. Small, superficial to slightly excavate confluent soralia, with very small isidiomorphs, Herrera-Campos 4762 (MEXU). — b. Punctiform, circular, slightly raised, separate soralia with or without isidiomorphs, Herrera-Campos 4692 (MEXU). — c. Wide , plain, discrete, and slightly raised soralia without isidiomorphs, Herrera-Campos 4685 (MEXU). — d. Small to broad soralia, tuberculate, with or without margin, partially to totally confluent, plain to convex, Herrera-Campos 20 (MEXU). — e. Small to broad tuberculate, convex soralia, with margin, partially confluent, producing masses of soredia, Herrera-Campos 4693 (MEXU). — f. Small to broad, plain to slightly excavate soralia, partially confluent, with margin and sparse small isidiomorphs, Herrera-Campos 4693 (MEXU).

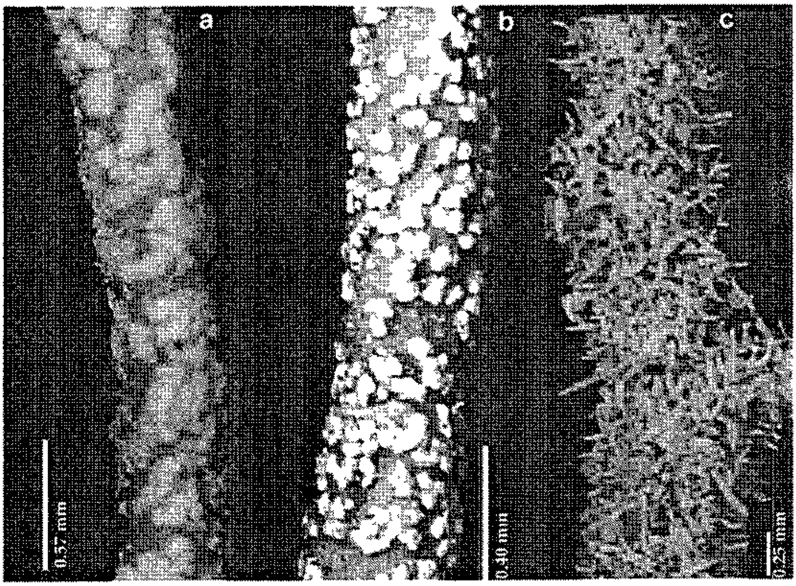


Figure 7. Typical soralia of U. cornuta s. str. — a. Punctiform, plain, totally confluent soralia, Herrera-Campos 4691 (MEXU).— b. Punctiform, slightly raised, partially to totally confluent soralia, Herrera-Campos 36 (MEXU). — c. Heavily isidiate branch segment, Herrera-Campos 1385 (MEXU).

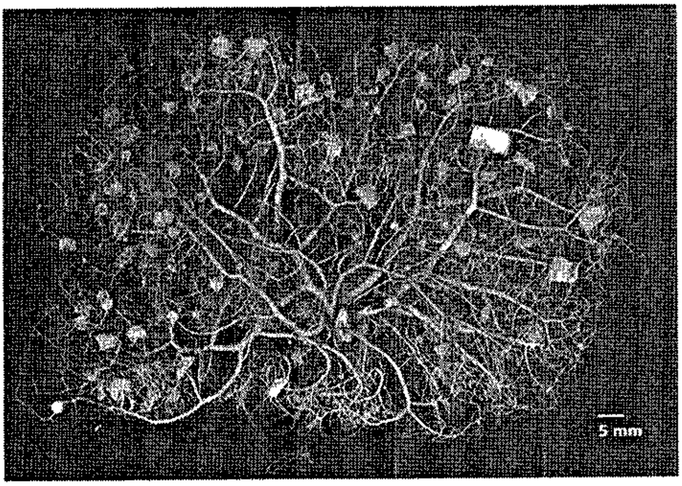


Figure 6. U. jamaicensis. Shrubby, densely ramified thallus with long slender fibrils, Herrera-Campos 4942 (MEXU).

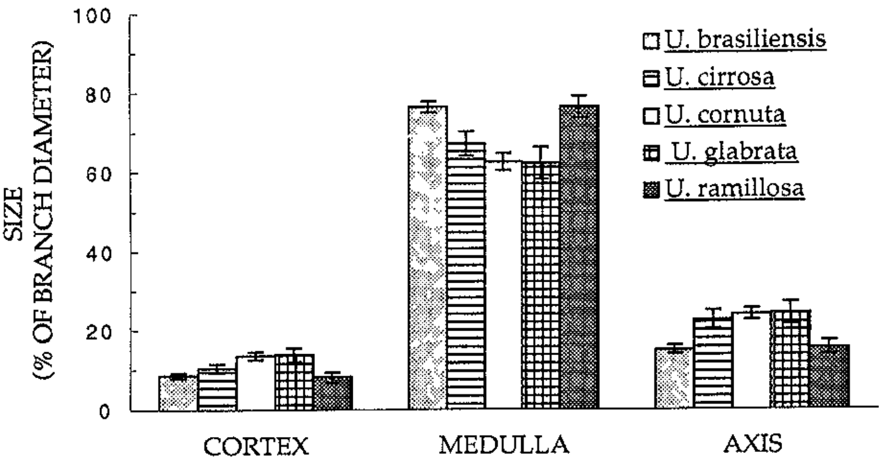
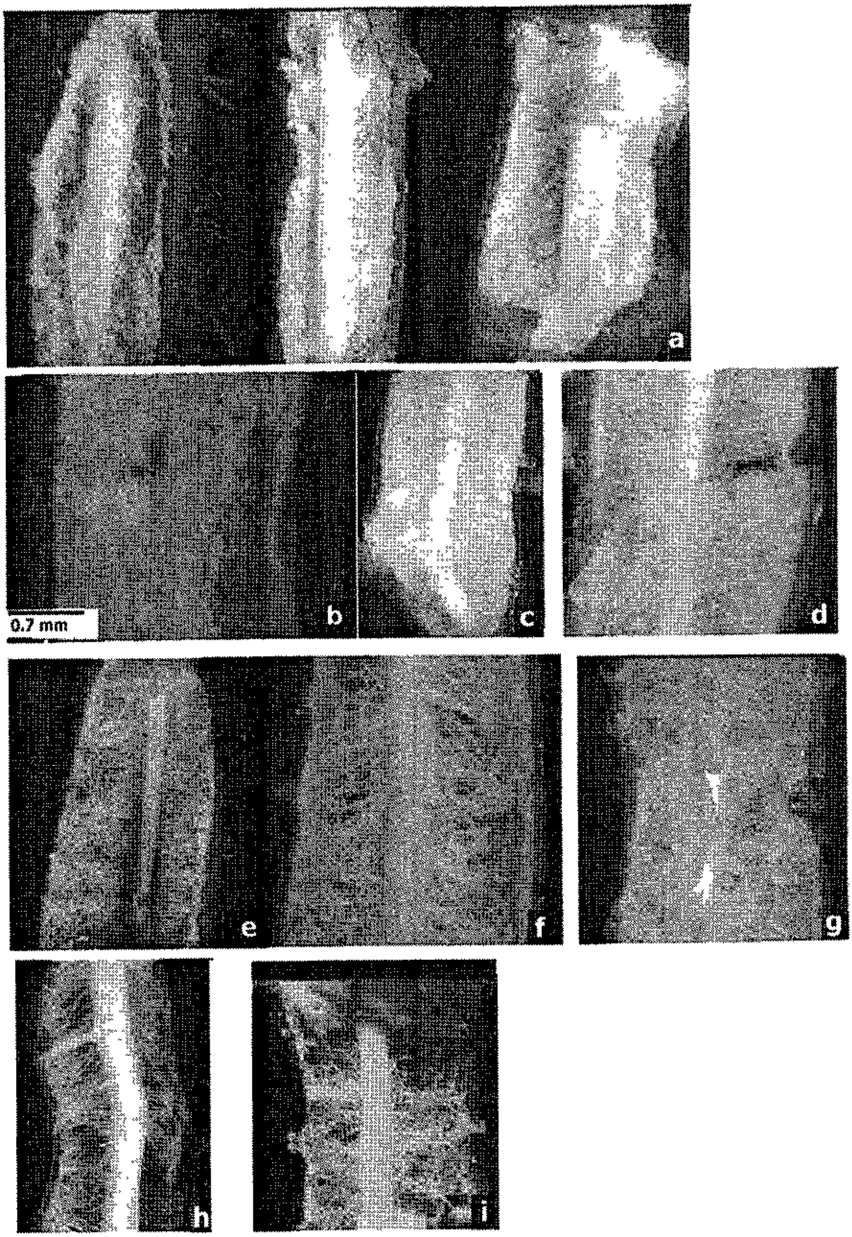


Figure 12. Relative size of the cortex, medulla, and axis in five Usnea species. Bars are mean values (n = 60, 58, 67, 43, and 38 for U. brasiliensis, U. cirrosa, U. cornuta, U. glabrata, and U. ramillosa, respectively). Error bars represent the 95% confidence interval of the mean.

Figure 13. Longitudinal sections showing the cortex, medulla and axis – a. Variation of U cornuta s. lat., Herrera-Campos 63, 4680, 20 (MEXU) – b-c. Variation of U. brasiliensis, Herrera-Campos 4817, 4816 (MEXU).–d U. fragilescens, Herrera-Campos 2708 (MEXU). –e-f. Variation of U. ramillosa, Herrera-Campos 4905, 4906 (MEXU).–g. U. jamaicensis, Herrera-Campos 4941 (MEXU). –h. U cirrosa, Herrera-Campos 4937 (MEXU). –i. U glabrata, Herrera-Campos 2729 (MEXU).


a
0.7 mm
b
c
d
e
f
g
h
i

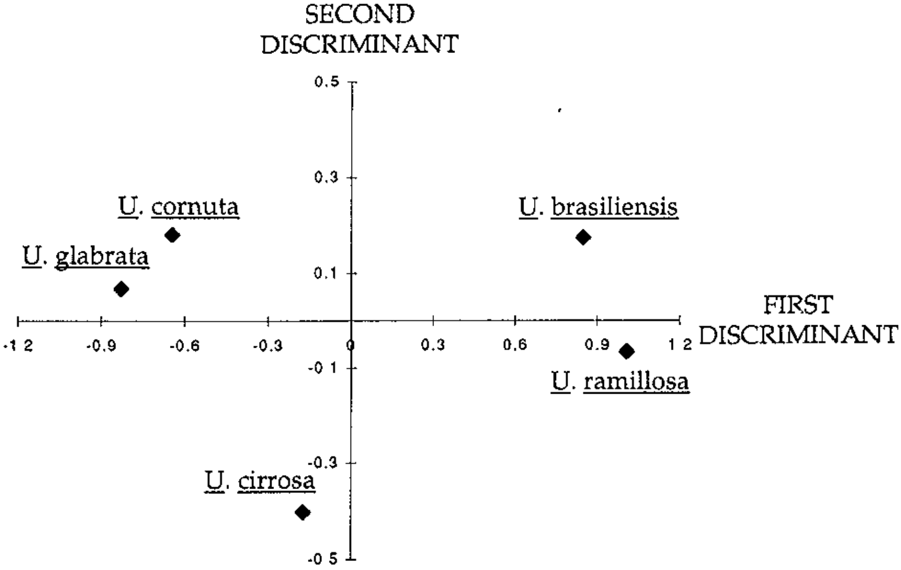
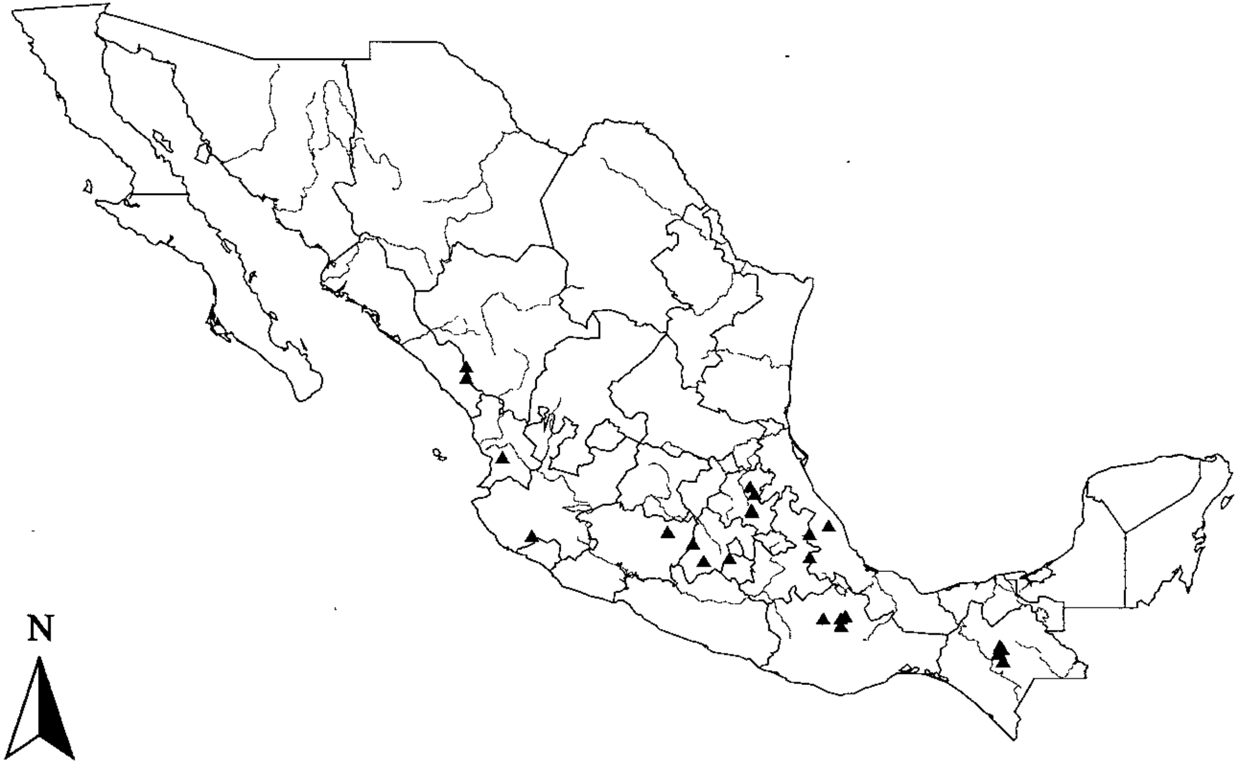


Figure 14. Species means on the first and second discriminant functions.

