appearing flat on upper surface, with yellow pruina, with thin algal sheath, evanescent; **Ascomata:** immersed, punctiform, perithecioid, 0.1-0.25 in diam., usually appearing darker than wart; **true exciple:** colorless; **hymenium:** hyaline; periphysoids 20-30 µm long, branched and easily detached in sectioning; without paraphyses. **asci:** 100-160 long and swollen, *I*+ pale blue, eventually dissolving when spores are mature, multispored; **ascospores:** hyaline, simple, ellipsoid, 3-4.5 x 1.5-2 µm; **Pycnidia:** not found; **Secondary metabolites:** not investigated.

**Substrate and ecology:** on wood, leather, rocks, cow manure, or decaying lichens; **World distribution:** North America and Europe; **Sonoran distribution:** mainland of southern California, presently known only from one collection in Santa Monica Mountains, non-lichenized on decaying *Lecanora muralis*.

**Notes:** *Thelocarpon intermediellum* is a rare species of North America and Europe. It is characterized by its yellow pruina, its usual lack of a photobiont, the presence of periphysoids, and the lack of paraphyses.

**Thelocarpon lichenicola** (Fuckel) Poelt & Hafellner, Phyton, Horn 17: 69 (1975).


**Habit:** not lichenized, lichenicolous; **Thallus:** absent, not lichenized; **Ascomata:** initially perithecioid, later expanding and appearing apothecioid, solitary, immersed to adnate, 0.1-0.35 mm in diam.; **disc:** pale orange-brown, concave to plane; **true exciple:** pale greenish yellow-brown; **hymenium:** hyaline, 65-75 µm tall, hymenial gel non-amyloid; paraphyses: simple to sparingly branched, c. 1 µm thick, without apical thickening, without periphysoids; **asci:** flask-shaped, thin-walled, apex slightly thickened, 60-65(-75) x 12-14 µm, with an amyloid tube structures (*I*+ pale blue with a darker blue apex), multispored; **ascospores:** hyaline, simple, ellipsoid, 4-6(-7.5) x 1.5-2 µm; **Pycnidia:** not found; **Secondary metabolites:** pulvinic acid derivates.

**Substrate and ecology:** on wood, soil, sandstone, or lichenicolous on various lichens; **World distribution:** North America and Europe; **Sonoran distribution:** mainland of southern California, presently known only from one collection on Palomar Mountain.

**Notes:** *Thelocarpon lichenicola* is one of the more common species of the genus. It is characterized by the presence of simple to sparingly branched paraphyses, the absence of periphysoids, slightly thickened ascus apices, and the absence of a photobiont.

**USNEA**

*by P. Clerc*

**Usnea** Dill. ex Adans., Fam. Pl. 2: 7 (1763).


**Life habit:** lichenized; **Thallus:** fruticose, erect, decumbent (prostrate), supendent or longly pendant, usually attached by a basal holdfast; branching isometric- or anisometric-dichotomous; **basal part:** jet black to reddish-brown pigmented or concolorous with branches; continuous or with annular or longitudinal cracks; **branches:** longitudinally cylindric, fusiform, tapered or irregular; transversely terete, flattened, striated, ridged or alate; constricted or not at attachment points; with or without annulations; divided into ±conspicuous segments which may be cylindric, ±sausage-like or trapezoidal; with or without papillae, fibrils, tubercles, fibercles, pseudocyphellae; without true isidia; **soralia:** present or absent; punctiform and indistinct to enlarged and conspicuous; even, excavate or stipitate; plane, convex or concave; rounded to longitudinally or transversally elliptical with or without a sharply
USNEA

Notes: The fruticose thallus and the presence of the elastic central chord (seen by stretching a branch) readily separates Usnea from all other lichen genera. Each species of Usnea accepted here consists of a distinctive combination of morphological, anatomical and chemical characters [for discussion, see Clerc (1998)]. However, quite often one or more rarely two diagnostic characters are lacking, or are not interpretable, especially when specimens are young or growing in an extreme locality (for example with high insolation or with strong winds, or with very high humidity, etc.) or if they are infected by a lichenicolous fungus or when they are necrotic (in specimens collected on the ground). When such difficulties are encountered, chemistry should be investigated with t.l.c. and possibly specialists should be consulted.

Key to the species of Usnea from the Sonoran region: (species in brackets have so far not been found but are likely to occur in the Sonorn region)

1. Soralia absent; apothecia present or absent .............. 2
   1. Soralia or “soralia-like” structures present; apothecia
      absent or few ............................................... 19
2. Wine red, red, pink, reddish orange, orange, pink
   or yellow pigment present (be careful not to con-
   found with necrotic zones due to lichenicolous fungi
   or rotting when the specimen has been collected on
   the ground) .................................................... 3
2. Wine red, red, reddish orange, orange, pink or yel-
   low pigment absent ......................................... 8
3. Red pigment present in the edges of the apothecia .......
   ............................................................... U. cirrosa
3. Edges of apothecia without red pigment ................. 4
   4. Red or orange cortical pigment .......... U. erinacea
   4. Red cortical or orange cortical pigment absent ...... 5
5. Orange reddish medullary subcortical pigment present;
   P-, K- ......................................................... U. horrida
   5. Pigment not subcortical; P+, K+ .......................... 6
6. Medulla KC+ yellow, C+ yellow, K+ yellow, P-;
   wine red, pink or yellow medullary pigment pres-
   ent; medullary periaxial orangish pigment absent;
   diffractaic acid present ................................. U. cristatula
6. Medulla C-, KC-, K+ yellow turning red, P+ orang-
   ish yellow; wine red, pink or yellow medullary pig-
   ment absent, medullary periaxial orangish pigment
   present; galbinic, norstictic, salazinic acids present . 7
7. Branches cylindrical, densely covered with spinules;
   papillae and tubercles absent ...................... U. subelegans
7. Branches irregular, not densely covered with spinules;
   papillae and tubercles present .................... U. shimadai
8. Thallus pendulous when mature; branches parallel
   for most of the length of thallus; apothecia absent to
   numerous .................................................... 9
8. Thallus shrubby to subpendant when mature, rarely
   pendant; branches mostly divergent along the entire
   length of thallus; apothecia usually numerous .... 10
9. Central axis relatively thin (27-48%), serpentine; me-
   dulla relatively thick (19-31%), dense; thallus flaccid
   with distinct thin, fusiform to elongate-sinuous pseudo-
9. Central axis thick (49-80%), straight; medulla thin (4-15%) and compact; thallus ±stiff without distinct, thin fusiform to elongate-sinuous pseudocyphellae; papillae conspicuous, abundant, large, cylindrical to truncate-conical, paler at top .......................... U. goniodes

10. Branches densely covered with spinules; papillae and/or tubercles absent ........................................ 11

10. Branches not so densely covered with spinules; papillae and/or tubercles usually present ........ 14

11. Branches cylindrical; segments terete and ±cylindrical; foveoles and transversal furrows absent; K-, P- ................................................................. 12

11. Medulla one layered, dense to compact, sometimes with distinct annular cracks; spores 7.5-9 µm long; mountains of Arizona ..... U. parvula

11. Medulla distinctly two layered, compact and thin subcorticaly, large and lax subaxially; cortex of main branches with few indistinct annular cracks; spores 7.5-9 µm long; mountains of Arizona .... U. parvula

12. Medulla with diffractaic acid present; cortex thin to thick (6-10%); spores 9-11 µm long; southern Baja California .................. U. strigosa s.l.

12. Medulla without diffractaic acid but with fatty acids; cortex very thin to moderately thin (2-8%); spores 7.5-11 µm long ..................................... 13

13. Medulla distinctly two layerd, compact and thin subcorticaly, large and lax subaxially; cortex of main branches with few indistinct annular cracks; spores 9-11 µm long; coastal range of Baja California .... U. horrida

13. Medulla one layered, dense to compact, sometimes locally chalky; cortex of main branches with distinct annular and ±transverse cracks; spores 9-11 µm long; coastal range of Baja California .... U. horrida

14. Cortex shiny to vitreous; basal part without any jet black pigmentation, concolorous with or paler than main branches ........................................ 15

14. Cortex mat; basal part jet black pigmented at least on the first mm, rarely concolorous .................... 16

15. Large white tubercles present on branches supporting the apothecia; lateral branches constricted or not at attachment point ..................... U. shimadai

15. Tubercles absent; lateral branches distinctly constricted at attachment point .................... U. cirrosoa

16. Branches irregular; segments ±swollen; basal part often indistinctly (only on the first mm) black pigmented; spores 7-9 µm long .... U. intermedia

16. Branches cylindrical to tapered; segments cylindrical and terete; basal part distinctly jet black pigmented; spores 7-11 µm long .................. 17

17. Lateral branches ±distinctly ridged; fibrils numerous, regularly disposed on branches (in fish bone like pattern); only norstictic acid; mountains of Arizona ...... ........................................ U. myrmaiacacina

17. Lateral branches cylindrical and terete; fibrils few to numerous, irregularly disposed on branches; when norstictic acid present then together with salazinic acid; Sierra Madre Occidental ............. 18

18. Spores 7-9 µm long; salazinic acid [U. subfusca] ........................................................... U. florida s.l.

18. Spores 9-11 µm long; chemistry varied ........... 24

19. Wine red, red, pink, reddish orange, orange, pink, yellow or (only in central axis) ochraceous brown pigment present (be careful not to confound with necrotic zones due to lichenicolous fungi or rotting when the specimen has been collected on the ground) .................................................. 20

19. Wine red, red, pink, reddish orange, orange, pink, yellow or (only in central axis) ochraceous brown pigment absent .............................................. 35

20. Central axis with ochraceous brown pigment ...... ................................................................. U. mexicana

20. Central axis without an ochraceous brown pigment ......................................................... 21

21. Central axis fistulose (in all branches) with loose hyphae inside, extremely thick (usually > 80%), sometimes with a yellow pigment; medulla thin and compact, with a periaxial pink-red pigment U. baylei

21. Central axis not fistulose (except sometimes in large branches close to the basal part), thinner; medulla of variable width, pigmented or not ........ 22

22. Cortex of branches with a red or orange pigment 23

22. Cortex of branches without a red or orange pigment ......................................................... 27

23. Red pigment present as minute spots on the branches ......................................................... 24

23. Red or orange pigment not forming minute red spots on the branches ................................. 25

24. Thallus stiff with extremely thick central axis
(50-80%); minute red spots covering some papil-
lae of main branches; soralia minute often coales-
cing and forming extensive larger soralia-like ar-
eas; terminal branches ±tortuous, with greenish
parts crowded with soralia separated by discolored
white to light brownish parts without soralia; peri-
axial medulla and axis unpigmented .. *U. brattiae*

24. Thallus not stiff, with thin to moderately thick
axis (<40%); red spots ±homogeneously present
in the cortex of every branches; soralia large ±ho-
mogenously distributed on terminal branches; peri-
axial medulla and axis yellow to yellow-orange
(sometimes unpigmented) ........ *U. flavocarida*

25. Cortex ±light orange-brown pigmented; soralia puncti-
tiform minute; cortex thin; fibrils spinulous; papil-
lae absent ..................... *U. hirta* subsp. *trachista*

26. Medulla P+, K- or P-, K-; red cortical pigment
present only close to the basal part; cortex thick
(11-19%) and shiny-vitreous ........ *U. subscabrosa*

27. Medulla C+ yellow-orange intense with a pink,
wine red, yellow to yellow-orange pigment (pig-
ment sometimes very faint) .................... 28

28. Medulla with a peraxial yellow or yellow-orange
pigment ........................................ *U. flavocarida*

29. Soralia minute, developing on the cortex, plane, not
well delimited and with an irregular outline, coales-
cing and covering densely the apices of the branches;
fatty acids of the murolic acid group .. *U. mutabilis*

30. Basal part distinctly jet black; lateral branches not
narrowed at attachment points ....... *U. praetervisa*

31. Basal part paler or concolorous; lateral branches
slightly to distinctly narrowed at attachment points
........................................................ 31

32. Cortex mat; soralia ±stipitate and convex when ma-
ture, with numerous and clustered isidiomorphs; fi-
bercles usually absent; galbinic acid absent .......... 32

33. Soralia minute, developing on the cortex, plane, not
well delimited and with an irregular outline, coales-
cing and covering densely the apices of the branches;
fatty acids of the murolic acid group .. *U. amblyoclada*

34. Fibrils short and spinulose, densely but ±irregularly
covering restricted parts (rarely the entire length)
of branches; soralia enlarged to 1/2 branch diam-
eter or more when mature, often slightly fusiform,
not coalescing; galbinic acid present .... *U. dasaea*

35. Fibrils usually longer and slender, scattered on
whole thallus; soralia punctiform, often coales-
cing and forming extensive larger soralia-like ar-
eas; galbinic acid absent ........... *U. cornuta*

36. Fibercles numerous on the whole thallus, large,
with conspicuous white summits and thus “soralia-
like”; short isidiomorph-like fibrils occurring on fi-
bercles; true soralia absent; on rock .......... \textit{U. nashii}

36. Large fibercles with conspicuous white summits and isidiomorph-like fibrils absent; true soralia present; primarily on bark .......................................... 37

37. Lateral branches not constricted at attachment points; cortex thick (9-19%), mat or shiny; medulla thin and compact; thallus bushy erect to subpendulous or pendulous; basal part with or without a red pigment .. 38

37. Lateral branches distinctly constricted at attachment points; cortex thin (3-6%) and shiny; medulla thick, very loose; thallus bushy erect; basal part without a red pigment ................................ 39

38. Cortex distinctly shiny and vitreous; basal part often with red pigment; thallus bushy erect to subpendulous or pendulous ..... \textit{U. subscabrosa}

38. Cortex mat to sometimes slightly shiny, never vitreous; basal part without red pigment; thallus pendulous .................................. \textit{U. schadenbergiana}

39. Soralia broad, larger than half the diameter of branch, plane to excavate ...................... \textit{U. glabrata}

39. Soralia typically minute, smaller than half the diameter of the branch, often fusing together thus looking like a single large soralium, never excavate .... \textit{U. esperantiana} subsp. \textit{brasiliensis}

40. Isidiomorphs thick, not clustered but often sitting alone on soralium, often black-tipped, always present; soralia punctiform, never enlarged, ±stipitate, numerous, densely disposed, developing on fibercles; primarily on rock, rarely on bark ..................................... \textit{U. amblyoclada}

40. Isidiomorphs thin, clustered, rarely black-tipped or absent; soralia punctiform to distinctly enlarged, ±level with the cortex or slightly stipitate, developing initially on the cortex or on fibercles; primarily on bark, rarely on rock (see however \textit{U. halei}) ...................................................... 41

41. Lateral branches distinctly narrowed at point of attachment; cortex shiny ........................................ 42

41. Lateral branches not narrowed at point of attachment; cortex mat or shiny ......................... 46

42. Fibrils short and spinulose, densely but ±irregularly covering restricted parts (rarely the entire length) of branches; galbinic acid usually present ................................................................. \textit{U. dasaea}

42. Fibrils usually longer and slender, scattered on whole thallus, not very densely covering branches or restricted parts of branches; galbinic never present ............................................................................................................. 43

43. Isidiomorphs absent; soralia larger than half the diameter of the bearing branch, ±level with the cortex or convex, without margin, mainly covering the terminal parts of branches; bourgeanic acid usually present ................................\textit{U. esperantiana}

43. Isidiomorphs usually present (sometimes absent in old herbarium specimens); soralia punctiform to enlarged, ±level with the cortex or stipitate, with or without margins, covering main branches and terminal parts or only terminal parts; bourgeanic acid absent .. 44

44. Cortex mat; lateral branches slightly or not constricted at attachment points; basal part concolorous with the branches or brown-red pigmented; salazinic and norstictic acids .................. \textit{U. halei}

44. Cortex shiny; lateral branches distinctly constricted at attachment points; basal part concolorous with the branches or black; chemistry diverse ...... 45

45. Soralia covering mainly the terminal branches (last third of the thallus length), minute and crowded (30-50 soralia/mm$^2$), often becoming confluent and thus looking like a single large soralium (be sure to look at single soralia), mostly of irregular shape, ±level with the cortex, usually without margin, arising mostly directly on the cortex, rarely efflorescent-excrecent; isidiomorphs rarely numerous; fibrils usually numerous on primary branches close to the basal part; psoromic acid absent ................... \textit{U. cornuta}

45. Soralia numerous on primary and terminal branches, usually not crowded but widely spaced (15-25 soralia/mm$^2$), rarely becoming confluent, larger than half the diameter of the bearing branch when mature, mostly rounded, usually slightly to distinctly stipitate, with a distinct margin, often efflorescent-excrecent; isidiomorphs often conspicuous and numerous; fibrils usually absent on primary branches close to the basal part; psoromic acid frequent .......... \textit{U. fragilescens}

46. Soralia deeply excavate when mature, reaching central axis, often exceeding width of branches, with the adjacent cortex being torn off; isidi-
omorphs never present ......................................... 47
46. Soralia slightly concave, or ±even with the cortex or ±stipitate but never deeply excavate and reaching the central axis, never exceeding width of branches, with adjacent cortex never torn off; isidiomorphs present or absent ...................... 48
47. Branching mostly anisotomic-dichotomous; branches irregular; fibrils unevenly distributed; medulla in average thick (21-30%); norstictic acid absent ........... 

U. lapponica
47. Branching mostly isotomic-dichotomous; branches tapering; fibrils usually numerous, in fish-bone like pattern; medulla in average thin (14-22%); norstictic acid mostly present ...........

U. fulvoreagens
48. Medulla C+, CK+ deep yellow-orange, diffraactaic acid present; soralia conspicuously stipitate ...........................................................

U. ceratina
48. Medulla C-, CK-, diffraactaic acid absent; soralia stipitate or not .................................... 49
49. Branch segments distinctly ridged to slightly alate with small to extensive areas where cortex is erose; thallus pendulous with branches running parallel to each other; central axis very thick (50-80%) .. 

U. transitoria
49. Thallus not at the same time pendulous, with branch segments ridged and areas with erose cortex and with thick central axis ...................... 50
50. Soralia minute, smaller than half the diameter of the bearing branch (be sure to look at single soralia and not at coalescing minute soralia forming extensive larger soralia-like structures) ............ 51
50. Soralia large, larger than half the diameter of the bearing branch ................................................. 60
51. Thallus stiff with extremely thick central axis (50-80%) and thin medulla; soralia often coalescing and forming extensive larger soralia-like areas; terminal branches ±tortuous, with greenish parts crowded with soralia separated by discolored white to light brown parts without soralia ........... Usnea brattiae
51. Thallus not so stiff, with thinner central axis (<40%) and larger medulla; soralia ±homogeneously distributed on terminal branches, usually without discolored parts ......................................................... 52
52. Branches typically obtusely angular (ridged) and deformed ......................................................... 53
52. Branches terete ............................................................. 55
53. Tubercles numerous; soredia ±stipitate growing on the summit of tubercles, with clustered isidiomorphs; basal part brownish black to distinctly jet black; foveoles and transversal furrows absent .. U. cedrosiana
53. Tubercles absent; soredia growing on fibrercles; isidiomorphs absent (do not confound with young fibrils!); basal part pale or concolorous with the branches; foveoles and transversal furrows frequent 54
54. Thallus flaccid; cortex thin (3-7%), mat to ±shiny, never pigmented; medulla lax U. hirta subsp. hirta
54. Thallus stiff; cortex thick (6-14%), distinctly shiny, sometimes ±orange pigmented; medulla compact ..

U. hirta subsp. trachista
55. Thalle pendulous when mature with branches parallel for most of the length of the thallus; branches irregular; segment often ±swollen; usnic, ±salazinic acids ................................................................. 56
55. Thallus shrubby to subpendulous with branches mostly divergent along most of the thallus length; branches tapering; segment cylindrical; chemistry various ................................................................. 56
56. Fibrils short and spinulose; basal part pale or concolorous with branches; isidiomorphs clustered or not, few or numerous; galbinic acid usually present .. 57
56. Fibrils longer, not spinulose; basal part usually black; isidiomorphs clustered, usually numerous; galbinic acid never present ................... 58
57. Isidiomorph thick, usually not clustered but often sitting alone on soralium, black-tipped, always present; soralia punctiform never enlarged, ±stipitate, numerous, densely disposed; fibrils scattered on whole thallus, not very densely covering branches or restricted parts of branches; primarily on rock .... U. amblyoclada
57. Isidiomorphs thin, clustered, never black-tipped, sometimes absent; soralia punctiform to ± enlarged, especially on terminal branches, ±level with the cortex, developing initially on the cortex or on fibrercles; fibrils short and spinulose, densely but ± irregularly covering restricted parts (rarely the entire length) of branches; primarily on bark .... U. dasaea
58. Terminal branches mostly anitotomic-dichotomous, not tapered but similar in diameter over their entire length; often sinuose, not all of the same length; usnic ± salazinic, ± barbatic acids  \textit{U. diplotypus}

58. Terminal branches mostly isotomic-dichotomous, tapered, usually not sinuose, all ± of the same length; thamnolic acid or norstictic acid or squamatic acid ............................................. 59

59. Soralia developing initially on the cortex, usually with a cortical rim, shortly stipitate, ± circular slightly convex at the top and usually not coalescing; K+ yellow intense turning slowly orange, P+ orange (thamnolic acid) or K-, P- (squamatic acid) ....  \textit{U. subfloridana}

59. Soralia developing on fibercles, without a cortical rim, of irregular shape, often coalescing and looking like a large diffuse and even soralia; K+ dull yellow turning reddish orange, P+ deep yellow (norstictic acid) ........................................ 60

60. Branches tapering, without foveoles or transversal furrows ............................................. 61

60. Branches irregular, uneven in thickness, often with foveoles or transversal furrows ............................................. 61

61. On rock; branching isotomic-dichotomous; isidiomorphs numerous  \textit{U. ammannii}

61. On bark; branching anisotomic-dichotomous; isidiomorphs few or absent  \textit{U. substerilis}

62. Basal part concolorous with branches, never black; norstictic and salazinic acids ...............  \textit{U. halei}

62. Basal part distinctly jet black; other chemistry 63

63. Basal part with small but distinct longitudinal cracks (at 50x magnification) and few annular cracks; mature soralia usually longitudinally stretched; barbatic acid present or absent ........  \textit{U. wasmuthii}

63. Basal part without longitudinal cracks, with few to numerous annular cracks; mature soralia not distinctly longitudinally stretched but ±circular; barbatic acid absent ............................................. 64

64. Isidiomorphs usually numerous on young and mature soralia; few annular cracks; basal part usually with short black pigmentation; thamnolic or squamatic acids ................. \textit{U. subfloridana} (rare morphotype with large and ± concave soralia)

64. Few isidiomorphs on young soralia only; annular cracks usually numerous (6-9/5mm); basal part with conspicuous black pigmentation; salazinic acid ...... .................................................................  \textit{U. silesiaca}

The Species


\textbf{Thallus}: shrubby, compact, 2-10 cm long; \textbf{branching}: isotomic-dichotomous, branches divergent; \textbf{basal part}: distinctly paler than branches or of same color, with numerous and conspicuous annular cracks; \textbf{branches}: usually ±irregular, lateral branches not narrowed or slightly to distinctly narrowed at point of attachment; \textbf{segments}: terete to distinctly ridged, cylindrical to weakly sausage-like; \textbf{foveoles}: absent; \textbf{transversal furrows}: absent; \textbf{apices}: short, thick, usually sparsely branched; \textbf{papillae}: absent; \textbf{tubercles}: absent; \textbf{fibercles}: low, numerous, mostly sorediate; \textbf{fibrils}: short (1-3 mm) often spinulous, mostly present in oldest part of thallus; \textbf{soralia}: punctiform, smaller than half the diameter of branches, densely disposed, usually ±irregular, lateral branches not narrowed or slightly to distinctly narrowed at point of attachment; \textbf{isidio-morphs}: on soralia or isolated on plain cortex, sometimes on ridges, frequently black pigmented at tips; \textbf{cortex}: moderately thin (5-9%), shiny, distinctly transversely, and longitudinally cracked at the base of main branches; \textbf{medulla}: compact to dense and often orange pigmented close to the axis; \textbf{axis}: thick; \textbf{Apothecia}: rare; \textbf{Spot tests}: medulla K+ yellow turning red, C-, KC-, P+ pale orange-yellow; \textbf{Secondary metabolites}: cortex with usnic acid; medulla always with norstictic and salazinic acids, and almost always with galbinic acid.