Figure 15 Distribution maps of the species studied

U. brasiliensis



__U. cirrosa__

__U__. __cornuta__ __s__. __lat__.

U. dasaea

U. esperantiana

U. fragilescens

U. glabrata

U. jamaicensis

U. ramillosa s. str.

U. wirthii

Table 1 Main (+) and accesory (±) secondary chemical compounds of the species. U =usnic acid, St = stictic acid, Cst = constictic acid, S = salazinic acid, Cs= consalazinic acid, N = norstictic acid, P = protocetraric acid, Ps = fumarpsoromic acid, Cr = cryptostictic acid, Ca = caperatic acid, Bo = bourgeonic acid, UF = unknown fatty acid, and G = galbinic acid.

Species	U	St	CSt	S	CS	N	P	Ps	Cr	Ca	Bo	UF	G
U. brasiliensis	+						+						
U. cirrosa	+			+		+	±						
U. cornuta s. lat.	+		±	+	+							±	
U. dasasea	+			±		±							+
U. esperantiana	+	+	±								+		
U. fragilescens	+		±	±									
U. glabrata	+	+	±			+							
U. ramillosa s. str.	+						+						
U. jamaicensis	+			+					+				
U. wirthii	+	±		+		+		±					

Table 2. F test for square distance between species (Sharma 1996). *** = $p < 0.001$. ns = non-significant. Sample size: U. brasiliensis, 60; U. cornuta, 68; U. cirrosa, 58; U. glabrata, 43, U. ramillosa, 38.

	U. brasiliensis	U. cornuta	U. cirrosa	U. glabrata	U. ramillosa
U. brasiliensis	1	***	***	***	ns
U. cornuta	***	1	***	ns	***
U. cirrosa	***	***	1	***	***
U. glabrata	***	ns	***	1	***
U. ramillosa	ns	***	***	***	1

Las especies tratadas en esta sección son especies de reproducción asexual, talos erectos a subpéndulos, ramas no constreñidas en la base, segmentos de cilíndricos a irregulares; con o isn foveolas; corteza generalmente gruesa aunque en ocasiones es delgada, médula densa a compacta, rara vez laxa; eje principalmente grueso, ocasionalmente delgado; soralios variables, pequeños puntiformes o grandes (mayores a la mitad del diámetro de la rama), superficiales a excavados; circulares, oblongos o irregulares; con o sin margen; isidiomorfos abundantes en los soralios y/o en la corteza; apotecios ausentes o raros.

Se presenta la descripción y la distribución geográfica de: U. fulvoreagens (Räs.) Räs., U hirta (L.) Wigg , U madeirensis Mot., U setulosa Mot., U. subfloridana Stirton y U. wasmuthii (Ras.).

Usnea fulvoreagens (Räs.) Räs.

TIPO: Kl. Kurkijoki, Lapinhlahti, 22.8.93, leg V. Räsänen. (H!). Chemistry: ácidos úsnico, norestíctico, criptoestíctico, estíctico y menegaziaico

Talo verde olivo claro, algo pruinoso, arbustivo, hasta 9 cm de largo, moderadamente rígido, ramifiiciación dicotómica anisotóma o isótoma, ramas divergentes, fijo al sustrato en sólo punto; tronco recto o triangular, más amplio en la base, pocas veces atenuado o continuo con la rama principal, y raramente indistinto, comúnmente 5 mm de largo, ocasionalmente 13 mm, café obscuro a negro; hasta 6 grietas transversales/0.5 cm; ramas 0.81 ± 57.36 mm de diámetro, cilíndricas, agudizándose lentamente hacia las puntas; segmentos cilíndricos; ápices generalmente largos, curvos o sinuosos, a veces cortos, ramificados a 90°; papilas indistintas, de escasas a abundantes, distribuidas irregularmente en el talo; tubérculos pequeños, erosionados, dispersos y escasos; fibérculos pocos; fibrillas cortas (3-7 mm) espinulosas o finas, irregularmente distribuidas principalmente sobre las ramas secundarias, abundantes, permanentes; pseudocifelas ausentes; soralios originándose en la corteza, en pequeñas papilas o tubérculos erosionados y/o en las grietas entre las ramas y las fibrillas; localizados en ramas secundarias o terminales y en fibrillas; ligera a profundamente excavados, sin exponer el eje; pequeños, menores que la mitad de la rama donde se desarrollan; circulares, con o sin margen; algunos separados pero en su mayoría total o parcialmente confluentes, sobre todo hacia las puntas; producen abundantes soredios granulares muy polvorientos que llegan a deformar las puntas de las ramas; isidiomorfos ausentes o muy raros en los soralios inmaduros; corteza 23 77 ± 1.32 % de la rama, brillante u opaca, no agrietada; médula 35.14 ± 2.94 % de la rama, desna, fibrilosa, de compacta y casi inconspicua a moderadamente laxa, pero no ancha, eje 41.08 ± 2.44 % de la rama, sólido y recto; apotecios ausentes; química: ácidos úsnico, salazínico, norestíctico y difractaico

Variación.– Los caracteres variables de U. fulvoreagens son los soralios, en confluencia y densidad, la densidad de soredios, el aspecto de los ápices y la localización de las fibrillas.

Los soralios varían de separados a confluentes, algunas veces con margen bien desarrollado que se desintegra conforme los soralios confluyen En ejemplares densamente sorediados los ápices son cortos y deformados, en lugar de largos y relativamente finos. La producción de soredios puede ser tan abundante que en ocasiones no es posible distinguir la forma de los soralios.

Características distintivas.– U. fulvoreagens puede ser distinguida de U. subfloridana por las diferencias en los soralios y en la química. La segunda especie tiene soralios puntiformes, no excavados y regularmente con abundantes isidiomorfos; los compuestos secundarios diagnósticos son los ácidos escuamático y tamnólico. En contraste, a U fulvoreagens tiene soralios excavados que se agrandan, nunca isidiados, y ácido salazínico como principal sustancia diagnóstica.

Distribución y ecología.– U fulvoreagens es una especie ampliamente distribuida, reportada para África, Europa y Norteamérica (Clerc 1992, James et. al. 1992; Motyka 1936-1938), particularmente en la región de los Apalaches del Sur y en el norte de México (Dey 1978; Hale 1979) y en el Pacífico Norteamericano (McCune y Geiser 1997). Las recolectas recientes en México son de los estados de Chihuahua, Chiapas, Colima-Jalisco, Hidalgo, Puebla y Veracruz entre 1600 m y los 3650 m en bosques de coníferas mixtos con Quercus, Alnus o Juniperus y en plantaciones de Prunus, epífita en Pinus, Quercus, Burlegia, Alnus y Abies.

Usnea hirta (L.) F.H. Wigg. Prim. Fl. Hols 91. 1780;
TIPO: SUECIA, Fries, Lich. Suec. Exc. 150 (UPS) holotipo, typ cons. prop. (Jørgensen et al. 1994a, 1994b: 652). Química: ácido úsnico y ácidos del complejo del ácido murólico. El rechazo del neotipo ('typus reconstructus') de Motyka (1936.86) fue propuesto por Jørgensen et al. 1994a (Halonen & Puolasmaa 1995).
Usnea glaucescens Vain., Medd Soc. Fauna Fl. Fenn. 48: 172.1925
TIPO: Rusia, región de Leningrado, Vyborg (Viipuri), Hovi, Picea (kussi), 1919 Pulkkinen (TUR-V 369, lectotype by Clerc 1987: 494). Química: ácidos úsnico y del complejo murólico.

Talo verde brillante a verde olivo obscuro, arbustivo a subpéndulo, con un punto de fijación, 8 cm de longitud, poco a densamente ramificado, ramificación dicotómica anisótoma, simpodial, ramas divergentes; tronco mayormente indistinto, corto, 2 mm de largo, base pálida, más o menos blanquecina, o concolora; ramas 0.71 ± 0.035 mm de diámetro, cilíndricas a irregulares, adelgazándose lentamente hacia las puntas, frecuentemente deformadas por pequeñas depresiones, foveolas, surcos transversales y costillas pequeñas y discontinuas que a veces se erosionan, segmentos cilíndricos, irregulares o ligeramente acostillados en secciones transversal y longitudinal; ápices cortos a medianos, finos, ramificados a 90°; papilas, tubérculos y fibérculos ausentes; fibrillas cortas, espinulosas, usualmente más abundantes en la base, dispersas hacia las puntas de las ramas; pseudocifelas ausentes, soralios originados en la corteza, superficiales, planos, puntiformes, isidiados; isidiomorfos pequeños, abundantes, corticales, en soralios o en costillas, rara vez con puntas negras, más abundantes en las puntas de las ramas; corteza 10.89 ± 1.14% de la rama principal, brillante; médula 50 08 ± 4.32%, laxa, fibrosa; eje 39 02 ± 3.43%, sólido, recto; apotecios ausentes o raros, terminales, química ácidos úsnico y murólico.

Variación.– La variación de esta especie en México coincide con la observada en Colombia Británica por Halonen et al. (1998) y en Europa (Clerc 1997). El hábito de los talos varía de arbustivo a subpéndulo, la densidad de la ramificación de los mismos va de talos con pocas ramas a talos muy densamente ramificados. Sin embargo, el carácter más variable es la forma de las ramas y segmentos, conferida por la presencia de depresiones, foveolas y costillas; las ramas en U hirta pueden ser claramente cilíndricas o marcadamente deformadas.

Características distintivas.– Los caracteres distintivos de esta especie son la base clara del tronco, las ramas deformadas, los abundantes isidimorfos y la presencia de ácido murólico.

Distribución y ecología.– U. hirta es una especie de amplia distribución mundial (Clerc 1997). En el continente americano se extiende desde las zonas boreales de Canadá hasta México (Halonen et. al. 1998). En México se conoce en pocas localidades en los bosques de coníferas de Baja California y Baja California Sur, Sonora, Chihuahua y Durango, a altitudes que van de 1900 a 2500 msnm.

Usnea madeirensis Motyka in C. N. Tavares, Revista de Biología 4(1-2):131-134 (1964). TIPO: Madeira, Paul da Serra, abajo de Rabaçal y Bica de Cana. H. Persson (holotype, S).%C%M%A:12/12.5/50. Química: ácidos úsnico y salazínico.

Talo verde-amarillento, arbustivo a péndulo con ramas divergentes, de 6 a 18 (raramente 30 cm) de longitud, ramificación dicotómica isótoma o anisótoma, densamente ramificado, con un punto de fijación; tronco bien desarrollado, recto, hasta 7 mm de longitud, muy rara vez indistinto, agrietado transversalmente, anillado hasta 10 grietas/ 0.5 cm, negro, a menudo la pigmentación se extiende hasta la base de las ramas principales; ramas 0. 88 ± 37 mm de diámetro, cilíndricas, agudizándose lentamente hacia las puntas; segmentos cilíndricos; ápices finos, ramificados a 90°; papilas cilíndricas, abundantes, regularmente distribuidas en ramas principales, secundarias y terminales; tubérculos ausentes; fibérculos a veces presentes; fibrillas cortas (1-3 mm) espinulosas, y largas y aguda (hasta 10 mm), localizadas principalmente en las ramas principales y secundarias, aunque en ocasiones son más abundantes en las terminales, ocasionalmente pueden estar alrededor de los soralios; pseudocifelas ausentes; soralia originados en la corteza, fibérculos o en nódulos, principalmente en ramas secundarias, terminales y fibrillas, mayormente superficiales, algunos ligeramente tuberculados; planos, convexos o ligeramene excavados, pequeños, cuando se agrandan no son mayores que la mitad de la rama donde se desarrollan, aunque rara vez la rodean; de circulares a irregulares, con o sin margen; de separados a parcialamente confluentes; isidiomorfos más frecuentes en soralios maduros, abundantes, cortos y redondeados, o largos y agudos, éstos últimos a veces pueden ser confundidos con espínulas pequeñas; apotecios generalmente ausentes, cuando se presentan son subterminales; corteza 27.92 ± 1.15 % de la rama, opaca, agrietada; médula 25.43 ± 2.07 % de la rama, compacta, algodonosa; eje 46.63 ± 1.98 % de la rama, sólido y recto; química: ácidos úsnico y salazínico.

Variación.– La variación de esta especie puede ser apreciada en el hábito de crecimiento del talo, los soralios y las fibrillas. El hábito de crecimiento varía de arbustivo a péndulo. Los soralios pueden ser superficiales o ligeramente tuberculados, su superficie puede variar de plana, convexa o ligeramente excavada, así como la forma de circular a irregular. Las fibrillas pueden ser cortas o espínulas, o largas; en ocasiones las espínulas pueden disponerse en el conocido "fish-bone pattern", pero las largas casi siempre están distribuidas de manera irregular en el talo.

Características distintivas.– U. madeirensis puede ser distinguida de otras especies por la pigmentación negra que se extiende con frecuencia desde la base del tronco hasta la base de las ramas principales, por la combinación anatómica de corteza opaca y gruesa, médula compacta y eje grueso y por la constante presencia de ácido salazínico como sustancia diagnóstica. En particular, U. madeirensis contrasta con la especie arbustiva U. subfloridana, que también presenta una base negra, en que en ésta última el pigmento no se extiende a las ramas principales; los soralios son pequeños, planos y confluentes, y tiene una química totalmente diferente: ácidos escuamático, tamnólico y baeomicésico.

Distribución y ecología.– U. madeirensis tiene una distribución discontinua en Europa, Norteamérica y Macaronesia (Clerc 1991; Halonen et. al. 1998) En México las localidades donde ha sido colectada son escasas y dispersas en los estados de Chihuahua, Durango, Hidalgo, Veracruz, Chiapas y en Oaxaca donde fue encontrada en un número mayor de localidades. Crece en la corteza de diferentes árboles en bosques mixtos de Pinus-Quercus con elementos de Alnus o Juniperus, entre 1600 y 2850 msnm. No ha sido colectada en bosque de Abies, puro o mixto

Usnea setulosa Mot. Lich. Gen. Usnea Stud Monogr. Pars. Syst. 2: 313 1938.
TIPO: Cuba, Loma del Gato, 900 m, 1935. Hioram. (holotipo, LUBL).