\textbf{Substrate and ecology}: growing mainly on acidic and volcanic rocks, rarely on limestone, very rarely on bark, usually in shady situations, in mixed pine-oak-juniper forests or in canyons, between 200 and 2530 m; \textbf{World distribution}: southern North America; \textbf{Sonoran distribution}: [map]
eastern and southeastern Arizona, Baja California Sur, Chihuahua and Sonora.

Notes: *Usnea amblyoclada* is closely related to *U. dasaea*, and they differ ecologically (the latter species grows primarily on bark) and morphologically (mainly through their different type of soralia and isidiomorphs). For differences from *U. shimadai*, see under that species.


**Thallus:** shrubby, 1.5 to 3 cm long; **branching:** anisotomic dichotomous, branches divergent; **basal part:** short, not conspicuous, black pigmented; **branches:** usually tapering, sometimes ±irregular, with inconspicuous segmentation (3-5 segments/0.5 cm), lateral branches not narrowed at point of attachment; **segments:** terete to slightly ridged, cylindrical to slightly sausage-like; **foveoles:** absent; transversal furrows: present; **papillae:** verrucous, irregularly distributed on main branches; **tubercles and fiberels:** absent; **fibrils:** short spinulous, 1-2(-3) mm long, irregularly distributed on the whole thallus; **soralia:** superficial to slightly stipitated, as large as the branches when mature, sometimes ±encircling the end of the branches, circular to oblong transversely, without margin, usually not confluent, arising initially on the cortex; **isidiomorphs:** small, and sometimes black-tipped, mainly on young soralia, usually few on mature soralia; **cortex:** ±smooth, and glossy, thin (5-8%); **medulla:** loose to dense, extruding between the segments, especially at ramification points, moderately large; **axis:** moderately thick; **Apothecia:** rare; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolite:** salazinic acid.

**Substrate and ecology:** growing on rock, at 1950-2800 m; **World and Sonoran distribution:** endemic to Mexico where it is reported from Chihuahua.

Notes: The lateral branches which are not narrowed at ramification point make *Usnea ammannii* distinct from all species of the *U. fragilascens* agg. Characteristic are the large, and ± circular soralia with few isidiomorphs when mature. *Usnea substerilis* Motyka has the same kind of soralia but has, however, a different ecology, a dull cortex, and normally no isidiomorphs in mature soralia. *Usnea lapponica*, and *U. fulvoreagens* have large soralia as well but they are deeply excavate, reach the central axis, and never produce isidiomorphs.


**Thallus:** erect-shrubby to subpendulous, very stiff; **branching:** anisotomic-dichotomous, divergent; **basal part:** concolorous with branches or dark brown to black; **branches:** not segmented, only here and there with thin and ±incomplete annular cracks, cylindrical or irregular, terete; lateral branches: not narrowed at attachment points; **segments:** absent; **papillae:** absent; **tubercles:** nearly absent to numerous, low-verrucous to truncate-conic, paler at top, sometimes eroded, irregularly distributed mainly on secondary branches; **fiberels:** nearly absent; **fibrils:** long (2-6 mm) and slender, irregularly distributed mainly on main branches; **soralia:** punctiform, of irregular outline, smaller than half the diameter of the branch, even or slightly stipitate, developed from the top of tubercles or initially from the cortex, mainly on secondary and terminal branches; **isidiomorphs:** nearly absent to numerous and conspicuous, giving a spinulous appearance to the thallus (lens at 10x); **pseudocyphellae:** absent; **cortex:** thin (2-4%), **medulla:** thin and compact, with a pink-red pigment in the area close to the axis; **axis:** very thick (usually > 80%), fistulose (whole thallus) with loose hyphae inside, sometimes with a yellow pigment; **Apothecia:** not seen; **Spot tests:** medulla K+ yellowish, C+ yellow, KC+ yellow, P-; **Secondary metabolites:** diffractaic acid (major), ±barbatic acid (minor), eumitrins.

**Substrate and ecology:** on bark and on rock; **World dis-
distribution: pantropical; Sonoran distribution: one old collection from the San Gabriel Mountains in southern California, probably extinct.

Notes: The stiff thallus, the thin pink pigmented medulla and the fistulose axis clearly define *Usnea baileyi* and make it easily recognizable.

**Usnea brattiae** P. Clerc, sp. nov.


Type: U.S.A., California, Santa Barbara Co.: Santa Cruz Island, Ridge Road, Laguna Canyon road turnover, 200 m, 32°54’N, 118°30’W, on *Arctostaphylos* sp., 29.03.2000, P. Clerc and C. Bratt (Holotype, G).

**Thallus:** erect-shrubby to subpendulous, 1.5 to 9 cm long, stiff; **branching:** ±isotomic-dichotomous especially towards the tips, divergent to subparallel; **basal part:** concolorous to reddish brown, pigmented at the very base, rarely black; **branches:** cylindrical to tapered, lateral branches not narrowed at attachment point, foveoles or transversal furrows absent; **segments:** terete and cylindrical; **papillae:** few to numerous, irregularly distributed on secondary branches; **tubercles:** absent; **fibrils:** nearly absent to few, rarely numerous, slender (2–3 mm long) scattered on the branches, especially close to basal part; **soralia:** numerous on secondary and terminal branches, punctiform, minute, smaller than half the diameter of the branch, fusing together and looking thus like a single large soralium, circular or of irregular shape, without a sharply delimited cortical rim, even, developing initially on the cortex; **isidio-morphs:** numerous on mature soralia but sometimes covering densely all the branches; **pseudocyphellae:** absent; **cortex:** thin to moderately thick (6–9%), dull to slightly shiny, without distinct cracks, often parasitized by lichenicolous fungi and then with pale brown or pale red pigmented zones (sometimes with small aggregated red dots at summits of papillae); **medulla:** extremely thin (5–14%), dense to compact, unpigmented; **central axis:** extremely large (50–80%); **Apothecia:** not seen; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow, or K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow, or K-, C-, KC-, P-; **Secondary metabolites:** either salazinic acid or norstictic acid and fatty acids or none detected.

**Substrate and ecology:** on bark on *Quercus* spp. (but especially *Q. pacifica*) and *Arctostaphylos* spp. in oak stands or scrubs between 200 and 500 m; **World and Sonoran distribution:** Channel Islands of southern California.
and Isla Cedros in Baja California.

**Notes:** The thick axis and thin medulla giving the stiffness to the thallus, the absence of tubercles, the numerous punctiform soralia with isidiomorphs make *Usnea brattiae* very distinct. Among other species with such a thick central axis, *U. schadenbergiana* differs by the pendulous habitus, the numerous and long fibrils arranged in ±fish-bone like pattern, the sparse isidiomorphs and the chemistry; *Usnea transitoria* differs by the pendulous habitus and ridged to distinctly alate branch segments; *Usnea baileyi* differs by the pink pigmented medulla, the fistulose axis and the chemistry.

**Usnea cavernosa** Tuck. in Agassiz, Lake Superior: 171 (1850).

**Synonym:** *Usnea microcarpa* Arn.; Illustrations: Herrera-Campos et al. (1998), figs. 5g & 10a; Clerc (1998), figs. 5, 6 & 8; Brodo et al. (2001), p. 714.

**Thallus:** pendulous, up to 60 cm long, flaccid hanging loosely on branches and twigs; **branching:** isotomic-di-chotomous, distinctly parallel; **basal part:** paler than or concolorous with the branches, sometimes with several attachment points; **branches:** cylindrical to irregular, tapering very slowly, commonly conspicuously foveolate; **segments:** not conspicuous, terete, striate, or weakly ridged, cylindrical; **papillae, tubercles** and **fibercles:** absent; **fibrils:** absent to scarce and irregularly distributed, 1-3 (5) mm long; **soralia** and **isidiomorphs:** absent; **pseudocyphellae:** thin fusiform to elongate-sinuous; **cortex:** thin (4-8%), shiny and smooth, with thin transverse cracks; **medulla:** dense, not pigmented; **axis:** typically sinuous; **Apothecia:** very rare; **Spot tests:** K-, C-, KC-, P- or K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** either no medullary substances or salazinic acid.

**Substrate and ecology:** on bark, rarely on wood, in mountains in moist habitats between 2000 and 3300 m; **World distribution:** Eurasia and North America; **Sonoran distribution:** Arizona, Baja California, Chihuahua, Sinaloa and Sonora.

**Notes:** *Usnea cavernosa* is easily distinguished by its pendant and flaccid habit, the slender, smooth and foveolate branches with numerous thin elongate-sinuous pseudocyphellae not developing into soralia and lacking papillae.

**Usnea cedrosiana** P. Clerc, sp. nov.

**Diagnosis:** *Fungus corticola. Thallus 4-9 cm altus, erectus vel subpendulus; ad basim brunneolus niger ad distinctum nigrum. Rami irregular, not tumidi et contracti, leviter complanati ad distinctos porcatos. Papillae et tuberculae numerosae verrucatae. Fibrillae numerosae, magnitudine variantes, irregular dispositus et sinuosae, praecipue in ramis principalibus. Soralia isidiosa punctiformia praecipue in apex tuberculorum evolens. Cortex nitidus, moderate crassus (9.5%). Medulla moderate crassa (26%). Axis moderate crassus (29%). Apothecia desunt. Acidum usnicum et acidum norsticticum continens.*

**Type:** Mexico, Baja California: Isla Cedros, north-facing slope on NE ridge top with pines at north end of the island, 28°22’N, 115°15’W, c. 400 m, on *Pinus muricata*, 18 Mar. 1994, T. H. Nash III 34.267 (Holotype, ASU; isotype, G).

**Fig. 7:** *Usnea cedrosiana,* photo by P. Clerc

**Other specimens examined:** Mexico, Baja California: Isla Cedros, ridge crest overlooking western shore and adjacent canyon to the E at the NW corner of the island,


Thallus: erect-shrubby, subpendulous to pendulous, up to 30 cm long, coarse to slender, stiff to flaccid; branching: isometric- to anisometric-dichotomous, divergent to parallel; basal part: concolorous to the branches, often with a brownish-orange pigment, sometimes brownish-black pigmented at the very base; branches: cylindrical to irregular; lateral branches: narrowed or not at point of attachment; segments: terete to ridged, cylindrical to ±sausage-like; foveoles and transversal furrows: absent to frequent; papillae: nearly absent to frequent especially on main branches, low and indistinct to verrucous; tubercles: sparse to numerous, conspicuously raised, at first eroded and white at summit, then bursting to form ulcerose soralia; fibercles: absent; fibrils: nearly absent to numerous, spinulous (1-3 mm) to long (up to 10 mm), irregularly distributed; soralia: nearly absent to numerous, sometimes covering completely the apices, located mainly on young branches or fibrils, arising mainly on the tubercles, plane to convex, frequently capitate; isidiomorphs: few to numerous, tufted on soralia; pseudocyphellae: absent; cortex: thick (6-12%), shiny to vitreous, hard, smooth to densely cracked; medulla: thick, dense to compact, rarely loose, pink to wine red pigmented, sometimes not pigmented at all; axis: thick, white to pink or yellow pigmented; Apothecia: not seen in the area; Spot tests: K+ yellowish, C+ yellow, KC+ yellow, P-; Secondary metabolites: diffractaic acid (major), barbatic acid (minor), ±4-O-demethylbarbatic acid (minor), ±several accessory substances and fatty acids.

Substrate and ecology: coastal to montane areas, mainly on bark of Pinus spp. or sometimes Quercus spp. in low forests on exposed ridges between 200 and 450 m or at high altitude in the mountains of the Sierra Madre Occidental; World distribution: Eurasia,
eastern, western and south eastern North America, and South America; **Sonoran distribution:** southeastern Arizona, southern California including the Channel Islands, Chihuahua and Sierra Madre Occidental of Sinaloa.

**Notes:** *Usnea ceratina* is characterized by its tuberculate soralia, its vitreous cortex, its ± pinkish pigmented and compact medulla, its pale base sometimes with a yellowish hue and its production of diffractaic and barbatic acids in the medulla that reacts C+ yellow.


Illustrations: Herrera-Campos et al. (2001), figs. 2g & 13h.

**Thallus:** erect-shrubby, tufted, 2-7 cm long; **branching:** the whole thallus anisotomic-dichotomous; **basal part:** paler than or concolorous to branches or ±pale brown; **branches:** tapering; lateral branches: distinctly narrowed at attachment point; **segments:** terete, ±cylindrical to strongly sausage-like; **papillae/tubercles:** verrucous, few to numerous, irregularly distributed; **fibercles:** absent; **fibrils:** short (< 3mm) and thick, spinulous, unevenly distributed on the whole thallus, often numerous on the apices, giving a spinulous aspect to the terminal part of the thallus; **soralia and isidiomorphs:** absent; **pseudocyphellae:** absent; **cortex:** thin (3-7%), shiny; **medulla:** moderately thick to thick, lax to dense; **central axis:** thin to moderately thick; **Apothecia:** usually numerous, terminal or lateral; **ascospores:** elliptical, 9-12 x 6-8 μm; **Spot tests:** K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow; **Secondary metabolites:** norstictic acid (major), ±salazinic acid (major).

**Substrate and ecology:** on bark, on *Abies* spp., *Quercus* spp. and *Pinus* spp. in the temperate forests in mountainous area between 1500 and 3650 m; **World distribution:** North and South America; **Sonoran distribution:** Arizona and southern California.

**Notes:** *Usnea cirrosa* is distinguished by its lateral branch-
es that are distinctly constricted at ramification points, its swollen branch segments, its thin and shiny cortex and the numerous apothecia. *Usnea cirrosa* can be considered as the primary species of *U. cornuta*. It is closely related to if not identical to *U. ramillosa* Motyka that produces proto-

**Usnea cornuta** Körb., Parerga Lichenol. 2 (1859).

**Thallus:** erect-shrubby, tufted, 2-5 cm long; **branching:** the whole thallus anisotomic-dichotomous; **basal part:** paler than or concolorous to branches or ±pale brown; **branches:** tapering; lateral branches: distinctly narrowed at attachment point; **segments:** terete, ±cylindrical to strongly sausage-like; **papillae/tubercles:** verrucous, few to numerous, irregularly distributed mainly on secondary branches; **fibercles:** absent; **fibrils:** short (< 3mm) and thick, spinulous, unevenly distributed on the whole thallus, often numerous on the apices, giving a spinulous aspect to the terminal part of the thallus; **soralia:** typically minute, smaller than half the diameter of the branch, often fusing together thus looking like a single large soralium, typically even to sometimes ±stipitate, not efflorescent-excrecent, primarily developing initially on the cortex (secondary branches and apices), rarely on top of tubercles (main and secondary branches), rarely present on main branches but mainly on terminal branches, plane, of irregular shape, usually without a sharply delimited cortical rim; **isidiomorphs:** short (0.1-0.2 mm), numerous at the beginning but often absent on mature soralia; **pseudocyphellae:** absent; **cortex:** thin to moderately thick (5-9%), shiny; **medulla:** moderately thick to thick, lax to dense; **central axis:** thin to moderately thick, sometimes orange pigmented; **Apothecia:** not seen; **Spot tests:** either K+ yellow turning red, C-, KC-, P+ orangish yellow, or K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow, or K+ yellow slowly turning orangish, C-, KC-, P+ deep orange, or K-, C-, KC-, P+ orangish yellow or K-, C-, KC-, P-; **Secondary metabolites:** salazinic acid (major), ±consalazinic acid.
USNEA

(subsp. cornuta)


**Segments:** ±cylindrical to moderately sausage-like; cortex: thin to moderately thick (5-9%); medulla: moderately thick (25-36%), lax to dense; central axis: thin to moderately thick (17-30%); *Spot tests:* K+ yellow turning red, C-, KC-, P+ orangish yellow, or K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow, or K+ yellow slowly turning pale orange, C-, KC-, P+ deep orange of K-, C-, KC-, P-; **Secondary metabolites:** salazinic acid (major), ±consalazinic acid (minor), ±protocetraric acid (minor), ±norstictic acid (minor), ±lobaric acid (minor), ±fatty acids (minor); norstictic acid (major), ±fatty acids (minor) or norstictic acid (major), lobaric acid (major), or stictic acid (major), norstictic acid (major), ±constictic acid (minor), ±cryptostictic acid (minor), ±menegazziaic acid (minor); or none detected.

**Substrate and ecology:** on bark, rarely on wood, in mixed oak-conifer or spruce-fir forests at high elevations or in coastal areas with chaparral or exposed low oak forests, more rarely on rock in the chaparral; **World distribution:** Europe, Macaronesia, eastern and western North America, South America, Japan, and Australia; **Sonoran distribution:** mountains of SE Arizona, southern California, Cedros Island in Baja California, and the Sierra Madre Occidental of Sinaloa.

Notes: Typical for *U. cornuta* are the lateral branches distinctly narrowed at the ramification points, the glossy cortex and the minute soralia with isidiomorphs on the terminal branches. In western North America *U. cornuta* and *U. fragilesens* are harder to distinguish than in Europe and eastern North America because of the presence of intermediate forms and a larger range of morphological variation. In some populations of western America these two species are indeed very difficult to distinguish. There are morphotypes that are intermediate between the two species, e.g. a specimen collected on Cedros Island with a typical *U. cornuta* thallus morphology but with soralia of the *U. fragilesens* type and norstictic acid in the medulla.


**Segments:** strongly sausage-like (on main branches only); cortex: (3-6%); medulla: thick (35-40%) and very lax; central axis: thin (11-20%); *Spot tests:* K-, C-, KC-, P+ orangish yellow; **Secondary metabolite:** protocetraric acid (major).

**Substrate and ecology:** on bark; **World distribution:** North and South America; **Sonoran distribution:** southern California and the Sierra Madre Occidental.

Notes: There is a tendency for the protocetraric acid chemotype to have segments that are more “sausage-like” with thinner cortex and larger medulla than in the other chemotypes (Herrera-Campos et al. 2001). However this separation is not complete yet and lots of intermediates still occur (*U. brasiliensis* morphotypes without protocetraric acid or protocetraric acid in typical *U. cornuta*). For this reason I recognize these two taxa at the subspecific level.

Synonym: *Usnea grandisca* Motyka.

**Thallus:** erect-shrubby, subpendulous to pendulous, up to 50 cm long, coarse and ±stiff; **branching:** isometric- to anisometric-dichotomous, divergent to parallel; **basal part:** concolorous with or paler than the branches, sometimes with a pale yellow to dark brown pigment; **branches:** cylindrical to irregular; **segment:** conspicuous, terete to strongly ridged, cylindrical to slightly sausage-like or trapezoidal; **papillae:** nearly absent to frequent especially on main branches, low and indistinct to verrucose; **tubercles:** sparse to numerous, especially on smaller branches, conspicuously raised, sometimes eroded at summit, never bursting into ulcersor soralia; **fibercles:** irregularly present; **fibrils:** nearly absent to numerous, spinulous, 1-3(-10) mm, usually conspicuous, easily breaking away, usually densely disposed on some parts of the branches, giving spinulous appearance to this part of the thallus; **soralia:** punctiform to slightly elliptic longitudinally (especially on terminal branches), raised, smaller than half the diameter of main branches where they arise usually on branches, typically enlarged on apices where they mainly arise on cortex ab initio, appearing ±fusiform; **isidiomorphs:** occurring on soralia, not blackened at tips; **cortex:** thin (5-9%), glossy, not conspicuously cracked; **medulla:** large, compact to dense, often internally pinkish pigmented; **axis:** moderately thick, often peripherally pinkish pigmented; **Apothecia:** not seen; **Spot tests:** medulla K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** cortex with usnic acid; medulla with norstictic (major), galbinic (major) and salazinic (major) acids, or very rarely only with salazinic (major) and norstictic (major) acids or with psoromic acid (major).

**Substrate and ecology:** mainly on bark, rarely on wood or rock, mainly coastal, between 0 and 500 m, on Quercus spp., Pinus spp. in oak-pine forests or on diverse scrubs in the chaparral; **World distribution:** world-wide, North and South America, Africa, Asia and Europe; **Sonoran distribution:** southern California, Baja California, Chihuahua, and Sonora.
Notes: This species can be recognized by its lateral branches constricted at ramification points, its numerous spinulous fibrils covering the branches, its minute soralia with isidiomorphs and the presence of galbinic acid in the medulla. Badly developed or old specimens with few fibrils may be difficult to separate from *U. cornuta* without investigation with t.l.c.


**Thallus:** shrubby, 4 to 8 cm long, forming dense erect to subpendant tufts; **branching:** anisotomic-dichotomous; **basal part:** concolorous with the branches to distinctly blackened; **branches:** irregular, rarely cylindrical, inconspicuously segmented; **segments:** not narrowed at point of attachment; **papillae:** usually numerous especially on main branches, usually cylindrical; **tubercles and fibreles:** generally absent; **fibrils:** few and unevenly distributed to numerous and ±fish bone-like; **soralia:** punctiform, smaller than half the diameter of the branch, plane to convex and then efflorescent, sometimes confluent, arising initially on cortex; **isidiomorphs:** generally numerous, in clusters on young and mature soralia; **Apothecia:** not seen; **cortex:** dull, thin to moderately thick (5-9%); **medulla:** moderately thick, dense; **axis:** moderately thick; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow (salazinic acid) or K-, C-, KC-, P-, **Secondary metabolites:** salazinic acid (major), ±caperatic acid, ±lobaric acid, or none detected.

**Substrate and ecology:** on bark of *Pinus* spp. and *Quercus* spp., mainly in mixed deciduous-conifers forests between 1900 and 2600 m; **World distribution:** Europe, western North America, and northern Mexico; **Sonoran distribution:** mountains of SE Arizona, Sonora and Chihuahua.