Talo verde olivo obscuro, arbustivo a péndulo, 11.5 cm de longitud, ramificación dicotómica anisótoma o simpodial, con ramas paralelas, con un punto de fijación al sustrato; tronco recto, triangular (más ancho en la base) o continuo con la rama principal, 6 mm de largo, café obscuro a negro con tintes anaranjados, con pocas grietas transversales (4/0.5 cm); ramas 0.639 ± 42.26 mm de diámetro, cilíndricas, poco o no segmentadas, agudizándose gradualmente hacia la punta; segmentos cilíndricos; ápices largos, delgados a capilares, ramificados a 90° y 45°; papilas ausentes o escasas, indistintas; tubérculos y fibérculos ausentes; fibrillas escasas, muy largas y finas (hasta 25 mm), distribuidas irregularmente; pseudocifelas ausentes o raras, transversalmente oblongas, delgadas; soralios orignados en la corteza, localizados a todo lo largo de las ramas secundarias, terminales y fibrillas, superficiales, pocos ligeramente levantados, planos, puntiformes, muy rara vez agrandados, sin margen, separados, a veces totalmente confluentes; isidiomorfos ausentes o escasos, más frecuentemente en los soralios que en la corteza; corteza 24.82 ± 1.74 % de la rama, opaca, sin grietas; médula 17.36 ± 1.53 % de la rama, compacta, algodonosa, a veces incospicua; eje 57.76 ± 2.13 % de la rama, sólido y recto; apotecios ausentes; química: ácidos úsnico y salazínico.

Variación.– U. setulosa parece tener muy poca variación entre los ejemplares recolectados hasta ahora en México. Los soralios varían ligeramente de superficiales a ligeramente levantados y aunque generalmente son puntiformes, en algunos casos se observan soralios más grandes, sin embargo, nunca son mayores a la mitad del diámetro de la rama sorediada. En cuanto a la segmentación del tronco, se observó un ejemplar extremo con 15 grietas/0.5 cm.

Características distintivas.– Los rasgos distintivos de U. setulosa son los soralios, el patrón de ramificación y los ápices o terminales. Los soralios puntiformes y separados, muy abundantes en toda la longitud de las ramas, con escasos y pequeños isidiomorfos o carentes de los mismos. El patrón de ramificación en el cual predomina la rama principal, con las ramas secundarias ramificándose en un solo lado y creciendo paralelamente. Finalmente, las terminales largas y capilares no se observan en ninguna otra especie del agregado artificial U. subloridana-U. madeirensis.

Distribución y ecología.– Especie cortícola reportada por Motyka (1938) para México, San Salvador, Panamá, Colombia, Cuba, Brasil, República Dominicana, Jamaica y Perú. Recientemente, en México ha sido colectada en bosques mixtos de Pinus-Quercus-Abies, bosque mesófilo y en localidades donde Quercus se desarrolla como vegetación secundaria en los estados de Chiapas, Durango-Sinaloa, Hidalgo, Jalisco, Michoacán y Veracruz a una altitud de 1000 a 2825 msnm.

Usnea subfloridana Stirton

Scott. Naturalist 6: 294. 1882.

TIPO: Scotland, Killin, 19.7.1881, leg.? (BM). Química: ácidos úsnico y thamnólico.

U. comosa (Ach.) Vain. Lectotipo: Suecia, 1857C (H-ACH). Química: ácidos úsnico, thamnólico e hipothamnólico.

Talo verde olivo, 5.5-9 (11) cm de longitud, arbustivo, dicotómico isótomo, ramas divergentes, densamente ramificado, un punto de fijación; tronco bien desarrollado, más ancho en la base, hasta 6 mm de longitud, café obscuro con tonalidades naranja a negro, con pocas grietas transversales 4/0.5 cm; ramas 1.15 ± 0.128 mm de diámetro, cylíndricas, agudizándose gradualmente hacia las puntas; segmentos cilíndricos, ápices cortos y gruesos, y largos y finos, ramificados a 60°, deformados cuando están densamente isidiados, papilas indistintas, abundantes o no, regularmente distribuidas en las ramas; tubérculos generalmente pequeños, pocos grandes; fibérculos escasos; fibrillas largas y finas hasta de 10 mm de largo, distribuídas irregularmente, a veces con pequeñas espínulas alrededor de los soralios, algunas permanentes; pseudocifelas ausentes; soralios originados en la corteza y en fibérculos, en ramas secundarias y terminales, superficiales a ligeramente tuberculados, mayormente planos a ligeramente excavados, pocos son convexos, puntiformes, si se agrandan casi nunca son mayores que la mitad del diámetro de la rama donde se desarrollan, circulares a irregulares, la mayoría sin margen, si éste se presenta es muy delgado e inconspicuo, separados, rara vez parcialmente confluentes, algunos talos con soralios P+ amarillo a anaranjado, soradios granulares; isidiomorfos numerosos, en soralios jóvenes y maduros; corteza 20.21 ± 1.14 %, opaca a ligeramente brillosa; médula 43 54 ± 2.79 %, densa a compacta, algodonosa; eje 36.23 ± 2.50 %, sólido y recto; apotecios extremadamente raros, sólo se observó uno subterminal en un ejemplar; química: ácidos úsnico, escuamático, tamnólico y/o baeomycésico, a veces únicamente ácido úsnico.

Variación.– La combinación química de los talos varía, la forma y densidad de los soralios también es variable, así como la densidad de los isidiomorfos.

Características distintivas.– Aunque variables, los soralios en U. subfloridana son característicamente pequeños, no confluentes, regulares y más isidiados comparados con los de U. madeirensis y U. wasmuthii. La presencia de los ácidos escuamático, tamnólico y/o baeomycésico distingue a U. subfloridana de estas dos especies.

Distribución y ecología.– U. subfloridana es una especie cortícola que se desarrolla desde las zonas boreales y templadas de Alaska y Canadá hasta México (Motyka 1936-1938; Hale 1979; Halonen et. al. 1998; McCune y Geiser 1997). En Europa es muy abundante en Inglaterra y es considerada como una de las especies más tolerantes a la contaminación atmosférica (James et al. 1992).

En México su distribución es discontinua en bosque de coníferas de Chihuahua, Nuevo León, Colima-Jalisco y Veracruz, concentrándose en los bosques de Abies del Estado de México y el Distrito Federal. El espectro altitudinal de U. subfloridana es de 1500 a 3650 msnm, los forofitos más comunes son Pinus, Abies, Quercus y Alnus.

Usnea wasmuthii Räs.

Fletch. Estlands I., Suom. Tidenknd. Taim. 34 (4):17-19 (1931).

TIPO· Rusia, Esthonia, Tallinna, Kakumäem en Picea excelsa, 13-7-1908. Wasmuthii (holotipo?H).%C%M%A: 13 5/14.5/44 (talo A), 9.5/11./58 (talo B); química: ácidos úsnico y barbático.

Talo verde olivo obscuro, arbustivo, hasta 9 cm de longitud, más o menos rígido, rara vez flácido, poco o densamente ramificado; ramificación dicotómica anisótoma, ramas divergentes, con un punto de fijación al sustrato; tronco más ancho en la base, a veces atenuado, o también continuo con la rama principal, 5-10 mm largo, negro, con finas grietas longitudinales en la base; ramas 1.01 ± 47.65 mm de diámetro, cilíndricas, agudizándose gradualmente hacia las puntas; segmentos cilíndricos, rara vez ligeramente constreñidos en los extremos; ápices laxos y más o menos largos, a veces sinuosos, ramificados a 90°; papilas indistintas, distribuidas irregularmente; tubérculos escasos; fibrillas cortas (3-5 mm) espinulosas y largas (10-15 mm), distribuidas irregularmente en el talo, escasas, permanentes; pseudocifelas ausentes; soralios originados en la corteza, en ramas secundarias, terminales y en fibrillas, superficiales a ligeramente excavados, planos a cóncavos, pequeños, longitudinalmente oblongos a circulares, a veces irregulares, con o sin margen, parcialmente confluentes, a veces se les observa oblicuamente alrededor de la rama; isidiomorfos pequeños escasos y largos abundantes, especialmente en los ápices, en soralios inmaduros y maduros, algunos tienen las puntas negras; corteza 19.89 ± 0.95 % de la rama, opaca, no agrietada; médula 44.80 ± 1 87 % de la rama, heterogénea, compacta, densa y a veces laxa, generalmente algodonosa y brillante; eje 35.30 ± 1.73 % de la rama, sólido y recto, apotecios ausentes; picnidios raros (observados sólo en un ejemplar); química: ácidos úsnico y salazínico y una sustancia desconocida café C: 5.

Variación.— La médula es compacta por debajo la corteza, hacia el eje se vuelve densa e incluso laxa, aunque nunca llega a ser tan ancha como en las especies del complejo U. fragilescens. Algunos ejemplares carecen de soralios bien desarrollados y en su lugar presentan estados iniciales de desarrollo en los cuales se asemejan a pseudocifelas oblongas y lineales.

Características distintivas.— Clerc (1987b) menciona como una característica típica de U. wasmuthii las finas grietas longitudinales en la base del tronco. Sin embargo en los ejemplares mexicanos dichas grietas no son tan abundantes ni conspicuas como en los ejemplares europeos. Hasta ahora, estas grietas no se han observado en ninguna otra especie.

U. wasmuthii y U. madeirensis presentan la misma combinación química pero se distinguen porque en la primera especie la pigmentación negra del tronco no se extiende a las ramas principales, la frecuencia de grietas transversales en el tronco no es tan alta como en la segunda especie; los soralios oblongos de U. wasmuthii no se observan dentro de la variación de los soralios de U. madeirensis. Finalmente U. wasmuthii es una especie arbustiva que no ha sido observada con talos péndulos como es el caso de U. madeirensis.

Otra especie con base negra es U. subfloridana, la cual frecuentemente crece mezclada junto con U. wasmuthii y aunque se distingue de ella en los soralios y en la química, hay ocasiones en que la distinción entre ambas no es posible por la existencia de morfos con "la química equivocada", es decir, la morfología corresponde a U. subfloridana pero la química a U wasmuthii o viceversa Clerc (1992). Esto ha sido interpretado por Clerc como posibles híbridos vegetativos, y ha sido observado en otros grupos como en el agregado U. fragilescens entre U. cornuta s. lat. y U. brasiliensis.

Distribución y ecología.— Motyka (1936-1938) menciona la ocurrencia de esta especie en Eurasia, James et. al. 1992 la confirma para Inglaterra y el norte de Europa. Distintos reportes en Norteamérica se basaron en ejemplares correspondientes a U. substerilis o U. lapponica por lo que fue excluida de las especies de Usnea de Columbia Británica, Canadá (Halonen et al. 1998).

En México, U. wasmuthii está limitada a regiones de alta montaña en el Eje Neovolcánico Transversal, entre 2950 y 3900 msnm en el Pico de Orizaba, Cofre de Perote, Sierra Nevada, La Malinche, Nevado de Toluca, Ajusco y Contreras

Especies pigmentadas de Usnea

Las especies pigmentadas de Usnea para México que a continuación se incluyen en esta sección no representan un grupo natural. Son especies con talos arbustivos o péndulos, apoteciados y sorediados y/o isidiados que presenta pigmentos corticales y/o medulares, cuya naturaleza es desconocida en la mayoría de los casos. Los caractereres morfológicos, anatómicos y químicos las separan una de la otra. Esta agrupación obedece a fines prácticos y no sugiere una relación filogenética entre las especies incluidas.

Se incluyen la descripción y distribución geográfica de: Usnea mutabilis Stirton, Usnea rubicunda Stirton, Usnea sanguinea Swinscow y Krog y Usnea baileyi Striton (Zahlbr.) s. lat., representante del subgénero Eumitria. Otras especies pigmentadas descritas en diferentes secciones de este trabajo son: las especies péndulas U. ceratina, U cristatula y U mexicana; y las especies arbustivas U cirrosa y U. wirthii del complejo U. fragilescens.

Usnea mutabilis Stirton

Scot. Natur. 6: 107 (1881).

TIPO: U S.A. Alabama, Cedar villa, Mrs. Hawley (holotype, BM).

Talo verde amarillo claro, arbustivo, no rígido, densamente ramificado, dicotómico anisótomo o isótomo, ramas divergente, talo con un punto de fijación; tronco recto o bifurcado, hasta 3 mm de largo, del mismo color que las ramas principales; ramas agudizándose lentamente hacia las puntas; segmentos cilíndricos; ápices cortos y gruesos a medianos y finos, ramificados a 90° o 45°; papilas ausentes; tubérculos pequeños e irregularmente distribuidos en ramas principales y secundarias; fibérculos ausentes; fibrillas cortas (1-2 mm de largo), irregularmente distribuidas en el talo, pseudocifelas ausentes; soralia orignados en la corteza, mayormente superficiles, pocos ligeramente tuberculados, planos a ligeramente convexos, pequeñs y puntiformes a alargados y circulares, nunca mayores a la mitad del diámetro de la rama donde se desarrollan, sin margen, separados a totalmente confluentes, producen soradios granulares; corteza 19 3% (n=3) ligeramente brillosa, médula 40.34 % (n=3) compacta y algodonosa, pigmenta de color rojo vino claro a obscuro, no siempre continuo; eje 40.34% (n=3), sólido y recto, a veces del mismo color que la médula; apotecios ausentes; química: únicamente ácido úsnico o con ácidos grasos del grupo del ácido murólico.

Variación.– Los caracteres variables de U. mutabilis son los soralios y la distribución del pigmento en la médula. Los soralios varían de puntiformes a alargados, éstos últimos resultado de la fusión de lo soralios pequeños (Clerc 1994). El pigmento medular a veces se observa más concentrado en un área central entre dos zonas más pálidas.

Cracterísticas distintivas.– U. mutabilis se caracteriza por el color rojo vino de la médula, los soralios puntiformes y planos, y la presencia del complejo de ácido murólico como principa metabolito secundario Esta especie se distingue de U. ceratina; que también tiene la médula pigmentada, porque el color del pigmento medular nunca es tan obscuro en U ceratina, los soralios de ésta última son tuberculados, más grandes y no confluentes, y tiene ácido difractaico, nunca ácido murólico, como metabolito secundario principal U. hirta tiene ácido murólico, pero carece de pigmento en la médula y es abundantemente isidiada. Finalmente, otra especie que presenta ácidos grasos, particularmente ácido bourgéonico, es U. esperantiana la cual tiene soralios ligeramente planos, a veces excavados, y circulares, no puntiformes y carece de pigmento medular.