**Usnea erinacea** Vain., Dansk Botanisk Archiv. 4: 3 (1926).

**Synonym:** *Usnea sanguinea* Swinscow & Krog; Illustrations: Swinscow and Krog (1979), figs. 16 & 17.

**Thallus:** erect-shrubby to subpendant, 2-15 cm long; **branching:** anisotomic-dichotomous, divergent; **basal part:** concolorous with branches; **branches:** tapered, lateral branches not narrowed at attachment points; **segments:** terete, cylindrical; **papillae:** nearly absent to numerous (young fibrils?); **tubercles:** absent; **fibreles:** few to numerous; **fibrils:** numerous, short (<3mm) and thick, giving a spinulous aspect to the branches; **soralia** and **isidiomorphs:** absent; **pseudocyphellae:** absent; **cortex:** thick (9-12%), shiny with a red pigment sometimes spotty and sparse at the surface; **medulla:** compact, thin to moderately thick, sometimes ±slightly orange pigmented; **axis:** thick, fistulose in the thickest branches; **Apothecia:** usually present, sometimes nearly absent, subterminal to terminal; **Spot tests:** medulla K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** medulla with norstictic (major) and salazinic (major) acids and ±protocetraric acid (minor).

**Substrate and ecology:** on bark of *Quercus* at 2300 m in mixed pine-oak forest; **World distribution:** East Africa, southern North America and South America (?); **Sonoran distribution:** Sierra Madre Occidental of Sinaloa.

**Notes:** *Usnea erinacea* is easily distinguished from all other species of the area by its numerous apothecia, the absence of soralia, its red pigmented cortex, and its chemistry.


Thallus: erect-shrubby and compact, up to 5 cm long; branching: richly anisotomic to isotomic dichotomously branched, divergent; basal part: concolorous to branches or light brown; branches: cylindrical to ±irregular; lateral branches: ±constricted at attachment points, ±deformed by the presence of foveoles or transverse furrows; apices: sparsely branched, thick, ±distinctly twisted and recurved, resembling skeletal fingers, especially when heavily sorediate; segments: terete, ±sausage-like; papillae: small, verrucous, ±sparsely and unevenly distributed; tubercles and fibrices: absent; fibrils: short (1-2 mm) spinulous, sparsely and irregularly distributed; soralia: broad, larger than half of diameter of branches, plane to slightly excavate, irregular shape, arising initially from cortex, mainly on terminal branches and fibrils, often confluent and covering most of the extremities of the branches; isidiomorphs: absent; pseudocyphellae: absent; cortex: thin (3-6%), shiny; medulla: dense, unpigmented; axis: usually thin, sometimes rose pigmented; Apothecia: unknown; Spot tests: K+ yellow turning red, C-, KC-, P+ orangish yellow; Secondary metabolites: salazinic (major) and bourgeanic (major) acids, rarely salazinic acid alone, or rarely salazinic and norstictic acids.

Substrate and ecology: on bark, sometimes on wood, rarely on rock in the chaparral, oak woodland, oak-pine forests; mainly on Quercus sp., Pinus sp. and diverse shrubs between 0 and 650 m of altitude; World distribution: southwestern Europe, Macaronesia, western North America and South America; Sonoran distribution: coastal, southern California in the Channel Islands, and Isla Cedros in Baja California.

Notes: The main diagnostic characters of U. esperantiana are its constricted branches at attachment points, its large and even soralia without isidiomorphs and the usual presence of bourgeanic acid.

Usnea flavocardia Räsänen, Revista Universitaria (Santiago) 21 (1): 139 (1936).


Thallus: erect-shrubby, short, 1.5-5 cm long; branching: anisotomic dichotomous, divergent; basal part: concolorous to branches or pale brown to brownish black; branches: cylindrical to irregular, swollen or fusiform, lateral branches distinctly to not narrowed at point of attachment; foveoles or transversal furrows: present or absent; segments: terete, cylindrical to strongly sausage-like; papillae: nearly absent to numerous, irregularly distributed on main branches; tubercles and fibrices: absent to few; fibrils: short (1-2 mm) and slender, few to numerous, irregularly distributed on branches, giving sometimes a spinulous aspect to the branches; soralia: usually numerous, as large or larger than half the diameter of the branch, convex, plane or slightly excavate, developing initially on the cortex or at the top of eroded tubercles, especially at the apical part of the branches, fusing together and often covering entirely the apices; isidiomorphs: present on young soralia, rarely on mature ones; cortex: thin (4-6%), shiny, with minute purple red spots (sometimes absent or rare); medulla: thin to most frequently thick, usually two layered: compact close to the cortex and lax around the axis, sometimes pale yellow peripherally; axis: thin to thick, unpigmented or yellowish orange to pale orange (especially at the apices); Apothecia: not seen; Spot tests: K+ intense yellow, C+ intense yellow, KC+ intense yellow, P+ orangish, or K-, C-, KC-, P-; Secondary metabolites: fatty acids, or norstictic ±fatty acids, or none detected.

Substrate and ecology: on bark or rock, rarely on wood, mainly coastal between 200 and 800 m, on Quercus spp., Pinus spp. and diverse shrubs in Quercus woodland, Quercus forests or in the chaparral; World distribution: Europe, North Africa, North and South America, Macaronesia; So-
noran distribution: common on the Channel Islands and mainland of southern California and scattered in coastal Baja California.

Notes: In eastern North America the red dots covering the cortex are diagnostic for *U. flavocardia*. *Usnea brattiae* may also have some red spots on the cortex as well, but these are very localized on some of the papillae.


**Thallus:** shrubby to subpendant, 2-10 cm long; **branching:** both isotomic- and anisotomic-dichotomous, divergent; **basal part:** usually conspicuously blackened on 2-4 mm or more; **branches:** tapered, lateral branches not constricted at attachment point; **annulations:** numerous and conspicuous with white rings of medullary tissue; **segments:** terete and cylindrical; **papillae:** verrucous to cylindrical, usually numerous and irregularly to densely disposed on main and secondary branches; **tubercles:** usually present and numerous, often eroded and white at their top, mainly on terminal branches bearing apothecia; **fibercles:** rare, irregularly distributed; **fibrils:** slender, 1-6 mm long; **soralia** and **isidiomorphs:** absent; **pseudocyphellae:** present on fibrils growing on branches or at the edge of apothecia; **cortex:** thick (9-15 %) dull; **medulla:** thin and compact, unpigmented; **axis:** at least twice as much larger than the medulla; **Apothecia:** 2-12 mm in diam., terminal and lateral; **ascospores:** ellipsoid, 10-11 x 6-7 µm; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** salazinic acid; norstictic and salazinic (weak) acid.

**Substrate and ecology:** mainly on bark of *Pinus* spp. and *Quercus* spp. in pine-oak forests, between 1800 and 2550 m; **World distribution:** Europe, Taiwan, and Mexico; **Sonoran distribution:** Sierra Madre Occidental.

**Notes:** The Mexican specimens agree morphologically and anatomically well with the European specimens, but differ chemically. Although it is well known that, in species occurring both in Europe and North America, the secondary products diversity in North America is larger, it is still unsure whether such specimens with salazinic and/or norstictic acid can be accepted as chemical variants of the thamnolic/squamatic acid containing *U. florida* s. str. *Usnea subfuscja* Stirt. with salazinic acid, occuring in northeastern U.S.A. and in central Mexico, is morphologically identical with *U. florida* but has smaller spores (7-9 x 5-6 µm).


Illustrations: Clerc (1987a), figs 7, 10, 13, 14, 15, 16, 19, 25 & 26; Ohmura et al. (2000), fig. 1; Herrera-Campos et al. (2001), figs. 10 & 13d; and Brodo et al. (2001), p. 719.

**Thallus:** erect-shrubby to subpendulous, 3-8 cm long; **branching:** main branches and secondary ones anisotomic-dichotomous; **apices:** ±isotomic-dichotomous; **basal part:** concolorous with the branches to pale brown or black; **branches:** irregular to tapering; lateral branches: distinctly narrowed at attachment points; **segments:** terete, ±sausage-like; **papillae/tubercles:** low, hemispherical to verrucose, primarily on main branches, ±densely and regularly distributed; **fibercles:** absent to few on main branches; **fibrils:** rather long, 2-4 mm, slender, unevenly distributed, sparse to numerous; **soralia:** punctiform to enlarged and thus wider than half the diameter of the branch, stipitate, developing mainly on top of tubercles typically on main and secondary branches or initiated on the cortex (apices), plane or often efflorescent-excrecent, circular with a distinct and sharply delimited cortical rim (especially on main branches), sometimes confluent but mainly remaining distinct; **isidiomorphs:** sparse to typically numerous and long (up to 0.3 mm); **pseudocyphellae:** absent; **cortex:** thin to moderately thick (5-9%), shiny; **medulla:** thick, lax to dense; **central axis:** thin to moderately thick, unpigmented; **Apothecia:** not seen; **Spot tests:** K+ slowly yellowish to dull yellow, C-, KC-, P+ deep yellow, or K+ yellow slowly turning orangish, C-, KC-, P+ deep orange.
or K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow; **Secondary metabolites:** psoromic acid (major), ±2-O-demethylpsoromic acid (minor), or stictic acid (major), norstictic acid (major), ±constrictic acid (minor), ±cryptostictic acid (minor), ±menegazziaic acid (minor), or norstictic acid (major), ±connorstictic acid (minor), salazinic acid (major)

**Substrate and ecology:** on bark of *Quercus* spp. and *Pinus* spp. or on scrubs, rarely on dead wood or on rock; in low *Quercus* forests on ridges, in oak-pine woodlands, pine forests or in the chaparral, between 30 and 550 m; **World distribution:** northwestern Europe, eastern and western North America, and Japan; **Sonoran distribution:** common on the Channel Islands (especially Santa Cruz Island) and coastal areas of southern California and scattered in Baja California.

**Notes:** When well developed, *Usnea fragilescens* is easy to recognize. It is distinguished by its large, ±circular and even to slightly concave soralia with numerous isidiomorphs present on main and terminal branches, its constricted branches at attachment points, its glossy and thin cortex and the presence of psoromic acid (main chemotype in the area). When soralia are not well developed, distinction from *U. cornuta* requires careful examination (soralia usually absent on main branches of *U. cornuta*) and chemical analysis. There is, for instance, a morphotype with psoromic acid collected on rocks in Santa Rosa Island that is morphologically close to *U. fragilescens*, but that has numerous minute and irregularly shaped soralia covered with isidiomorphs on the main and secondary branches. Such a morphotype can be interpreted as being an intermediate between *U. cornuta* and *U. fragilescens*.


**Thallus:** shrubby, compact, 2-5 cm long; **branching:** isometric- to anisometric-dichotomous, divergent; **basal part:** usually distinctly jet black; **branches:** tapered, lateral branches not narrowed at attachment points; **segments:** terete, cylindrical; **papillae:** few to numerous, verrucous, irregularly distributed; **tubercles** and **fibercles:** generally absent; **fibrils:** usually slender and ±long (2-3 mm long when mature), few to numerous especially on main branches, ±regularly distributed; **soralia:** deeply excavate, tearing off the cortex around the soralia, as large as the branches when mature, often reaching the central axis and encircling the branches, ±widely spaced and usually not confluent, arising initially on the cortex; **isidiomorphs:** always absent; **cortex:** dull to shiny, thick (7-14%); **medulla:** in average thin, dense; **axis:** thick; **Apothecia:** not seen; **Spot tests:** medulla K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow, or K+ yellow slowly turning pale orange, C-, KC-, P+ deep orange, or K-, KC-, C-, P-; **Secondary metabolites:** norstictic acid ±zeorin or stictic acid group ±zeorin or only usnic acid.

**Substrate and ecology:** mainly on bark of *Quercus* spp. in low forests on exposed ridges or on shrubs in the chaparral between 200 and 500 m; **World distribution:** Europe, western and eastern North America; **Sonoran distribution:** coastal, southern California, including the Channel Islands.

**Notes:** Besides *Usnea lapponica*, *U. fulvoreagens* is the only species in the area, that has lateral branches not narrowed at attachment points and deeply excavate soralia without isidiomorphs. *Usnea fulvoreagens* has an isotomic-dichotomous branching pattern, tapered branches, a thinner medulla, a complex chemistry and belongs to the “*Usnea florida* group” whereas *U. lapponica* has an anisotomic-dichotomous branching, cylindrical to irregular branches, a thicker medulla, mostly salazinic acid, a different distribution pattern and belongs to the “*U. rigida (= U. intermedia)*.group”. For differences from *U. substerilis* and *U. diplotypus*, see the discussion under *U. substerilis*. 


Thallus: erect-shrubby, 2-5(-7) cm long; branching: glossy on the surface, mostly anisotomic-dichotomous, divergent; basal part: concolorous to branches or brown to black at the very base; branches: ±inflated and fusiform, distinctly narrowed at attachment points, ±foveolate or with transverse furrows; apices: often thick and recurved; segments: terete and ±sausage-like or irregular; papillae: absent or indistinct and irregularly distributed, rarely abundant; tubercles: absent; fibercles: absent; fibrils: absent to abundant, short (1-2 mm) and spinulous, irregularly distributed on the whole thallus; soralia: broad, larger than half of diameter of branches, plane to excavate and exposing axis, circular to irregular, arising initially from the cortex, mainly on terminal branches and fibrils, often confluent and covering the whole extremities of the branches; soredia: granular; isidiomorphs: absent; pseudocyphellae: absent; cortex: thin (3-5%) and smooth, shiny to vitreous; medulla: usually thick, very loose, unpigmented; axis: usually thin, unpigmented; Apothecia: not seen; Spot tests: K- brownish-greenish, C-, KC-, P+ orangish yellow to orange; Secondary metabolites: medulla with protocetraric acid, ±fumarprotocetraric acid, ± diverse unknowns, ±fatty acids.

Substrate and ecology: on bark of Quercus spp. and Pinus spp., and diverse scrubs in the chaparral or low oak and pine forests, between 0 and 500 m; World distribution: circumpolar in boreal, temperate and Mediterranean regions of the Northern Hemisphere; Sonoran distribution: coastal, southern California, including the Channel Islands.

Notes: Usnea glabrata is a small species with very characteristic features: distinctly swollen branches and segments, large and excavate soralia without isidiomorphs, thin cortex and very lax medulla with protocetraric acid.


Thallus: pendulous, up to 250 cm long, stiff, poorly to moderately branched; branching: anisotomous-dichotomous, parallel; basal part: concolor with or paler than branches, with distinct annulations, often with many points of attachment; branches: cylindrical to irregular; lateral branches: not narrowed at point of attachment; segments: cylindrical to slightly trapezoidal, weakly to strongly ridged, sometimes slightly alate, rarely with erose cortex; papillae: conspicuous, abundant, large, cylindrical to truncate-conical, paler at top, sometimes eroded, irregularly distributed mainly on secondary and thinner branches; tubercles and fibercles: absent; fibrils: short (0.5-2 mm) to long (3-10 mm), mostly spinulose, in a fish-bone like arrangement; soralia and isidiomorphs: absent; pseudocyphellae: short and linear, inconspicuous on secondary and thin branches; cortex: thin to moderately thick (5-12%); medulla: thin and compact, non pigmented; axis: thick, often fistulose at base of main branches; Apothecia: up to 2 cm in diameter, lateral; Spot tests: K+ yellow turning red, C-, KC-, P+ orangish yellow, or K-, C-, KC-, P-; Secondary metabolites: salazinic acid or caperatic acid.

Substrate and ecology: on bark; World distribution: Africa and southern North America; Sonoran distribution: Baja California Sur and Chihuahua.

Notes: Usnea goniodes is closely related to U. transitoria, differing only by the production of numerous apothecia and the absence of soralia.


Synonym: Usnea herrei Hale, nom. illeg.; Illustrations:

**Usnea hirta** (L.) F. H. Wigg., Prim. Fl. Holst. 91 (1780).

**Thallus:** erect-shrubby to supendant, usually between 2 and 6 cm long; **branching:** isometric-dichotomous at least in apical parts, mostly divergent; **basal part:** mostly with reddish brown pigment or of the same color as branches, with conspicuous annular cracks; **branches:** usually tapering, sometimes slightly irregular; lateral branches: not or slightly to distinctly narrowed at ramification point; foveoles and transversal furrows: sometimes present; **segments:** terete to slightly ridged, cylindrical to slightly sausage-like, with slightly inturned ends; **papillae** and **tubercles:** verrucose, sparsely and unevenly distributed; **fibercles:** absent; **fibrils:** 2-4 mm long, slender sparsely and unevenly distributed close to basal part, absent in upper parts; **soralia:** punctiform to large, slightly stipitate, smaller than half diameter of branches but often enlarged, few to numerous, arising on low tubercles in lower part of thallus, and initially on the cortex of the apices; **isidiomorphs:** mostly visible on young soralia but sometimes densely covering mature, large and capitate soralia, never single on plain cortex, rarely slightly blackened at tips; **pseudocyphellae:** absent; **cortex:** thin to thick (5-9%), dull, distinctly transversely cracked at base of main branches; edges of cracks: even or slightly inturned; **medulla:** thick, compact to dense, and often rose pigmented periaxially; **axis:** moderately thick, almost always pink pigmented; **Apothecia:** not seen; **Spot tests:** medulla K+ yellow turning red, C-, KC-, P + orangish yellow; **Secondary metabolites:** medulla with norstictic and salazinic acids (major) and ±protoproterteric acid (accessory).

**Substrate and ecology:** on acidic rock in the mountains between 2300 and 2800 m; **World distribution:** so far only known from North America; **Sonoran distribution:** Santa Rita Mountains in Arizona and Sierra Madre Occidental in Chihuahua and Sinaloa.

**Notes:** Potentially **U. halei** may be confused with **U. amblyoclada** as both occur on rock in the area. **Usnea halei** differs from **U. amblyoclada** by having a dull cortex, a different type of soralia with a different ontogeny, fibrils that are never spinulosus although slender, short papillae and a different chemistry.

**Substrate and ecology:** on bark and dead trees or wood, occasionally on rock in the area. **World distribution:** probably cosmopolitan on every continent; **Sonoran distribution:** mountains of Arizona, southern California, Baja California and Sinaloa.

**Note:** Two subspecies of **U. hirta** are recognized, one widely distributed and one restricted to Baja California. Intermediate specimens occur in the area of overlap.

**Usnea hirta** ssp. hirta

Thallus: usually flaccid; cortex: thin (3-7%) dull to ±shiny; medulla: lax, rarely dense.

Substrate and ecology: inland on bark (on *Pinus* spp., *Quercus* spp., *Pseudotsuga menziesii*, *Abies* spp., *Picea* spp., etc.) or on wood, very rarely on rock, mainly in mixed conifer-oak forests, ponderosa pine forests, spruce-fir communities, oak-juniper woodlands, between 650 and 3600 m; World distribution: probably cosmopolitan on every continent; Sonoran distribution: a frequent inland taxon in the mountains of Arizona, the Sierra Madre Occidental of Chihuahua, and northern Baja California, rarely in southern California and Baja California (Isla Cedros) near the ocean at low altitudes.

subsp. **trachista** (Motyka) P. Clerc, **comb. nov.**


Thallus: stiff; cortex: thick (6-14%) distinctly shiny, sometimes orange pigmented, at least in part, especially on main branches; medulla: compact, rarely dense.

Substrate and ecology: on bark in desert coastal scrub communities, on *Fouqueria* spp., on *Machaerocereus* spp., etc. between 0 and 220 m or in oak forests, on *Quercus* spp. between 1200 and 1400 m; World and Sonoran distribution: Baja California and Baja California Sur.


Thallus: shrubby, usually short, 3 to 6 cm long, ±stiff; branching: anisotomic-dichotomous, divergent; basal part: concolorous with the branches to pale; branches: main ones: irregular, distinctly segmented, ±swollen; lateral branches: not narrowed at point of attachment; segments: terete to strongly ridged, cylindrical to ± sausage-like; transversal furrows/foveoles: numerous on main branches; papillae: absent (can be mistaken with young fibrils); tubercles: absent; fibercles: nearly absent to numerous; fibrils: short and thick, spinulous, numerous and crowded (80-100 fibrils/0.5 cm on main branches); soralia and isidiomorphs: absent; cortex: thin (3-7%), distinctly shiny, often distinctly cracked on main branches; medulla: dense to compact, often partly chalky, with subcortical orange to red orange pigment, sometimes very faint, rarely absent; axis: thin to wide; Apothecia: often on short lateral branches, sometimes terminal to subterminal, 2 to 15 mm in diam.; ascospores: ellipsoid, 9-11 x 5-7 µm; Spot tests: medulla K-, C-, KC-, P-; Secondary metabolites: usnic acid, ±fatty acids (major), ±unknowns (minor).

Notes: *Usnea horrida* is morphologically and chemically

![Fig. 8: Usnea horrida, photo by P. Clerc](image-url)
close to *U. parvula*. It differs by its reddish orange subcortical pigment, its dense to compact single layered medulla and its distributional range.


**Thallus:** shrubby to subpendant, 2-12 cm long, compact to loose; **branching:** anisotomic-dichotomous; **basal part:** usually black on a narrow and irregular zone, rarely conspicuously blackened on 2-4 mm, sometimes concolorous with the branches, with few indistinct annular cracks; **branches:** irregular; lateral branches: not narrowed at attachment point, but sometimes ±fusiform; annulations usually few (1-4/0.5 cm) and indistinct, rarely conspicuous and numerous; **segments:** terete to flattened, slightly to distinctly sausage-like, usually with foveoles and/or transverse furrows; **papillae:** verrucose, few to numerous, irregularly to dense on main and secondary branches; **fibrules:** few to numerous, ±large and conspicuous, sometimes of irregular shape, often eroded and white at their tip, mainly on *Quercus* spp., *Pinus* spp., and *Pseudotsuga* in mixed conifer forests or pine-oak-fir forests or Douglas fir forests or in the spruce fir zone, between 1800 and 2900 m; **World distribution:** Europe and western North America; **Sonoran distribution:** mountains of Arizona and Sierra Madre Occidental of Chihuahua.

**Notes:** There are no visible differences between the western North American (*U. arizonica*, *U. retifera*) and the European specimens (*U. intermedia*), and therefore they are considered here as conspecific. *Usnea lecanorica* W. Culb., C. Culb & Fiscus with lecanoric acid is also morphologically and anatomically close to *Usnea intermedia*. Moreover, a specimen with thamnolic acid has been found in New Mexico. Detailed studies are needed to understand the signification of these different chemistries.


**Thallus:** shrubby to subpendant, 2 to 12 cm long, forming dense erect to subpendant tufts; **branching:** anisotomic-dichotomous; **basal part:** concolorous with the branches, to distinctly blackened; **branches:** cylindrical to irregular, inconspicuously segmented; lateral branches: not narrowed at point of attachment; **segments:** terete and ±cylindrical, sometimes slightly swollen, foveoles or transversal furrows often present; **papillae:** usually numerous especially on main branches, verrucose to cylindrical; **fibrules** and **fibrils** generally absent; **soralia** and **isidiomorphs** absent; **pseudocyphellae** present on fibrils growing on branches or at the edge of apothecia; **cortex:** thin to moderately thick (5-8%), dull to ±shiny; **medulla:** lax to dense, unpigmented; **axis:** usually of the same width than medulla; **Apothecia:** 2-13 mm in diam., terminal, subterminal or lateral; **ascospores:** broadly ellipsoid, 7-9 x 5-6 µm; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow, or K-, C-, KC-, P-; **Secondary metabolites:** salazinic acid (major) or no medullary substances.