Distribución y ecología.— U. mutabilis fue reportada para México por Bouly De Lesdain (1933), posteriormente Motyka (1936-1938) la reporta para España, norte de Africa, Estados Unidos, Canadá, México y Costa Rica.

En un estudio reciente, Clerc (1994) puntualiza que la distribución de esta especie es disjunta en el hemisferio norte principalmente en regiones con clima de tipo mediterráneo como España, Francia y Portugal en Europa, Marruecos en África y California en Estados Unidos. También la menciona para Japón.

Recientemente ha sido recolectada únicamente en Baja California. Los registros de Bouly De Lesdain (1933) y de Motyka (1936-1938) la menciona para Veracruz y Guerrero pueden tratarse de ejemplares jóvenes con soralios poco desarrollados de U. ceratina, los cuales sin el conocimiento de los metabolitos secundarios, podrían ser confundidos fácilmente con U. mutabilis.

Usnea rubicunda Stirton.

Scott. Nat. 6: 102 (1881). M. Holmes (BM).

Talo rosa coral, verde amarillento rojizo o café naranja, de 4 a 12 cm de largo, arbustivo a péndulo, a veces decumbente, más o menos rígido, poco o densamente ramificado, ramificación dicotómica isótoma o anisotóma, ramas divergentes, uno o más puntos de fijación; tronco del mismo color que la rama principal, negrusco al contacto con el punto de fijación, rara vez anulado, indistinto o bien desarrollado, pero generalmente de 3 a 5 mm de largo, rara vez más (8 mm), principalmente recto, a veces bifurcado, frecuentemente con pseudoraíces: ramas 1.00 ± 0 34 mm de diámetro, cilíndricas, agudizándose gradualmente hacia las puntas; segmentos circulares en sección transversal y cilíndricos a ligeramente fusiformes en sección longitudinal; ápices laxos y largos, a veces espinulosos, ramificados a 90°, ocasionalmente cortos, pero sólo un ejemplar los tenía realmente cortos y gruesos; papilas ausentes o presentes, indistintas a verrucosas, escasas o abundantes, distribuidas irregularmente en las ramas principales y secundarias; tubérculos pequeños, frecuentemente erosionados, abundantes a lo largo de todo el talo, fibérculos abundantes o escasos en las ramas principales y secundarias; fibrillas ausentes o numerosas, cortas y espinulosas, o largas y finas hasta de 10 mm de largo, de ddistribución irregular, rara vez arregladas como "vértebras de pez", a menudo más abundantes hacia los ápices, también creciendo a través de los soralios, frecuentemente se desprenden; pseudocifelas ausentes, soralios originándose en la corteza, tubérculos erosionados, fibérculos, o en las grietas entre los segmentos de las ramas, principalmente a los largo de ramas secundarias y terminales y en fibrillas; superficiales o tuberculados, rara vez excavados, la mayoría planos, pocos convexos a capitados, pequeños, cuando se agrandan rara vez son mayores que la mitad del diámetro de la rama sorediada, más comúnmente separados o parcialmente confluentes, pocos totalmente confluentes, producen soredios granulares; isidiomorfos pequeños o largos, corticales o en soralios, en ocasiones son producidos de manera secundaria en soralios muy viejos, corteza 25.47 ± 0.74 % de la rama (n=71), mayormente brillante, a veces vítrea, comúnmente muy dura y quebradiza, lisa o rugosa, rara vez con grietas profundas, con pigmento rojo-naranja o rojo brillante, este pigmento puede ser continuo o en manchas pequeñas e irregulares, a veces se puede observar un patrón bandeado de coloración, especialmente en las ramas más jóvenes, el pigmento está más concentrado en las partes basales del talo o de las ramas principales, en los ejemplares papilados se le observa en mayor concentración justo debajo de las papilas; médula 32.48 ± 1.18 % de la rama (n=71), compacta a densa, algodonosa, en ocasiones con aspecto farináceo; eje 2.03 ± 1.05 % de la rama (n=71), sólido y recto; apotecios ausentes o escasos; química: ácidos úsnico, estíctico, norestíctico, conestíctico, criptoestíctico, y/o salazínico; algunos ejemplares presentan la combinación de ácido úsnico y ácidos grasos.

Variación.— U rubicunda es conocida como una especie muy variable (James 1979), el talo puede fijarse al sustrato por medio de uno o dos "holdfasts". Las ramas pueden ser moderadamente delgadas a robustas Halonen et al (1998) reportan que U. rubicunda tiene base pálida, sin embargo, todos los ejemplares mexicanos presentan una base del mismo color que las ramas principales, aunque la concentración del pigmento varía, en ocasiones las partes basales presentan un color más intenso que el resto del talo. Algunos talos tienen un patrón ligeramente bandeado verde y rojo, sobre todo en las fibrillas y en ramas jóvenes. En los ejemplares papilados, al remover las papilas, es posible observar el pigmento más concentrado, como una pequeña mancha, en la área expuesta. La superficie cortical también cambia, generalmente es lisa a ligeramente rugosa. Sin embargo en algunos ejemplares se observa muy agrietada, con escamas grandes separadas por médula evertida entre las fracturas, como si ésta hubiera crecido y quebrado irregularmente la corteza. Otro rasgo inconstante de la superficie cortical es la presencia de depresiones pequeñas en las ramas secundarias o terciarias.

El desarrollo de soralios e isidiomorfos varía considerablemente. Los soralios son superficiales a tuberculados debido a que se originan planos en la corteza y en grietas o encima de pequeños tubérculos; la mayoría son pequeños, aunque en pocos ejemplares llegan a sobrepasar la mitad del diámetro de la rama donde se desarrollan. La superficie de los soralios es generalmente plana, aunque también se observan algunos soralios convexos o capitados. Cuando los soralios presentan isidiomorfos, éstos son principalmente de dos tipos, muy pequeños y de puntas redondeadas, y otros más bien largos y de puntas agudas. Los isidiomorfos también pueden ser corticales y son fácilmente confundibles con fibrillas jóvenes. James (1979) presenta una descripción detallada de los propágulos vegetativos de U. rubicunda.

Características distintivas.— El rasgo más característico de U. rubicunda es el pigmento cortical rojo-anaranjado.

Distribución y ecología.— U. rubicunda está ampliamente distribuida en regiones tropicales y templadas de Europa, Japón, China, Hawai, Nueva Zelanda, Australia, este y sur de África, sur de Norteamérica, norte de Sudamérica, las Islas Ascensión, Azores y Canarias (James 1979), este de África (Swinscow y Krog 1979). En Norteamérica, ha sido reportada para Columbia Británica en Canadá (Halonen et al. 1998), California, Carolina del Norte y Tennessee en Estados Unidos y Baja California en México (Clerc y Herrera-Campos 1997).

En México es una de las especies más ampliamente distribuidas. Es principalmente cortícola, aunque ocasionalmente también puede crecer en rocas. Tiene una amplitud altitudinal de 40 a 2825 m, creciendo en una numerosos de tipos de vegetación desde matorral xerófilo costero, bosque subtropical, bosque mesófilo y bosque de coníferas. Los estados en donde esta especie ha sido recolectada son: Baja California, Baja California Sur, Coahuila, Colima, Distrito Federal, Estado de México-Michoacán, Guanajuato, Hidalgo, Jalisco, Michoacán, Nuevo León, Nayarit, Puebla, San Luis Potosí, Sinaloa, Oaxaca y Veracruz.

Usnea sanguinea Swinscow y Krog.
The Lichenologist 11 (3): 207-253 (1979).

Talo rosa coral, verde amarillento rojizo o café naranja, de 4 a 12 cm de largo, arbustivo a péndulo, a veces decumbente, más o menos rígido, poco o densamente ramificado, ramificación dicotómica isótoma o anisotóma, ramas divergentes, uno o más puntos de fijación; tronco del mismo color que la rama principal, negrusco al contacto con el punto de fijación, rara vez anulado, indistinto o bien desarrollado, generalmente de 3 a 5 mm de largo, rara vez más (8 mm), principalmente recto, a veces bifurcado, frecuentemente con pseudoraíces: ramas 1 00 ± 0.34 mm de diámetro, cilíndricas, agudizándose gradualmente hacia las puntas, segmentos circular en sección transversal y cilíndricos a ligeramente fusiformes en sección longitudinal; papilas ausentes o presentes, indistintas a verrucosas, escasas o abundantes, distribuidas irregularmente en el talo; tubérculos pequeños, abundantes a lo largo de todo el talo, fibérculos abundantes o escasos en las ramas principales y secundarias; fibrillas ausentes o numerosas, cortas y espinulosas, o largas y finas hasta de 10 mm de largo, distribución irregular, rara vez arregladas como "vértebras de pez", a menudo más abundantes hacia los ápices, también creciendo a través de los soralios, frecuentemente se desprenden; corteza 25.47 ± 0.74 % de la rama, brillante, a veces vítrea, comúnmente muy dura y quebradiza, lisa o "arrugada", rara vez con grietas profundas, con pigmento rojo-naranja o rojo brillante, este pigmento. puede ser continuo o en manchas pequeñas e irregulares, a veces más concentrado en las partes basales del talo o de las ramas principales, en los ejemplares papilados se le observa en mayoar concentración justo debajo des las papilas; médula 32.48 ± 1.18 % de la rama, compacta a densa, algodonosa, en ocasiones con aspecto farináceo; eje 2.03 ± 1.05 % de la rama, sólido y recto, apotecios abundantes; química: ácidos úsnico, estíctico, norestíctico, conestíctico, criptoestíctico, y/o salazínico; algunos ejemplares presentan la combinación de ácido úsnico y ácidos grasos.

Variación.— U sanguinea presenta la misma variación que U. rubicunda de la cual es la especie primaria (Swinscow y Korg 1979), con excepción de las características de los soralios, de los cuales carece U. sanguinea, por lo tanto el lector es referido a la descripción de U. rubicunda.

Distribución y ecología.— U. sanguinea tiene una distribución geográfica conocida mucho más restringida que U. rubicunda; sólo ha sido reportada para el este de África (Swinscow y Krog 1979) En México, se ha colectado en menor número de localidades que U. rubicunda y únicamente en bosque mixto de coníferas y encinos y en bosque mesófilo de montaña, en los estado de Chiapas, Hidalgo, Oaxaca y Veracruz.

Usnea baileyi (Stirton) Zahlbr. s. lat. Denkschr. math.-naturw. Kais. Akad. Wiss Wien 83, 182 (1909).
Eumitria baileyi Stirton Scottish Naturalist 6, 100 (1881). Lectotipo Rogers y Stevens (1988). Australia, Queensland, prope Brisbane, sin fecha F M. Baileyi, 164 (BM).

Talo verde olivo claro, arbustivo a supéndulo, hasta 12 cm de largo, rígido y quebradizo, moderada a densamente ramificado, ramificación dicotómica anisótoma o isótoma, ramas divergentes, talo con un punto de fijación; tronco recto, hasta 3 mm de largo, del mismo color que el talo o café rojizo; ramas 1.14 ± 0 79 mm, no segmentadas, agudizándose lentamente hacia las puntas, circulares en sección transversal y de cilíndricas a ligeramente fusiformes en sección longitudinal, ápices largos y laxos, a veces espinulados, ramificados a 90° o 45°; papilas ausentes o escasas, indistintas a verrucosas; tubérculos muy pequeños, irregularmente distribuidos en las ramas principaless y secundarias, frecuentemente erosionados; fibrillas muy abundantes, cortas (1 mm) o largas (hasta 15 mm de largo), regularmente distribuídas alrededor de las ramas principales y secundarias, frecuentemente más abundantes en las parte basales, persistentes; pseudocifelas ausentes; soralios en ramas principales, secundarias, terminales y en fibrillas, originados principalmente en la corteza, también en papilas o tubérculos erosionados, superficiales a ligeramente levantados, planos, puntiformes a circulares, separados, sin margen, producen soradios farináceos; isidiomorfos escasos a moderadamente abundantes, corticales y en soralios, en soralios muy jóvenes los isidiomorfos son pequeños con puntas redondeadas, en soralios más viejos los isidiomorfos son más largos y agudos; corteza 12.85 ± 0.83 % del diámetro de la rama principal (n=22), brillante a vítrea; médula 6.21 ± 0.74 % del diámetro de la rama principal (n=22), compacta, algodonosa, pigmentada de anaranjado claro a color óxido obscuro , a veces amarillo, regularmente el pigmento es continuo, rara vez en pequeñas manchas; eje 80 92 ± 1.35 % del diámetro de la rama principal (n=22), recto hueco y con hifas laxas que a veces son amarillas o anaranjadas; apotecios ausentes; química: ácido úsnico con o sin ácido difractaico y eumitrinas

Variación.– El hábito de crecimiento varía entre arbustivo, subpéndulo a péndulo. La concentración del pigmento medular varía de tal manera que la médula puede ser de un anaranjado muy pálido, casi rosa, a un color obscuro casi café. Los isidiomorfos varían de pequeños redondeados a largos y agudos. Ambos pueden corresponder con los propágulos vegetativos observados en Neuropogon, los primeros probablemente correspondan a los pseudoisidios y los segundos a los isidios verdaderos (Walker 1985).

Características distintivas.– Morfológicamente indistinguibles entre sí, U. baileyii, U. perplectata Mot. y U. vainioi Mot. pueden ser diferenciadas fácilmente del resto de las especies estudiadas, por el eje central hueco, que las ubican en el subgénero Eumitria. Entre ellas, la presencia de eumitrinas distingue a U. baileyii de U. perplectata y U. vainioi las cuales carecen de eumitrinas pero tienen ácido difractaico, además, de acuerdo con Rogers y Stevens (1988), la única especie que produce soralios verdaderos es U. vainioi.

Sin embargo, los ejemplares examinados muestran características mezcladas, que hacen difícil la separación de las tres especies, por lo que es necesario un estudio más detallado de un mayor número de ejemplares para describir la variación de estos taxa y decidir si son conespecíficos o no.

Distribución y ecología.– Las especies del complejo U. baileyi están distribudas en zonas tropicales del mundo en Australia, el Archipiélago Filipino, África , Sudamérica, México, Florida en Estados Unidos (Motyka 1936-1938; Hale 1979; Rogers y Stevens 1988).