**Substrate and ecology:** on bark rarely on wood or rock,
tests: medulla K+ yellow turning dark red (or deep yellow), C-, KC-, P+ orange or K-, C-, KC-, P+ deep yellow; Secondary metabolite: salazinic acid (major) or psoromic acid (major), respectively relative to spot tests.

Substrate and ecology: on bark, especially on Abies spp., Pinus spp., Picea spp., and Quercus spp., usually in mixed conifer forests, between 2300 and 3400 m; World distribution: holarctic, mainly in continental areas; Sonoran distribution: common at upper elevations in Arizona and extending to Chihuahua, rare in coastal areas of southern California and Baja California.

Notes: For differences between Usnea lapponica and U. fulvopseudota, see under the latter species.  

Usnea mexicana Vain. Dansk Botanisk Archiv. 4: 3 (1926).

Synonym: Usnea duriuscula Motyka; Illustrations: Swinscow & Krog (1978), fig. 23 (as U. gigas); Stevens (1990), fig. 2 (as U. himantodes); Stevens (1999), fig. 3E (as U. himantodes).

Thallus: pendulous, 5 to 50 cm long, stiff and barely rami-fied; branching: anisotropic-dichotomous, parallel; basal part: concolorous with branches to brownish blackish, often with multiple attachment points; branches: cylindrical and distinctly segmented; lateral branches: not narrowed at point of attachment; segments: terete, slightly ridged to weakly alate, smooth to conspicuously cracked and areolated, with eroded cortex at some places especially at the edges; papillae: indistinct to verrucous, irregularly distributed, from scattered to abundant; tubercles: absent; fibers: few to numerous; fibrils: long (5-15 mm), abundant, usually in fish-bone like pattern; soralia: punctiform, smaller than the diameter of the branch, plane to slightly stipitate, arising on fibers and on cracks at the ridge of the ±alate branches, scattered to numerous; isidiomorph: nearly absent to numerous; pseudocystellae: inconspicuous, long and narrow on thin branches; cortex: thin to moderately thick (3-10%), dull to shiny; medulla: thin and compact, unpigmented; axis: thick, with ochraceous brown pigment, fistulose in thickest branches, brittle; Apothecia: not seen; Spot tests: K-, C-, KC-, P+ orangish yellow, or K+ yellow turning red, C-, KC-, P+ orangish yellow, C-; Secondary metabolites: diffractaic acid (major), ±salazinic acid (major), ±constictic acid (minor) or salazinic acid (major), ±protocetraric acid (minor) or protocetraric acid (major).

Substrate and ecology: on bark between 1200 and 1900 m in mixed conifer-oak forests; World distribution: pantropical: southern North America, South America, Africa, eastern Asia and Australia; Sonoran distribution: so far known only from Guadalupe Island in Baja California.

Notes: Usnea mexicana is closely related to U. himantodes, from which it seems to differ only by the reproductive strategy (U. himantodes produces no soralia, only apothecia). The pendulous habitus, its brown pigmented and ±fistulous central axis and its chemistry are diagnostic characters for U. mexicana.
±thick (6-11%), hard and shiny; medulla: ±thin, dense to compact, with pink to red-wine pigment; axis: thin to thick, sometimes pink pigmented; Apothecia: not seen; Spot tests: K± yellow, C+ orangish yellow, KC+ organish yellow P± orange; Secondary metabolites: Eumitrin A₂ (major), fatty acids of the murolic acid complex (major), norstictic acid (major), diverses unknowns (minor).

Substrate and ecology: on bark, rarely on rock, in the chaparral and other coastal shrub communities, on Quercus spp. and diverse shrubs, between 0 and 500 m; World distribution: southwestern Europe, eastern and western North America, eastern Asia; Sonoran distribution: Channel Islands (mainly Santa Catalina) of southern California and Baja California.

Notes: This species may morphologically and chemically somewhat ressemble U. hirta, but the presence of the wine red pigment in the medulla leaves no doubt about its identity. Moreover, U. mutabilis has a thicker cortex (6-11%) than U. hirta s. str. (3-7%). Finally, the medulla in U. hirta is lax; whereas, it is dense to compact in U. mutabilis.

Usnea myrmaiacaina P. Clerc, sp. nov.

Diagnosis: Fungus corticola. Thallus 9 cm altus, erectus.
Thallus: shrubby to subpendant, 2-10 cm long, compact to loose; branching: anisotomic-dichotomous, divergent; basal part: usually conspicuously blackened on 2-4 mm, rarely only on a narrow and irregular zone; branches: ±irregular to fusiform (secondary branches); lateral branches not narrowed at attachment point, but sometimes ±fusiform; usually with numerous annular cracks (4-8/0.5 cm) and conspicuous with white rings of medullary tissue (primary branches, close to basal part); often with distinct transversal furrows; segments: terete (primary branches), often and characteristically slightly ridged giving to the branch an angular aspect in surface view (secondary branches) or flattened; papillae: cylindrical, few to numerous, irregular to dense, on main and secondary branches; tubercles (young stage of fibrils?): usually absent to numerous (especially on terminal branches bearing apothecia), ±large and verrucous, conspicuous, irregular, rarely eroded; fibercles: present mainly on secondary and terminal branches bearing apothecia; fibrils: slender, 1-6 mm long, usually numerous, regularly distributed in fibbone-like pattern; soralia and isidiomorphs: absent; pseudocyphelae: present on fibrils growing on branches or at the edge of apothecia; cortex: moderately thick to thick (8-11 %), mat to ±shiny; medulla: dense to compact, unpigmented; axis: usually larger than medulla; Apothecia: 2-13 mm in diam., terminal or lateral; ascospores: broadly ellipsoid, 9-11.5 x 5-7 µm; Spot tests: K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow, or K-, C-, KC-, P-; Secondary metabolites: norstictic acid (major), ±fatty acids (minor), or rarely none detected.

Substrate and ecology: on bark (Quercus spp. and Pinus spp.), rarely on wood, in oak, pine-oak forests or thorn forests (southern area), between 1500 and 2600 m, especially on windy crests of mountains; World distribution: western coast of North America; Sonoran distribution: mountains of Arizona, Baja California Sur, Sinaloa, Chihuahua, and Sonora.

Notes: Morphologically, U. myrmaiacaina is close to U. intermedia (irregular branches with ridged segments) but it differs in its spore size and the chemistry, as well as in the width of the cortex, the numerous fibrils arranged in fishbone-like pattern and the distinct annulation pattern in the basal part. Anatomically, U. myrmaiacaina is close to U. florida (spore size, width of the cortex) but differs in having slightly irregular secondary branches with segments that are often ridged, cylindrical papillae as well as a different distribution range. Specimens collected in the southern and south western part of the Sonoran Desert area, with large spores and norstictic acid, can be for the moment only tentatively assigned either to U. myrmaiacaina or to U. florida. More detailed field and taxonomic studies are needed.


Thallus: shrubby, rigid, 2-12 cm long; branching: anisotomic-dichotomous, divergent; basal part: short (1-3 mm), variously pigmented but never jet black, sometimes barely developed, often rugose to ±decorticated; branches: usually tapering, conspicuous with few ramifications, distinctly segmented (especially the main branches) with conspicuous everted medulla between the segments; lateral branches: sometimes slightly narrowed at point of attachment; segments: terete to slightly ridged, cylindrical to slightly sausage-like; foveoles: absent; transversal furrows: sometimes present; papillae: minute, hardly distinct; tubercles: absent; fibercles: large (7-10 x 10-20 µm), conspicuous, and numerous over the whole thallus; fibrils: mature ones rather rare and only present near the basal part, short (1-3 mm), ±slender; short (0.5 mm) isidiomorph-like fibrils: produced (sometimes in bundles) on top of fibercles; soralia and isidiomorphs: absent; cortex: ±glossy, distinctly longitudinally, and transversally cracked with conspicuous medullary tissues coming out from the cracks, thin to moderately thick (5-10%); medulla: dense, moderately thick; axis: sometimes fistulose; Apothecia: not seen; Spot tests: K-, C-, KC-, P+ orangish yellow; Secondary metabolite: protocetraric acid (major).

Substrate and ecology: growing on rocks, at 1950-2800 m; World distribution: endemic to Mexico; Sonoran distribution: only one locality in the Sierra Madre Occidental.

Notes: Usnea nashii is distinguished by the large fibercles
producing short isidiomorph-like fibrils at their summit and the presence of protocetraric acid in the medulla.


Illustrations: Tavares and Sanders (1998), figs. 1 & 2 (as the “southwestern morphotype” of *U. cirrosa*); Brodo et al. (2001), fig. 879 (as *U. cirrosa*).

**Thallus:** shrubby, usually short, 3 to 8 cm long, ±stiff; **branching:** anisotomic-dichotomous, divergent; **basal part:** concolorous to the branches or paler; **branches:** main branches: irregular, distinctly segmented, ±swollen; lateral branches: not narrowed at point of attachment; **segments:** terete to strongly ridged, cylindrical to ±sausage-like; transversal furrows/foveoles: numerous on main branches; **papillae:** absent although young fibrils may be mistaken for such; **tubercles:** absent; **fibercles:** nearly absent to numerous, looking like pseudocyphellae; **fibrils:** short, spinulous, numerous and crowded (80-100 fibrils/0.5 cm on main branches); **soralia and isidiomorphs:** absent; **cortex:** thin (2-6%), dull to distinctly shiny, never cracked; **medulla:** usually two layered: compact close to the cortex and lax around the axis, not pigmented; **axis:** thin to wide; **Apothecia:** terminal to subterminal, 2 to 17 mm in diam.; **spores:** 7.5-9 x 3-5 µm; **Spot tests:** medulla K-, C-, KC-, P-; **Secondary metabolites:** usnic acid, ±fatty acids (minor), ±unknown (minor).

**Substrate and ecology:** mainly on bark of *Pinus* spp. and *Pseudotsuga menziesii* in coniferous forests or pine-oak vegetation in the mountains between 1800 and 3100 m and exceptionally coastal on shrubs; **World distribution:** southwestern U.S.A., Mexico, and South America; **Sonoran distribution:** mountains of Arizona, Sierra Madre Occidental of Chihuahua, exceptionally along coastal California (one specimen found on San Nicolas Island at 150 m).

**Notes:** The lack of soralia and the numerous apothecia in *U. parvula* separate it from the very similar *U. hirta*. *Usnea parvula* could be considered as the primary species of *U. hirta*. In *Usnea intermedia*, the short, numerous and crowded spinulous fibrils are absent, the basal part is usually black and salazinic acid is present in the medulla. *Usnea cirrosa* has lateral branches that are distinctly constricted at ramification points and nosrtictic acid in the medulla.

A few specimens from Mexico (Chihuahua, Sinaloa, and Sonora) agree morphologically and anatomically well with *U. parvula*. However, they produce salazinic acid, ±nrostictic or only constictic acid in the medulla. More field work and more specimens are needed to understand these chemical variants.