En México U. baileyi s. lat. ha sido colectada en bosque mesófilo de montaña y en bosques de pinos adyacentes en los estados de Chiapas, Hidalgo, Jalisco y Oaxaca.

A la fecha no se ha realizado ningún estudio extensivo de las especies fértiles del género Usnea. Los trabajos existentes son estudios aislados o locales como los de Asahina (1968; 1970) sobre U. florida y otras especies fértiles de Japón; Swinscow y Krog (1979) incluyen varias especies apoteciadas en su trabajo sobre las especies fruticosas del este de África; Clerc (1984a) sobre U florida en Europa, Tavares (1987) compara diferentes especies fértiles del este de Estados Unidos, Stevens (1992) estudia de los complejos U. scabrida y U. molliuscula para Australia y en 1998, Tavares y Sanders reportan una clave preliminar para las especies arbustivas fértiles del suroeste de Estados Unidos

El estudio de las especies fruticosas apoteciadas de Usnea en Norteamérica, ha sido enfocado directamente a las diferentes razas químicas con algunas consideraciones sobre su distribución (Hale 1962; Fiscus 1972) Queda por estudiar dicha variación química en relación con las características morfológicas y anatómicas. En México, sólo existen menciones aisladas de algunas especies fértiles (Álvarez y Guzmán-Dávalos 1988; Coutiño y Mojica 1985; Gómez-Peralta 1992; Ruiz-Oronoz; Welden y Guzmán 1978; Welden et al. 1979), pero dado que no se ha efectuado ningún análisis químico, se requiere verificar todas las especies reportadas ya que este grupo está integrado por agregados de especies polimórficas muy difíciles de caracterizar sin el conocimiento de los metabolitos secundarios diagnósticos.

El grupo comprende especies con talos arbustivos, generalmente rígidos, de 3 a 15 cm de largo con un punto de fijación al sustrato o "holdfast", tronco comúnmente bien desarrollado, aunque en algunos casos indistinto, negro, concoloro o más pálido que la rama principal; ramificación dicotómica isótoma, anisótoma o simpodial; ramas segmentadas o no, principalmente cilíndricas, en ocasiones ligeramente poligonales y menos frecuentemente irregulares; los segmentos son cilíndricos, moderadamente angulares, hinchados o irregulares; papilas, tubérculos y fibérculos presentes o no, variables en forma y distribución en el talo; fibrillas cortas y espinulosas, y/o largas y finas, regular o irregularmente distribuidas en las ramas, rara vez completamente ausentes; pseudocifelas ocasionalmente presentes, alargadas a nivel de corteza o en pequeñas costillas o estriaciones; foveolas raras; la corteza puede ser opaca, brillante o rara vez vítrea, delgada o gruesa, ocasionalmente rojiza; médula generalmente compacta o densa, en algunos casos laxa, algodonosa, con pigmentos subcorticales o periaxiales rosa, amarillo o anaranjado; eje moderada o considerablemente grueso, de vez en cuando pigmentado de rojo, sólido y recto; apotecios terminales, subterminales, laterales o seriales, muy variables en tamaño, en algunas especies alcanzan los 2.5 cm de diámetro;

disco pruinoso, casi siempre regular y con fibrillas en el margen, éstas varían en tamaño y densidad, el envés del apotecio es liso o rugoso, con o sin espínulas o fibrillas; esporas simples, hialinas, elipsoidales, química variable en distintas combinaciones, algunas de las cuales pueden corresponder a especies bien definidas y otras sólo a quimiotipos de una misma especie

Debido a que se requiere de una revisión mundial de las especies fértiles del género para obtener conclusiones sobre el estatus taxonómico de estos grupos, las decripciones que a continuación se presentan de los agregados o especies mexicanas son preliminares. Esta agrupación es artificial y está basada en características morfológicas y anatómicas gruesas que pueden o no estar relacionadas con las características químicas y no intenta ilustrar relaciones filogenéticas entre las especies o agregados tratados. Algunas de estas especies han sido mencionadas con anterioridad en este trabajo, por lo que sólo se referirá al lector a la sección correspondiente.

1.- Complejo U ramillosa.- Incluye especies con talos de 2-4 cm a 8-10 cm de largo; tronco recto o atenuado, a veces bifurcado, corto o bien desarrollado, concoloro, rojizo o parcialmente negro o café, ramas con segmentos hinchados en sección longitudinal y teretes en sección transversal; corteza delgada y brillante o vítrea, médula principalmente laxa y eje delgado, espínulas muy cortas y abundantes o fibrillas medianas dispersas en el talo, papilas presentes o no, ocasionalmente puede haber foveolas deformando las ramas. Los compuestos secundarios más frecuentemente encontrados en este agregado son ácidos úsnico, salazínico, protocetrárico, norestíctico, estíctico y galbínico.

Entre las especies que integran este agregado se pueden citar U. ramillosa s. str., U. cirrosa, algunas especies sudamericanas como U. meridionalis Zahlbr., U. steinerii Zahlbr., U. andina Mot. y U. subelegans (Vain.) Mot., así como el morfotipo de U. cirrosa reportado para el suroeste de Estados Unidos por Tavares y Sanders (1998). Las especies reportadas anteriormente para México son. U. andina (Bouly de Lesdain 1933, Motyka 1936-1938), U. cirrosa (Motyka 1936-1938; Coutño y Mojica 1985) y U. subelegans (Bouly de Lesdain 1933; Motyka 1936-1938). A la fecha, sólo se ha confirmado la ocurrencia en el país de U. cirrosa. U. ramillosa s. str. es un nuevo registro para México. Las descripciones de estas dos especies se presentan en la sección correspondiente al agregado U. fragilescens.

2.- Complejo U. strigosa .- Está compuesto por especies con talos hasta de 15 cm de largo, rígidos o no, poco o densamente ramificados; tronco principalmente recto, bien desarrollado, a veces conspicuamente más grueso que las ramas principales, en ocasiones con grietas transversales, concolor con el resto del talo, más claro o rojizo, nunca negro; ramas cilíndricas, con diámetro constante, segmentos cilíndricos, acostillados o ligeramente trapezoidales en sección longitudinal, circulares, alados o irregulares en seccón transversal; espínulas y fibrillas abundantes; corteza gruesa brillante y frecuentemente dura; médula compacta ocasionalmente densa, a veces con pigmento rosa o rojo; eje moderadamente grueso; química· ácidos úsnico, barbático, difractaico, bourgeónico, norestíctico, estíctico y salazínico.

En el este de Estados Unidos, este agregado está compuesto por especies como U strigosa (Ach.) A. Eaton, U erinacea, U. evansii Mot. y U. tristis. (Hale 1979; Tavares 1987; Clerc comunicación personal). Se incluyen tentativamente U arbusculiformis Mot. y U. cristatula Mot.

U. evansii y U. tristis no se conocen para México, mientras que U. strigosa ha sido registrada en varias ocasiones (Bouly de Lesdain 1929 como el sinónimo U. florida (L.) Hoffm. var. strigosa Ach. (González de la Rosa y Guzmán 1976; Tavares y Sanders 1998); Motyka 1936-1938; Welden y Guzmán 1978; Welden et al. 1979; Gómez-Peralta 1992). En ocasiones se menciona en la literatura la presencia de un pigmento medular rojo óxido o rosado (Hale 1962, Dey 1978; González de la Rosa y Guzmán 1976). Es probable que algunos de los registros mexicanos correspondan a U. cristatula la cual frecuentemente tiene la médula rosa, pero contiene ácido difractaico como sustancia secundaria principal a diferencia de U. strigosa que contiene ácido norestíctico. Por otra parte, en la península de Baja California, se han colectado algunos ejemplares apoteciados con pigmento rojo óxido en la médula y abundantes espínulas que parecen ser afines a U. subcornuta. La confirmación de los mismos se hará como parte del estudio de la flora liquénica del Desierto Sonorense

U. erinacea fue reportada para México por Vainio (1926), Bouly de Lesdain (1933) y Motyka (1936-1938). Tavares (en Tavares y Sanders 1998) menciona que esta especie se caracteriza por la presencia de un pigmento rojo-naranja en las células corticales parecido al de U. rubicunda, sin embargo en este trabajo no se ha sido observado.

U. arbusculiformis es mencionada para México por Motyka (1936-1938) y por Ruiz-Oronoz (1937). González de la Rosa y Guzmán (1976) consideran que los registros de Ruiz-Oronoz corresponden a U. strigosa, sin embargo no hacen mención de las características que distinguen a ambas especies En el presente trabajo, U. arbusculiformis es separada de U. strigosa, s. str., en la clave, por la presencia de ácido bourgeónico y otros ácidos grasos como rangifórmico, protoliquesterínico y caperático.

3.- Complejo U. florida.- Talo amarillo o verde claro, frecuentemente las ramas principales son más obscuras que las secundarias, arbustivo, hasta 10 cm de longitud, tronco recto, pocas veces atenuado, bien desarollado, con pocas grietas transversales, pigmentación negra que se torna café hacia la base de las ramas principales; ramas cilíndricas, cuyo diámetro disminuye ligeramente hacia las puntas; segmentos cilíndricos; papilas indistintas en las partes basales de las ramas y mejor desarrolladas y más abundantes cerca de los apotecios; fibrillas cortas espinulosas (1-5) y largas, (hasta 10 mm); corteza opaca a ligeramente brillante, gruesa; médula densa y algodonosa; eje grueso; sólido y recto, química: ácidos úsnico, escuamático, tamnólico y lecánorico. Las especies que hasta ahora han sido identifiadas en México son U. florida (L.) Wigg. emend. Clerc y U. lecanorica W. Culb , C Culb. y Fiscus

En sentido amplio, U. florida ha sido reportada para México en varias publicaciones (Nash et al. 1998), así como sus diferentes quimiotipos (Fiscus 1972),en algunos casos se establece que las deterinaciones son dudosas (Weber 1993), por lo tanto, es la primera vez que se confirma U. florida s. str. (Clerc 1984) para México. El quimiotipo del grupo U. florida que contiene ácido lecanórico fue mencionado por primera vez por Fiscus (1972) y U lecanorica es reportada para México por Culberson et al (1983).

4.-Complejo U. arizonica.- Talos de rigidez moderada, tronco recto, indistinto, bifurcado o continuo con la rama principal, base concolor al resto del talo, o negra parcial o totalmente, sin extenderse a las ramas principales, con pocas grietas transversales; ramas de delgadas a moderadamente gruesas, cilíndricas, diámetro más o menos constante; segmentos cilíndricos; papilas abundantes, fibrillas irregularmente distribuidas en el talo, en ocasiones más abudantes en la base de las ramas secundarias; corteza opaca y gruesa; médula compacta y algodonosa; eje grueso; química: ácidos úsnico y salazínico como sustancias principales, connorestíctico, estíctico, norestíctico, consalazínico y conestíctico como accesorias.

De acuerdo con Tavares y Sanders (1998), algunas de las especies de este complejo son: U. arizonica Mot , U. subfusca Mot., y U. retifera Mot. Clerc (comunicación personal) considera que U arizonica es parte del complejo U. rigida, sin embargo ninguna de las especies que lo integran (Clerc 1984) ha sido reportada para México, ni tampoco U. retifera.

U arizonica y U. subfusca han sido registradas para varias localidades del país (Álvarez y Guzmán-Dávalos 1988, Bouly de Lesdain 1933; Coutiño y Mojica 1982, 1985; Culberson et al. 1983; Gómez-Peralta 1992; Motyka 1936-1938; Ruiz-Oronoz 1937).

Morfotipo 14.-Talo verde olivo amarillento, los ejemplares de herbario observados presentan un color café rojizo resultado de la herborización, en ambos casos las ramas principales son más obscuras que las secundarias; hábito péndulo, hasta 15 cm de longitud, con un punto de fijación, ni rígido ni flácido, densamente ramificado; dicotómico isótomo, ramas divergentes al principio y luego paralelas, tronco recto o bifurcado, hasta 5 mm, frecuentemente anillado, concoloro o parcialmente negro; ramas delgadas, Clave para las especies mexicanas de Usnea

1. Talos péndulos........ ....SECCIÓN A
1 Talos erectos a subpéndulos............ 2
   2. Talos saxícolas .. .. SECCIÓN B
   2. Talos cortícolas........................... 3
3. Pigmento cortical, medular o axial presente ....SECCIÓN C
3 Pigmento ausente........................ 4
   4. Talos sorediados y/o isidiados, rara vez apoteciados 5
   4 Talos apoteciados, nunca sorediados ni isidiados...................... ....SECCIÓN D
5. Segmentos de las ramas de ligera a conspicuamente hinchados o rregulares ....SECCIÓN E
5. Segmentos de las ramas cilíndricos, nunca hinchados . ...SECCIÓN F

SECCIÓN A. Talos péndulos

1. Soralios y/o isidios presentes; apotecios ausentes o raros (los soralios a veces inmaduros, parecidos a pequeñas pseudocifelas circulares) 2
1. Soralios, isidios o estructuras similares a pseudocifelas ausentes; apotecios de escasos a abundantes 11

   2. Eje central ocráceo o café amarillento . . .. U. mexicana
   2. Eje central no ocráceo ni café amarillento 3

3 Médula con pigmento rosa y/o amarillo (a veces muy tenue); CK+ amarillo-naranja brillante, ácido difractaico presente... .. .. U. ceratina
3. Médula sin pigmento; CK- o CK+, nunca con ácido difractaico 4

   4. Médula K-, P+ rojo-naranja; ácido protocetrárico como metabolito secundario principal........................... 5
   4. Médula K+ amarillo o rojo, P+ amarillo o rojo, o K- P-; ácido protocetrárico ausente...... 6

5. Corteza vítrea y dura; base a menudo con tintes rojos ....U. subscabrosa
5 Corteza opaca y blanda, base a menudo con tintes anaranjados...........7. U. hesperina

6. Segmentos de las ramas claramente acostillados o angulados; médula muy delgada (10-15%) y compacta; eje muy grueso (45-65%)... 7

6. Segmentos de las ramas sin costillas ni alas, cuando mucho estriados, médula más gruesa (20-30%), densa a compacta; eje más delgado (30-40%) 8

7. Segmentos de las ramas claramente alados, de forma trapezoidal; márgenes erosionados, abriéndose longitudinalmente y exponiendo la médula; ácido norestíctico presente .... U. angulata

7. Segmentos de las ramas no alados pero claramente acostillados, márgenes no abiertos longitudinalmente, médula no expuesta; ácido salazínico o ácido caperático presente . .. . U. transitoria

8. Ramas regular y conspicuamente segmentadas, con áreas de regeneración muy distintivas entre los segmentos... 9

8. Ramas irregularmente segmentadas, sin áreas de regeneración entre los segmentos. 10

9. Con pseudocifelas conspicuas, a menudo en grupos en las ramas principales;grietas longitudinales presentes; corteza vítrea y dura; ácido estíctico o metabolitos secundarios no identificados UP1 y UP2... U. malmei

9. Sin pseudocifelas conspicuas ni grietas longitudinales, corteza blanda de opaca a brillante; ácido salazínico presente... .. . .U. merrillii

10. Ramas irregulares; segmentos ligera o claramente hinchados; soralios sobre tubérculos pequeños; fibrillas de escasas a numerosas, dispuestas irregularmente en las ramas ....U. scabrata

10. Ramas adelazándose hacia las puntas; segmentos cilíndricos; soralios sobre fibérculos; fibrillas numerosas y dispuestas como "vértebras de pez" .. .. U. filipendula

11. Grietas longitudinales con márgenes involutos.. .... 18 U. sp 1

11. Grietas longitudinales sin márgenes involutos 12

12. Ramas distintivamente foveoladas; papilas ausentes; corteza delgada (4-8 %); eje central sinuoso .... U. cavernosa

12. Ramas no foveoladas; papilas comúnmente presentes; corteza más gruesa, eje rara vez sinuoso 13

13. Eje central ocráceo o café amarillento y quebradizo .... U. himantodes
13 Eje central ni ocráceo o café amarillento ni quebradizo 14

14. Médula con pigmento rosa y/o amarillo (a veces muy tenue); CK+ amarillo-naranja brillante, ácido difractaico presente .... U. cristatula
14. Médula sin pigmento, CK- o CK+, nunca con ácido difractaico 15

15. Médula K-, ácido protocetrárico como metabolito secundario principal 16
15. Médula K+ amarillo o rojo, ácido protocetrárico nunca como metabolito secundario principal 17

16. Corteza opaca y blanda; base conspicuamente anillada; con tintes anaranjados .... U. firma
16. Corteza vítrea y dura; base no conspicuamente anillada, con tintes Rojos .... U. vitrea.

17. Segmentos de las ramas claramente acostillados o angulados, médula muy delgada (10-15%) y compacta, eje muy grueso (45-65%) 18
17. Segmentos de las ramas sin costillas ni alas, cuando mucho estriados; médula más gruesa (20-30%), densa a compacta; eje más delgado (30-40%) 19

18. Segmentos de las ramas claramente alados, de forma trapezoidal, márgenes erosionados, abriéndose longitudinalmente y exponiendo la médula; ácido norestíctico presente .... U. alata
18 Segmentos de las ramas no alados pero claramente acostillados, márgenes no abiertos longitudinalmente, médula no expuesta; ácido salazínico o ácido caperárico presente .... U. goniodes

19. Con pseudocifelas conspicuas, a menudo en grupos en las ramas principales; grietas longitudinales presentes, corteza vítrea y dura; ácido estíctico o metabolitos secundarios no identificados UP1 y UP2 .... U. papillata
19. Sin pseudocifelas conspicuas ni grietas longitudinales, corteza blanda de opaca a brillante; ácido salazínico presente .... U. sanctaeritae

SECCIÓN B. Talos saxícolas.

1. Corteza con pigmento rojo, especialmente conspicuo en la parte basal, ramas laterales no constreñidas en la base .... U. rubicunda
1. Corteza sin pigmento rojo, o sólo como pequeñas manchas; ramas laterales constreñidas en la base 2

2. Médula C+ amarillo fuerte o anaranjado, con pigmento rosa en la médula, ácido difractaico presente .... U. ceratina
2. Médula C-, CK-, y K- o K+ rojo anaranjado, sin pigmento en la médula, ácido difractaico ausente 3

3. Médula con pigmento rojo vino; soralios puntiformes, con isidiomorfos numerosos; papilas ausentes; ácidos grasos del grupo del ácido murólico presentes; médula K-, PD- .... U. mutabilis
3. Médula sin pigmento rojo vino; soralios puntiformes o grandes, con o sin isidiomorfos; papilas presentes o ausentes; ácidos grasos del grupo del ácido murólico ausentes; médula comúnmente K+ o PD+ (rara vez ambas reacciones, checar el quimiotipo 5 de U. cornuta s. lat.) 4

4. Médula con pigmento amarillo; ramas laterales claramente constreñidas en la base; corteza brillante; ácido norestíctico o ácido psorómico en los soralios .... U. wirthii
4. Médula sin pigmento amarillo; ramas laterales constreñidas o no en la base; corteza brillante u opaca; ácido norestíctico o ácido psorómico presentes pero no restringidos a los soralios 5

5. Médula K- y P+ rojo-naranja; ácido protocetrárico como sustancia principal 6
5. Médula K- y P+ de amarillo a rojo; ácido protocetrárico nunca como sustancia principal 9

6. Fibérculos grandes con puntas blancas y fibrillas cortas parecidas a isidiomorfos alrededor; soralios ausentes .... U. nashii
6. Fibérculos grandes, sin puntas blancas, sin fibrillas parecidas a isidiomorfos; soralios generalmente presentes 7

7 Ramas laterales claramente constreñidas en la base; talo arbustivo, erecto con ramas divergentes . .. .quimiotipo 6 de U. cornuta

7. Ramas laterales no constreñidas en la base, talo subpéndulo o péndulo con ramas más o menos paralelas 8

8. Corteza distintivamente brillante o vítrea, ramas principales no anilladas .... U subscabrosa

8. Corteza opaca, ramas anilladas, principalmente en la base ....U. hesperina

9. Base negra; soralios grandes, más o menos circulares, al madurar alcanzan el tamaño del diámetro de la rama, a menudo la rodean, ligeramente cóncavos, con pocos isidiomorfos; ramas laterales no contreñidas en la base; sólo ácido salazínico presente ....U. ammannii

9. Base clara o de café a rojiza; soralios irregulares, rara vez alcanzan el tamaño del diámetro de la rama, nunca la rodean, planos o ligeramente tuberculados, con pocos o numerosos isidiomorfos; ramas laterales a menudo ligeramente constreñidas, sólo ácido salazínico presente (checar el quimiotipo 1 de U. cornuta s. lat.) 10

10. Corteza opaca; soralios más o menos tuberculados y convexos almadurar, usualmente alcanzan la mitad del diámetro de la rama o más, con numerosos isidiomorfos en grupos; fibérculos usualmente ausentes....... .... U. halei

10. Corteza brillante o vítrea; soralios más o menos planos, puntiformes, rara vez grandes (sin embargo checar U. dasaea), sobre los fibérculos o no, con o sin isidiomorfos, simples o en grupos; fibérculos de ausentes a numerosos 11

11. Isidiomorfos gruesos, usualmente solitarios, a menudo uno solo sobre un soralio, con puntas negras, siempre presentes; soralios puntiformes, nunca grandes, más o menos tuberculados, numerosos, densamente distribuidos, originándose en fibérculos .... U. amblyoclada

11. Isidiomorfos delgados, en grupos, nunca con puntas negras o ausentes; soralios puntiformes a más o menos agrandados, especialmente en las ramas terminales, más o menos planos, originándose en la corteza

o en fibérculos 12

12. Fibrillas cortas y espinulosas, densa pero irregularmente distribuidas en porciones restringidas de las ramas, rara vez cubriéndolas totalmente, soralios grandes, al madurar alcanzan la mitad de la rama o más, a menudo ligeramente fusiformes, no confluentes; ácido galbínico presente .... U. dasaea
12. Fibrillas usualmente más largas y delgadas, dispersas en todo el talo; soralios puntiformes, a menudo confluentes y cubriendo grandes áreas; ácido galbínico ausente .... U. cornuta s. lat.

SECCIÓN C Talos arbustivos a péndulos, sorediado-isidiados o apoteciados, regularmente con pigmento cortical, medular y/o axial.

1. Eje hueco .... 2 Eumitria
1. Eje sólido o fistuloso 3

2. Eumitrinas presentes, CK-, ácido difractaico ausente .... U. baileyi
2. Eumitrinas ausentes, CK+ amarillo-naranja brillante, ácido difractaico presente (con soralios: U. vainioi) .... U. perplectata

3. Eje central ocráceo o café amarillento, fistuloso .... U. mexicana
3. Eje central no ocráceo ni café amarillento, sólido 4

4. Pigmento cortical rojo o rojo-naranja, continuo o discontinuo, en las ramas o en los apotecios, con o sin pigmento medular o axial 5
4. Sin pigmento cortical, pero con pigmento medular y/o axial 6

5. Pigmento cortical en los apotecios .... U. cirrosa
5. Pigmento cortical en las ramas 7

6. Médula con pigmento rosa y/o amarillo; ocasionalmente eje rojo; CK+ amarillo-naranja brillante; ácido difractaico presente 8
6. Médula únicamente con pigmento rosa o únicamente con pigmento amarillo; eje blanco o amarillo; CK- or CK+, rosa, nunca con ácido

difractaico 9

7. Pigmento cortical continuo, en bandas en las ramas más jóvenes y en las fibrillas..... 10
7 Pigmento cortical discontinuo en pequeñas manchas de densidad variable.......... ... . U wirthii

8 Talos soredio-isidiados, apotecios ausentes o raros................ .... U ceratina
8. Talos nunca soredio-isidiados, siempre apoteciados..... .... U cristatula

9. Médula y/o eje amarillos, a veces muy tenue, nunca con ácido murólico como metabolito secundario principal. .. . . U. wirthii
9. Médula rosa, a veces muy intenso hasta rojo vino, ácido murólico como metabolito secundario principal . ...U. mutabilis

10. Talos soredio-isidiados, apotecios ausentes o raros................. U. rubicunda
10. Talos nunca soredio-isidiados, siempre apoteciados......... .. ... U. sanguinea

SECCIÓN D. Agregados de especies apoteciadas mexicanas de Usnea

1. Talos con pigmento cortical, medular o axial 2
1. Talos sin pigmentos..... 5

2. Pigmento cortical rojo 3
2. Pigmento medular. 4

3. Ramas no constreñidas en la base, segmentos principalmente cilíndricos, pigmento rojo naranja continuo o en bandas, frecuentemente más concentrado en las partes basales del talo .... U. sanguinea
3. Ramas constreñidas en la base, segmentos principalmente hinchados, pigmento rojo vino en el borde del disco apotecial (a veces ausente) y en los picnidios..... ... .U cirrosa

4. Médula con pigmento rosa y/o amarillo (a veces muy tenue); CK+ amarillo-naranja brillante, ácido difractaico presente.............. U. cristatula
4. Médula rojo naranja; CK- o CK+, nunca con ácido

difractaico .... U strigosa s. str.

5. Segmentos de las ramas cilíndricos, corteza gruesa, brillante u opaca, médula densa a compacta, talos arbustivos con terminales cortas o subpéndulos con terminales largas 6
5. Segmentos de las ramas hinchados o irregulares, corteza delgada, brillante o vítrea, médula laxa a densa, talos siempre arbustivos con terminales cortas 11

6. Talos subpéndulos. .. .. Morfotipo 14
6 Talos siempre arbustivos....... 7

7 Base del talo parcialmente negra, del mismo color o más clara que las ramas principales, rojiza o amarillenta........... 9
7 Base del talo totalmente negra 8

8. Ácidos escuamático, tamnólico como metabolitos secundarios principales .... U. florida
8. Ácido lecánorico como metabolito secundario principal .... U lecanorica

9. Base del talo negra sólo al al contacto con el sustrato, corteza opaca y suave. .... U. arizonica s. lat.
9. Base del talo del mismo color o más pálida que las ramas principales, corteza brillante y dura 10

10. Ácido burgeónico como metabolito principal ... . U. arbusculiformis
10. Ácido bougónico nunca como metabolito secundario principal .. .. U. strigosa s. lat.

11. Ramas principalmente hinchadas, espínulas y fibrillas de abundantes a escasas, irregularmente distribuidas en las ramas y al borde de los apotecios, sin cubrirlas por completo 12
11. Ramas principalmente irregulares o angulares, espínulas abundantes cubriendo totalmente las ramas y al borde y el envés de los apotecios .... U. sabrida

12. Médula K-, P+ rojo-naranja; ácido protocetrárico como metabolito secundario principal............ .... U. ramillosa s str.

12. Médula K+ amarillo o rojo, P+ amarillo o rojo, o K- P-; ácido protocetrárico ausente ... . U. ramillosa s. lat.

SECCIÓN E. Agregado U. fragilescens

Talos erectos a subpéndulos, segmentos de las ramas constreñidos, ligera o fuertemente hinchados o irregulares, corteza delgada a moderadamente gruesa, médula laxa a densa, eje delgado a moderamente grueso; soralios variables en forma y tamaño.

1. Soralios y/o isidiomorfos presentes; apotecios ausentes o raros.......... 2
1. Soralios y/o isidiomorfos ausentes, apotecios escasos o abundantes............. 9

2. Soralios pequeños (menos que la mitad del ancho de la rama donde crecen) 3
2. Soralios grandes (más de la mitad del ancho de la rama donde crecen)........... 6

3. Pigmento amarillo en la médula (a veces muy tenue).................. .. . . U. wirthii
3. Pigmento ausente 4

4. Ramas con abundantes espínulas triangulares (a veces ausentes); ácido galbínico como metabolito secundario principal...... .... U. dasaea
4. Ramas sin espínulas triangulares, pero con fibrillas largas o cortas, ácidos salazínico o protocetrárico como metabolito secundario principal................................ .... 5.

5. Segmentos conspicuamente hinchados y/o irregulares en sección longitudinal; comúnmente ramas rígidas y gruesas, corteza delgada (x=8.5%), médula laxa (x=76%), eje delgado (x=15%),ácido protocetrárico como metabolito secundario principal.............................U brasilensis
5. Segmentos no conspicuamente hichados a irregulares; ramas de flácidas a rígidas, delgadas a gruesas; corteza moderadamente gruesa (x= 14%), médula de laxa a densa (x= 63%), eje moderadamente grueso (x= 23.5%); ácido salazínico y otras substancias del grupo del ácido estíctico como metabolitos secundarios prinicpales .... U. cornuta s. str.

6 Soralios circulres de ligeramente levantados a tuberculados,

algunas veces planos, principalmente separados, con margen definido; isidios presentes .... U. fragilescens

6. Soralios superficiales, a veces ligeramente levantados, casi siempre confluentes, ligeramente o muy excavados; margen desgarrado o no, isidiomorfos ausentes............................ 7

7. Soralios profundamente excavados, frecuentemente exponiendo el eje; ácidos protocetrático y/o estíctico como metabolito secundario principal............. U. glabrata

7. Soralios no excavados, o muy ligeramente, nunca exponiendo el eje; ácido bourgeónico como metabolitio secundario principal...... ... ... U. esperantiana

8. Pigmento rojo vino en el borde del disco apotecial; picnidios rojos frecuentes (a veces ausentes), espínulas cortas abundantes ...... U. cirrosa

8. Pigmento y picnidios siempre ausentes, fibrillas medianas oconspicuamente largas de densidad variable 9

9. Segmentos claramente hinchados; tubérculos no conspicuos; ácido protocetrárico como principal metabolito secundario .... U. ramillosa s. str.

9. Segmentos cilíndricos o ligeramente hinchados; tubérculos grandes; ácido criptoestíctico o salazínico como principal metabolito secundario ... . U. jamaicensis

SECCIÓN F. Agregado Usnea subfloridana-Usnea madeirensis

Talos erectos a subpéndulos, segmentos de las ramas cilíndricos, corteza gruesa, médula densa a compacta, eje grueso; soralios variables; apotecios raros o ausentes .

1. Abundantes pseudocifelas isidiadas o soralios isidiados, ácidos grasos comúnmente como metabolitos secundarios principales .... U hirta

1. Pseudocifelas ausentes, soralios isidiados o no; ácidos grasos nunca como metabolitos secundarios principales 2

2. Soralios principalmente puntiformes, circulares, nunca o rara vez excavados 3

2. Soralios variables, frecuentemente excavados 5

3. Soralios confluentes, con frecuencia densamente isidiados, a veces P+ amarillo a anaranjado; ácidos escuamático, tamnólico y/o baeomisésico como metabolitos secundarios principales.. ....U. subfloridana

3. Soralios separados o parcialmente confluentes, no densamente isidiados, P-; ácido salazínico o norestíctico como metabolitos secundarios principales........... 4

4. Apices largos, finos y capilares; ácido salazínico como metabolito secundario principal............... ....U. setulosa

4. Apices cortos y gruesos, rara vez finos, nunca capilares; ácido norestíctico como metabolito secundario principal .... U. sp 2

5. Soralios circulares, ligera a profundamente excavados, a veces exponiendo el eje, parcial o totalmente confluentes; ácidos salazínico, norestíctico y/o difractaico como metabolitos secundarios ....U. fulvoreagens

5. Soralios de forma variable, ligeramente excavados o no, nunca exponiendo el eje, ácido salazínico como metabolito secundario principal 6

6. Soralios circulares a irregulares; tronco con numerosas grietas transversales, sin finas grietas longitudinales, con pigmentación negra se extiende frecuentemente a la base de las ramas principales; médula compacta........................ ....U. madeirensis

6. Soralios oblongos a circulares; tronco con pocas grietas transversales, pero con finas grietas longitudinales, la pigmentación negra nunca se extiende a la base de las ramas principales; médula variable..... ..U. wasmuthii

DISCUSIÓN

En sistemática se trata de establecer relaciones detectando semejanzas, comparando las diferencias, con la idea de que mientras más se parezcan dos entidades, más cercanas pueden ser. A su vez, es deseable construir sistemas de clasificación, lo más naturales posibles, que reflejen esas relaciones y su evolución (Jahns 1989 b; Tehler 1996). Sin embargo, uno de los aspectos más complicados de la taxonomía es la definición de los caracteres diagnósticos y la interpretación de su variación, ya sean éstos morfológicos, anatómicos, químicos o moleculares.

El estudio del género Usnea no está excento de controversia en la interpretación de los caracteres. Por ejemplo, en el caso de los caracteres químicos, Culberson et al. (1983) describieron una nueva especie, Usnea lecanorica Cul., Culb., y Fiscus basándose en la presencia de ácido lecanórico, distinguiéndola de U. arizonica, morfológicamente similar, que contiene ácido salazínico. Mientras que Stevens (1992) reagrupó las especies del complejo australiano U. scabrida-U. molliuscula en tan sólo dos especies con distintas subespecies de acuerdo a diferencias en morfología relacionadas con distintas regiones climáticas. En este nuevo arreglo, la química no fue considerada importante porque los compuestos encontrados correspondieron a ß-orcinol depsidonas. Para Swinscow y Krog (1979) los compuestos secundarios detectados en las especies fruticosas del este de Africa no fueron de valor taxonómico a menos que sean considerados en combinación con la morfología y/o la pigmentación de los talos. En estudios más recientes, los caracteres químicos han sido considerados como parte de la combinación de características que defininen a las especies, sin asignar ninguna categoría taxonómica a los quimiotipos morfológicamente indistinguibles (Clerc y Herrera-Campos 1997; Herrera-Campos et al. 1998; Halonen et al. 1998).

También los caracteres anatómicos de Usnea han sido interpretados de diferente manera, en particular el grosor de la corteza, de la médula y del eje. Motyka (1936-1938) incluyó los tamaños respectivos, en micrómetros, en las descripciones de las especies. Asahina (1956) reconoció la importancia de las dimensiones de estos estratos en la caracterización de las especies y propuso un método para calcular y graficar el "radio stratorum" tomando el grosor de la corteza como la unidad. Sin embargo, Swinscow y Krog (1979) consideraron impreciso el uso del grosor de la corteza, aunque reconocieron su utilidad en la determinación de U. picta (Steiner) Mot. Para otros autores Clerc 1984a, 1987; Clerc y Herrera-Campos 1997; Herrera-Campos et al. 1998), el grosor relativo de cada uno de estos estratos con respecto al diámetro total de la rama principal fue de utilidad en la distinción de las especies. En el presente trabajo se muestra, en el análisis de

U. cornuta s. lat. (Clerc 1987) y U brasiliensis, la utilidad de la química para identificar grupos morfológicamente cercanos que pueden distinguirse con estudios más detallados de anatomía y/o distribución geográfica.

La distribución geográfica de las especies estudiadas representa una importante adición a la distribución mundial conocida del género, no obstante, se reconoce que para algunas de ellas la distribución reportada aquí pudiera ser más amplia si la recolección se extendiera a otros tipos de vegetación. También cabe la posibilidad de que la distribución sea diferente en el caso de que la conceptualización de las especies se modifique. De cualquier manera, el conocimiento de la distribución geográfica de las especies mexicanas de Usnea no sólo resulta importante en su caracterización, sino que posibilita la realización de estudios biogeográficos que pongan de manifiesto el papel de México como corredor y/o barrera en la distribución de los líquenes, como ha sido documentado para otro tipos de organismos (Dávila y Herrera-MacBryde 1997, Delgadillo 1983, 1987, 1992, 1995; Graham 1993; Ramamoorthy et al 1993; Rzdowski 1981, 1991, 1993, Toledo 1993; Toledo y Ordóñez 1997).

Una aportación importante es la contribución a la definición de los caracteres diagnósticos y a la interpretación de su variación en Usnea. Sin embargo, aún quedan por definir nuevos caracteres -como características himeniales y/o de las acosporas- que sean útiles en el estudio de las especies fértiles. También es necesaria la evaluación de caracteres menormente utilizados en la sistemática del género, como la estructura microscópica de las células corticales (Tavares 1987, 1997; Tavares y Sanders 1998), y el estudio de la ontogenia de los propágulos vegetativos, la cual puede ayudar en el entendimiento de agregados como el de U. fragilescens.

A través del análisis de los caracteres taxonómicos, los métodos cladísticos permiten la inferencia de las homologías, de patrones filogenéticos y la clasificación de grupos monofiléticos (De Luna y Mishler 1996; Villaseñor y Dávila 1996). Como en todos los estudios taxonómicos, el trabajo realizado por los autores citados a lo largo de esta tesis y ésta misma, ha implicado la selección de distintos tipo de caracteres diagnósticos con diferentes estados que pueden ser analizados usando métodos cladísticos y de sistemática molecular para proponer hipótesis de relaciones filogenéticas de las especies estudiadas y construir un sistema de clasificación que las refleje.

ÁLVAREZ, I Y L. GUZMÁN-DÁVALOS. 1988. Nuevos registros de líquenes de Jalisco Revista Mexicana de Micologia 4: 89-56

ASAHINA, Y. 1956. Lichens of Japan. Vol. III Genus Usnea. Research Institute for Natural Resources Shinjuku, Tokio.

ASAHINA, Y 1968. New localities of Usnea florida (L) Wigg Journal of Japanese Botany 43 (3): 65-69.

ASAHINA, Y. 1970. On son Formosan Usneae with terminal peltate apothecia. Journal of Japanese Botany 45 (5): 129-133.

ASCASO, C , D H. BROWN, Y C. RAPSH. 1985. Ultrastructural studies or desicated lichens. En Brown, D. H. (ed.) Lichen physiology and cell biology. Plenum Press. New York.

AWASTHI, G. 1985. Two new commbinations in the genus Usnea. Current Science 54· 353-354.

AWASTHI, D. D. Y G, AWASTHI. 1985 Typifiction of Usnea compresa Taylor. The Lichenologist 17:309-311.

AWASTHI, G. 1986. Lichen Genus Usnea in India. Journal of Hattori Botany Laboratory 61· 333-421.

BOULY DE LESDAIN 1929. Lichens du Mexique. Deuxième Supplément. Annales de Crytogamie Exotique 2: 217-254

BOULY DE LESDAIN 1933. Lichens du Mexique. Troisième Supplément. Annales de Crytogamie Exotique 6· 99-130.

BRODO, I. 1978. Changing concepts regarding chemical diversity in lichens. Lichenologist 10: 3-11.

BRODO, I. 1973. Substrate ecolgy En The Lichens. Ahamadjian, V. y M. Hale (eds.), pp 401-442. Academic Press, New York.

BRODO, I. 1986. Interpreting chemical variation in lichens for systematic purposes . The Bryologist 89: 132-138 .

CARLIN, G. 1986 The chemical strains of Usnea lapponica and U. glabrescens in Sweden. Graphis Scripta 1. 29-32.

CLERC, P. 1984a. Contribution a la revision de la systematique des usnees (Ascomycotina, Usnea) d'Europe I.-Usnea florida (L.) Wigg. emend. Clerc . Cryptogamie, Bryologie et Lichenologie 5: 333-360.

CLERC, P. 1984b. Usnea wirthii – A new species of lichen from Europe and North Africa. Saussurea 15: 33-36.

CLERC, P. 1987a. Systematics of the Usnea fragilescens aggregateand its distribution in Scandinavia. Nordic Journal of Botany 7: 479-495.

CLERC, P. 1987 b. On the morphology of soralia in the genus Usnea. Bibliotheca Lichenologica 25: 99-102 .

CLERC, P. 1991. Usnea madeirensis Motyka (ascomycète lichénisé): une espèce méconnue de l'Europe et de l'Amèrique du Nord. Candollea 46: 427-438.

CLERC, P. 1992. Some new or interesting species of the genus Usnea (lichenised Ascomycetes) in the British Isles. Candollea 47: 513-526.

CLERC, P. 1994. Comment Usnea mutabilis Stirton, une espèce nord-américaine, se cache en Europe sous le nom d'Usnea morocana Motyka. Une contribution à la systématique du genre Usnea (ascomycètes lichénisés). Bull. Soc. linn. Provence 45: 309-316.

CLERC, P. 1997. Notes on the genus Usnea Dill. ex Adanson. Lichenologist 29: 209-215.

CLERC, P. Y DIEDERICH, P. 1991. Usnea wirthii Clerc new to North America and the British Isles. Lichenologist 23 (4): 405-407 .

CLERC, P. Y HERRERA-CAMPOS, M. A. 1997. Saxicolous species of the genus Usnea in North America. The Bryologist 100: 281-301.

COUTIÑO, B. Y MOJICA, A. 1982. Estudio de líquenes corticolas de bosque mesófilo de montaña y de coníferas del estado de Hidalgo. Boletín de la Sociedad Mexicana de Micología 17: 166-180.

COUTIÑO, B Y MOJICA, A. 1985. Líquenes de la región del Cofre de Perote-Xalapa. Revista Mexicana de Micología 1.379-399.

CULBERSON, C. 1986 a. Biogenetic relationships of the lichen substances in the framework of systematics. The Bryologist 89: 91-98.

CULBERSON, C. Y K. AMMANN. 1979. Standardmethode zur Dünnshichtchromatographie von Flechtensubstanzen. Herzogia 5: 1-24.

CULBERSON, C. Y A JOHNSON. 1982 Substitution of methyl tertbutyl ether for diethyl ether in standardized thin-layer chromatographic method for lichen products. Journal of Chromatography 238: 438-487.

CULBERSON, C. Y A. JOHNSON. 1988. Gene flow in lichens. American Journal of Botany 75: 1135-1139.

CULBERSON, W L 1969. Chemical and botanical guide to lichen products. Chapel Hill. The University of Carolina Press

CULBERSON, W. L. 1970. Chemosystematics and ecology of lichen-forming fungi. Annual Review of Eccology and Systematics 1: 153-170.

CULBERSON, W. L. 1986 b. Chemistry and sibling speciation in the lichen-forming fungi: Ecological and biological considerations. The Bryologist 89: 123-131 .

CULBERSON, L. W Y C. F. CULBERSON 1967. Habitat selection by chemically differentiated races of lichens. Science 158: 1195-1197.

CULBERSON, W. L. Y C. F. CULBERSON 1970. A phylogenetic view of chemical evolution in the Lichens. The Bryologist 73: 1-31.

CULBERSON, W. L., C. CULBERSON Y S. FISCUS. 1983. A new lecanoric acid-producing Usnea from Mexico. The Bryologist 86: 254-256.

CZECZUGA, B. 1979. Investigations on carotenoids in lichens II. Members of the Usneaceae family. Nova Hedwigia. XXXI, 1+2: 349-356.

CZECZUGA, B Y H S. OSORIO. 1989. Investigations on carotenoids in lichens. XX. Astaxanthin, the dominant carotenoid in some lichens from Uruguay. Israel Journal of Botany 38: 115-120.

CZECZUGA, B Y D. H. S. RICHARDSON 1989. Carotenoids in some lichen species from Ireland. Lichenologist: 21: 363-367.

DAVILA, P. Y O. HERRERA-MACBRYDE. 1997. In Davis, S. D., V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos & A. C. Hamilton (eds.) Centres of Plant Diversity. A guide and strategy for their conservation. The Wordl Wide Fund for Nature (WWF) and IUCN The World Conservtion Union.

DELGADILLO, C. 1983. Notas sobre la diversidad briológica de Mexico. Revista de la S ociedad Mexicana de Historia Natural 44: 93-97.

DELGADILLO, C. 1987. Moss distribution and the phytogeographical significance of the Neovolcanic Belt of Mexico. Journal of Biogeography 14: 69-78.

DELGADILLO, C. 1992. Moss interchange: Bryofloristic similarities between Mexico and Colombia and the phytogeographical role of the Central American bridge. The Bryologist 95: 261-265.

DELGADILLO, C. 1993. Diversity in the Mexican Bryoflora, pp. 365-377. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

DELGADILLO, C. 1995. Neotropical moss floras. Species common to North and South America. Tropical Biology 10: 1-6.

DE LUNA E Y B. MISHLER. 1996. El conepto de homología filogenética y la selección de caracteres taxonómicos. Boletín de la Sociedad Botánica de México 59. 131-146.

DEY J. P. 1978. Fruticose and foliose lichens of the high-mountain areas of the Southern Appalachians. The Bryologist 81: 1:93.

ELIX, J. A. 1996. Biochemistry and secondary metabolites. En Lichen Biology. T. H Nash III (ed.), pp 154-180. Cambridge University Press. New York

ERIKSSON, O. Y HAWKSORTH, D. (1983-91). Outline of Ascomycetes. Systema Ascomycetum 1-9.

FAHSELT, D. 1996. Individuals, populatoins aand population ecology, pp. 181-198. En T H. Nash (ed.), Lichen Biology. Cambridge University Press, New York.

FEIGE, G. B. Y T. LUMBSCH. Some types of chemical variation in lichens. Cryptogamic Botany 5: 31-35.

FISCUS, S. A. 1972. A survey of the chemistry of the Usnea florida group in North America 75 (3). 299-304.

GIBERT, A. 1935. Líquenes del Valle de México. Tesis de Maestría. Facultad de Ciencias. UNAM. México.

GÓMEZ-PERALTA, M. 1992. Contribución al conocimiento de los líquenes del campo geotérmico Los Azufres, Michoacán, México. Acta Botánica Mexicana 18: 31-53.

GUZMÁN G. Y M. E GONZÁLEZ DE LA ROSA. 1976. Estudios sobre los líquenes de México, IV. Especies de Usnea citadas por Motyka en 1936-1938 de México. Boletín de la Sociedad Mexicana de Micología 10: 65-70.

GRAHAM, A. 1993 Historical factors and biological diversity in Mexico, pp 109-127 In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

HAFELLNER, J. 1988. Principles of classification and main taxonomic groups. En Handbook of Lichenology. M. Galum (ed.), pp 41-55. CRC Press, Boca Raton, Florida , 41-52 .

HALE, M , JR. 1979. How to Know the Lichens. 2nd. Edition. Wm C. Brown. Dubuque, IA.

HALE, M., JR. 1962. The chemical strains of Usnea strigosa. The Bryologist 65 (4): 291-294 .

HALE, M., JR. 1965. A Revisvion of the Lichen Genus Hypotrachyna (Parmeliaceae) in Tropical America. Smithsonian Contributions to Botany 25: 1-73.

HALE, M., JR. 1983. The biology of lichens. London. Edward Arnold

HALONEN, P. Y A PUOLASMAA. 1995. The lichen genus Usnea in eastern Fennoscandia. I. Usnea hirta. Annales Botanici Fennici 32: 127-135.

HALONEN, P., P. CLERC, T. GOWARD, I. M. BRODO, Y K. WULFF. 1998. Synopsis of the genus Usnea (lichenized ascomycetes) in British Columbia, Canada. The Bryologist 101: 36-60.

HAWKSWORTH, D. L. 1976. Lichen chemotaxonomy. En Lichenology: Problemsand Progress. D. H. Brown, D. L., Hawksworth y R. H. Bailey (ed.), pp 139-184. Academic Press, London.

HAWKSWORTH, D. L. Y D. J. HILL. 1984 Lichen-forming fungi . London. Blackie.

HERRERA-CAMPOS, M. A., P CLERC Y T. H. NASH III. Pendulous species of Usnea from the temperate forests in Mexico. The Bryologist 101: 303-329.

JAHNS, H. M. 1989 a. Problems in lichen taxonomy. Abh. natruwiss. Ver. Hamburg 28: 247-252.

JAHNS, H. M 1989 b. Systematicis, morphology and ecology of lichenized fungi. Progress in Botany 50: 267-283.

JAMES, P. W. 1979 Notes on Usnea rubiginea and Usnea rubicunda. Lichenologist 11:322-323.

JAMES, P. W., P. CLERC Y W. PURVIS. 1992. Usnea, pp. 620-629. En O W. Purvis, B. J. Coopins, D. L. Hawksworth, P W. James y D. M. Moore (eds.), The Lichen Flora of Great Britain and Ireland. Edinburgh. Natural History Museum and British Lichenological Society.

JØRGENSEN, M. 1977. Foliose and fruticose lichens from Tristan da Cunha. I, Mat. - Naturv. Klasse Skrifter Ny Serie No. 36.

KILIAS, H. 1987. Protein characterization as a taxonomic tool in lichen systematics. Bibliotheca Lichenologica 50: 267-283.

KROG, H. 1976. Lethariella and Protousnea, two new lichens of the Parmeliaceae. Norwegian Journal of Botany 23.83-106.

KROG H. 1982. Evolutionary trends in the foliose and fruticose lichens of the Parmeliaceae. Journal of the Hattori Botany Laboratory 52: 303-311

LUTZONI, F. Y R. VILGALYS. 1995 a. Omphalina (Basidiomycota, Agaricales) as a model system for the study of coevolution in lichens. Cryptogamic Botany 5: 71-81.

LUTZONI, F. Y R, VILGALYS. 1995 b. Integration of morphologicaland molecular data sets in estimating fungal phylogenies Cryptogamic Botany 73 (Supp. 1): S649-S659.

MATTSON, J. Y T. H. LUMBSCH. 1989. The use of the species pair concept in lichen taxonomy. Taxon 38 (2): 238-241.

MCCUNE, B. Y L. GEISER. 1997. Macrolichens of the Pacific Northwest. Oregon State Univesity Press. Corvalis.

MCCUNE, B. Y T. GROWARD. 1995. Macrolichens of the Northern Rocky Mountains. Mad River Presss Inc. Eureka.

MOTYKA, J. 1936-1938. Lichenum Generis Usnea. Studium Monographicum, Pars Systematica. 1937. Leopoli.

MOTYKA, J. 1947. Lichenum Generis Usnea. Studium Monographicum. Pars Generalis. Annales Universitatis Mariae Curie-Sklodowska 1: 9 Sección C 277-470.

NASH III, T. H., B. RYAN & M. A. HERRERA-CAMPOS. Mexican Lichen Catalog. http://www.lichen.la.asu.edu.

POELT, J. 1972. Die taxonomishce Behandlung von Artenpaaren bei den Flechten Botanika Notiser 125: 77-81.

POELT, J. 1973 Appendix A: Classification. En The Lichens. V. Ahmadjian y M. Hale (eds.), pp 599-632. New York. Academic Press.

POELT, J 1994. Different species types in lichenized ascomycetes. En Ascomycete Systematics: Problems and Perspectives. D. L. Hawksworth (ed.), pp 273-278. Plenum Press. New York.

RAMAMOORTHY, T. P., R. BYE, A. LOT & J. FA. 1993. Introduction. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

ROBINSON, H. 1975. Considerations on the evolution of lichens. Phytologia 32: 407-413

ROGERS, R. W. 1989. Chemical variationand the species concept in lichenized ascomnycetes. Botanical of the Linnean Society: 101, 229-239.

ROGERS, R. Y G. STEVENS. 1988. The Usnea baileyi complex (Parmeliaceae, lichenised ascomycetes) in Australia. Australian Systematic Botany 1: 355-361.

RUIZ-ORONOZ, M 1937. Contribución al conocimiento de los líquenes del Valle del Mezquital. Anales del Insituto de Biología. UNAM 8: 117-131.

RZEDOWSKI, J. 1981. La Vegetación de México. Ed. Limusa. México.

RZEDOWSKI, J. 1991. El endemismo en la flora fanerogámica mexicana: una apreciación analítica preliminar Acta Botánica Mexicana 15: 47-64.

RZEDOWSKI, J. 1993 Diversity, and Origins of the Phanerogamic Flora of Mexico, pp. 129-143. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

SAS 1990 SAS/STAT User's Guide. Version G, 4 th ed. vol. I. SAS Institute, Cary, NC. USA.

SCOTT, G D. 1973. Evolutionary aspects of symbiosis. En V. Ahmadjian y M. Hale (eds.), The Lichens. New York. Academic Press.

STEVENS, G. N. 1990. Usnea himantodes Stirton and its synonyms. Lichenologist 22: 409-412.

STEVENS, G. N. 1991a. The tropical Pacific species of Usnea and Ramalina and their relationship to species in other parts of the world. En Tropical lichens: Their systematics, conservation and ecology D J. Galloway (ed.), pp Systematics Association no. 43. Calredon Press, Oxford.

STEVENS, G. N 1991b Usnea elixii, a new lichen species from Australia. Lichenologist 23: 53-56.

STEVENS, G. N. 1992. Variation in thallus morphology in response to climatic, and geographical distribution in an Usnea complex. Lichenologist, 24: 229-248.

SWINSCOW, T Y H. KROG. 1974. Usnea subgenus Eumitria in East Africa. Norwegian Journal of Botany 21: 165-185

SWINSCOW, T. Y H. KROG 1975. The Usnea undulata aggregate in East Africa. Lichenologist 7: 121-138.

SWINSCOW, T. Y H. KROG. 1976. The Usnea articulata aggregate in East Africa. Norwegian Journal of Botany 23. 261-268.

SWINSCOW, T. Y H. KROG. 1976. The Usnea bornmuelleri aggregate in East Africa. Norwegian Journal of Botany 23: 23-31

SWINSCOW, T Y H. KROG. 1978. Pendulous species of Usnea in East Africa. Norwegian Journal of Botany 25: 221-241.

SWINSCOW, T Y H. KROG. 1979. The fruticose species of Usnea subgenus Usnea in East Africa. Lichenologist 11: 207-252.

TAVARES, I. 1987. The taxa of Usnea (lichenes) described by Michaux from Eastern North America. Mycotaxon 30: 39-68.

TAVARES, I.. 1997. A preliminary key to Usnea in California. Bulletin of the California Lichen Society 4: 19-23.

TAVARES, I. Y W. SANDERS. 1998. Preliminary report on the short, apotheciate taxa of Usnea in the Southwestern United States. En Lichenographia Thomsoniana. North American Lichenology in Honor of John W. Thomson. M. G. Glenn, R. C. Harris, R. Dirig y M. S. Cole (eds.), pp 171-185. Mycotaxon LTD. New York.

TEHLER, A. 1982. The spececies pair concept in lichenology. Taxon 3 (4): 708-717.

TEHLER, A. 1995 a. Arthoniales phylogeny as indicated by morphologicaland rDNA sequence data. Cryptogamic Botany 5, 82-97.

TEHLER, A. 1995 b. Morphological data, molecular data,and total evidence in phylogenetic analysis. Cryptogamic Botany 73 (Supp. 1): S667-S676.

TEHLER, A. 1996. Systematics, phylogyand classification. En Lichen Biology. T. H. Nash III(ed.), pp 217-239 Cambridge University Press. New York.

TENHUNEN, J. D., O.L. LANGE, S. HAHN, R. SIEGWOLF Y S. F. OBERBAUER. The ecosystem of poikilohidric tundra plants. En Arctic Ecosystems in a Chanign Climate. F. S Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver y J. Svoboda. pp 213-237.

TOLEDO, V. & M. J. ORDONEZ. 1993. The biodiversity scenario of Mexico. A review of terrestrial habitats, pp. 757-777. In Ramamoorthy, T. P., R. Bye, A. Lot & J. Fa (eds.), Biological Diversity of Mexico. Origins and Distribution. Oxford University Press. Oxford.

TOLEDO. V., J RZEDOWSKI & J. VILLA-LOBOS 1997. Regional Overview: Middle America, pp. 97-124. In Davis, S. D., V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos & A. C. Hamilton (eds.) Centres of Plant Diversity. A guide and strategy for their conservation. The World Wide Fund for Nature (WWF) and IUCN The World Conservtion Union.

VAINIO, E. A. 1926. Lichenes Mexicani a F. M. LIEBMANN A 1841-43 collecti, in Museo Hauniensi asservati. Cansk Botanisk Arkiv 4: 1-25.

VILLASEÑOR, J. L. Y P DÁVILA. 1996. Introducción a la Metodología Cladística. Facultad de Ciencias, UNAM. México.

WALKER, F. J. 1985. The lichen genus Usnea subgenus Neuropogon. Bulletin of the British Museum Natural History (Botany) 13: 1-130.

WEBER, W. A. 1993. The Lichen flora of Guadalupe Island, Mexico, pp. 65-71. En F. J. Hochberg (ed.), Recent Advances on the California Islands. Santa Barbara Museum of Natural History. Santa Barbara.

WELDEN A. L. Y G. GUZMÁN. 1978. Lista preliminar de los hongos líquenes y mixomicetos de las regiones de Uxpanapa, Coatzacoalcos, Los Tuxtlas, Papaloapan y Xalapa (parte de los estados de Veracruz y Oaxaca). Boletín de la Sociedad Mexicana de Micología 12: 59-102.

WELDEN, A. L., L. DÁVALOS Y G. GUZMÁN. 1979. Segunda lista de los hongos, líquenes y mixomicetos de las regiones de Uxpanapa, Coatzacoalcos, Los Tuxtlas, Papaloapan y Xalapa (Mexico). Boletín de la Sociedad Mexicana de Micología 13: 151-161