**Thallus:** erect-shrubby, up to 2-6 cm long; **branching:** anisotomic- to isotomic-dichotomous; **basal part:** jet black to brownish black; **branches:** tapered; lateral branches: not narrowed at attachment points; **segments:** terete or sometimes slightly ridged, cylindrical; **papillae:** few to numerous, verrucous, principally on main branches; **tubercles:** few, irregularly distributed; **fibercles:** numerous on terminal branches, looking like pseudocyphellae, coalescing together, frequently evolving into soralia; **fibrils:** few to numerous, ±regularly distributed, short (< 3 mm); and
slender; *soralia*: minute, irregular, without a reflexed edge, smaller than half of the diameter of the branch, arising mainly on fibercles, even and plane, frequently fusing together and looking like a large soralium, generally numerous, sometimes covering entirely the terminal branches; *isidiomorphs*: short and spinulous, numerous especially on young soralia but present on mature soralia as well; *pseudocyphellae*: absent; *cortex*: thin to moderately thick (6-10%), dull to shiny, *medulla*: usually thin, dense to compact, sometimes peripherally orange pigmented; *axis*: thick, non pigmented; *Apothecia*: not seen; *Spot tests*: K+ dull yellow turning reddish orange, C-, KC-, P+ deep yellow; *Secondary metabolite*: norstictic acid (major).

**Substrate and ecology:** mainly on bark of *Quercus* spp. near the coast between 200 and 500 m or inland in the mountains on *Quercus hypoleucoides* at intermediate elevations; **World distribution**: Eurasia and North America; **Sonoran distribution**: southern California, especially the Channel Islands.

**Notes:** Morphologically *U. praeter** is difficult to separate from *U. subfloridana*. The latter species has soralia with slightly reflexed margins (50x!) producing a cortical rim that well delimits the soralia, that develop initially on the cortex. These soralia become shortly stipitate, slightly convex at the top and usually remaining separate. In contrast, *U. praeter** has ± diffuse soralia, unstipitate, developing on fibercles and coalescing together. The diameter of the soralia is smaller and the density of the soralia is on average higher in *U. praeter** than in *U. subfloridana*. Anatomically, *U. subfloridana* has a tendency to have a thicker cortex and a thinner central axis than *U. praeter**. Chemicaly, *U. praeter** has norstictic acid in the medulla whereas *U. subfloridana* produces thannolic and/or squamatic acids.


**Thallus:** erect-shrubby to subpendant, 3-15 cm long; **branching:** anisotomic-dichotomous, divergent; **basal part:** darker than branches or of the same color with conspicuous annular cracks; **branches:** tapering; lateral branches: not narrowed at attachment point; **segments:** terete and cylindrical; **papillae:** absent to numerous and indistinct on main branches; **tubercles:** absent to numerous on main and secondary branches, usually absent on the terminal branches, short and verrucous, sometimes eroded at top; **fibercles:** absent to numerous, irregularly distributed on main and secondary branches; **fibrils:** nearly absent to numerous, short and spinulous to long and slender, irregularly distributed on the whole thallus; **soralia:** punctiform, irregular in outline, even or slightly stipitate, plane to erumpent, developed initially from the cortex (on the whole thallus) or on top of tubercles (on main branches), or on fibercles (main and secondary branches), nearly absent to numerous, sometimes fusing together and entirely covering the terminal branches; **isidiomorphs:** always present, generally numerous and conspicuous on secondary and terminal branches; **pseudocyphellae:** absent; **cortex:** moderately thick to thick (6-15%), shiny to vitreous, hard, frequently transversely or longitudinally cracked, with a red pigment; **medulla:** thin to moderately thick, dense to compact, not pigmented; **axis:** moderately thick to thick, not pigmented; **Apothecia:** not seen; **Spot tests:** K+ dull yellow slowly turning orange, C-, KC-, P+ deep orange; **Secondary metabolites:** stictic (major), ±norstictic (minor), ±constictic (minor), ±cryptostictic (minor), ±menegazziaic (minor) acids.

**Substrate and ecology:** on bark of *Quercus* spp., *Pinus* spp., and diverse shrubs, rarely on rock, in oak, pine-oak forests and in chaparral or in coastal scrub communities between 0 and 500 m; or in the southern mountains between 1500 and 2500 m; **World distribution:** suboceanic, oceanic temperate and tropical regions: Europe, eastern Asia, Australasia, Africa, North and South America, and Macaronesia; **Sonoran distribution:** coastal areas of southern California (including the Channel Islands), Baja California, and Baja California Sur, and Sinaloa.
**Notes:** *Usnea rubicunda* is a very polymorphic species characterized by its red pigment in the cortex and the numerous minute soralia with conspicuous isidiomorphs.

**Usnea scabrata** Nyl. s.l., Flora 58: 103 (1875).

Synonym: *Usnea scabiosa* Motyka; Illustrations: Halonen et al. (1998), fig. 7; Herrera-Campos et al. (1998), figs. 5f and 10b; Brodo et al. (2001), p. 724.

**Thallus:** shrubby, subpendant to usually pendant, 5 to 15 cm long; **branching:** anisotomic-dichotomous, usually parallel; **basal part:** concolor with branches to brown or brownish black, with or without inconspicuous annular cracks; **branches:** irregular; lateral branches: not narrowed at point of attachment; **segments:** terete to ridged, cylindrical to slightly swollen or sausage-like; foveoles and transversal furrows: present or absent; apices: long, ± sinuous, often running parallel and densely packed; **papillae** and **tubercles:** nearly absent to numerous, indistinct to verrucose, often eroded and white at top, sometimes confluent and forming striations at the surface of the cortex; **fibercles:** absent and then fibrils numerous or usually and characteristically numerous and dense on main and secondary branches, with a distinct hole in the center; **fibrils:** usually numerous, irregular, and in some parts of the branches dense, polymorphic [short and isidiomorph-like to long and sinuous (2-3 mm)]; **soralia:** absent to numerous, punctiform, smaller than half the diameter of branches, developing on fibercles or on top of tubercles, even to slightly stipitate; **isidiomorphs:** absent to numerous (young fibrils?); **pseudocyphellae:** absent; **cortex:** thin to thick (6-13%), dull to slightly shiny; **medulla:** loose to dense; **axis:** moderately thick; **Apothecia:** absent to few; **Spot tests:** medulla K+ yellow turning red, C-, KC-, P+ orangish yellow, or K-, KC-, C-, P-; **Secondary metabolites:** usnic acid and salazinic acid (major), or rarely usnic acid alone.

**Substrate and ecology:** on bark (especially *Quercus* spp. and shrubs) in coastal chaparral or oak-pine woodlands at 200 and 400 m or in the mountains in mixed conifer forests between 2500 and 3000 m; **World distribution:** holarctic; **Sonoran distribution:** southern California, including the Channel Islands (Santa Cruz), and the high mountains of Arizona and Chihuahua.

**Notes:** *Usnea scabrata* s.l. is a very polymorphic species with numerous transition forms between the different morphs. Characteristic features include its pendulous habitus when optimally developed, numerous fibriles when the fibrils are shed, its irregular branches with ± swollen segments, and its short isidiomorph-like to ± long and sinuous polymorphic fibrils that are often very dense along the branches. *Usnea diploptypus* has punctiform soralia with clusters of true isidiomorphs; the fibrils are not so numerous and dense fibriles are usually absent. *Usnea filipendula* has a jet black basal part, branches and segments that are cylindrical and a thicker cortex.


**Thallus:** pendulous, up to 55 cm long; **branching:** isotomic to anisotomic dichotomous, mostly parallel; **basal part:** concolorous to or paler than branches, often with a orange-brown pigment, conspicuously annulate; **branches:** cylindrical to slowly tapering, distinctly segmented and annulated, slowly tapering; lateral branches: not narrowed at attachment points; apices: ± thick; **segments:** terete and cylindrical; **papillae, tubercles and fibercles:** absent; **fibrils:** long (5-20 mm), distinctly curved, often numerous and arranged in a ± fishbone-like pattern; **soralia:** punctiform, usually smaller than half of branch diameter, arising at surface of cortex from maculae or on small elevations and then slightly stipitate, convex, sometimes confluent, often immature and resembling pseudocyphellae, rarely mature and enlarged, formed mainly on lateral branches but on thicker branches too; **isidiomorphs:** not frequent, very small on young soralia and regenerative parts; **pseudocyphellae:** absent; **cortex:** thick (9-15% of the radius), dull; **medulla:** usually very thin, compact, unpigmented; **axis:** thick and unpigmented; **Apothecia:** not seen; **Spot tests:** K-, C-,
KC-, P+ orangish yellow; **Secondary metabolites:** protocetraric (major) and ±lobaric (minor) acids

**Substrate and ecology:** on bark, rarely on rock; **World distribution:** western Europe, Macaronesia, eastern and western North America, South America, Africa, and Asia; **Sonoran distribution:** Guadalupe Island (Baja California) and Sinaloa (Sierra Madre Occidental)

**Notes:** Its pendulous habitus, its cylindrical branch segments, the dull and soft cortex, its conspicuously annulated basal parts that are often orange-brown, its long and curved fibrils and its production of protocetraric acid in the medulla make *U. schadenbergiana* a very distinctive species. In the Caribbean Islands there is a chemotype with the stictic acid aggr. (*U. schadenbergiana* s. str.)


Illustration: Asahina (1970), fig. 6E.

**Fig. 11:** *Usnea shimadai*, photo by P. Clerc

**Thallus:** shrubby, compact, 2-8 cm long; **branching:** isometric-dichotomous, divergent; **basal part:** distinctly paler than branches or of same color, with numerous and conspicuous annular cracks; **branches:** usually ±irregular; lateral branches: not narrowed or slightly to distinctly narrowed at point of attachment; transverse furrows: rare on Mexican material but present on the type material from Taiwan; **segments:** terete to distinctly ridged, cylindrical to weakly sausage-like; **papillae:** absent; **tubercles:** present, low and verrucous, whitish or eroded on top (probably very young stages of fibrils), not sorediate; **fibercles:** low, numerous, not sorediate; **fibers:** short (1-3 mm), often spinulose, mostly present in oldest part of thallus; **soralia** and **isidiomorphs:** absent; **cortex:** thin to thick (7-10%), shiny like glass, distinctly transversally and longitudinally cracked at the base of main branches; **medulla:** compact to dense and often orange pigmented close to the axis; **axis:** thick; **Apothecia:** present but not numerous, up to 10 mm in diam., mainly terminal to subterminal on terminal branches; **ascospores:** ellipsoid, 8-10 x 5-6 µm; **Spot tests:** medulla K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** norstictic (major) and salazinic (major) and usually galbinic (major) acids, or diffractaic acid (major).

**Substrate and ecology:** on bark or rock in mixed pine-oak forests between 1600 and 2500 m or in thorn forest at lower elevations; **World distribution:** Taïwan and Mexico; **Sonoran distribution:** Sierra Madre Occidental in Chihuahua and Sierra de la Laguna in Baja California Sur.

**Notes:** Among the apotheciate species without soralia, *U. shimadai* is distinguished by the irregular branches, the tubercles that are whitish on the top, the shiny cortex that is conspicuously cracked at the base of main branches and the production of norstictic, salazinic and ±galbinic acids / diffractaic acids in the medulla. *Usnea strigosa* lacks the eroded tubercles and has more densely and regularly disposed fibrils. The relationships with *U. cristatula* Motyka are not well understood yet and further detailed taxonomical work is needed. The specimens with diffractaic acid are only tentatively placed here.

**Usnea silesiaca** Motyka, Wydawn. Muzeum Śląskiego w Katowicach, dz 2, 2: 19 (1930).

Synonym: *Usnea madeirensis* Motyka; Illustrations: Clerc (1987a), fig. 1e (as *U. madeirensis*); Clerc (1991), p. 430 & 431 (as *U. madeirensis*); Clerc (1998), fig. 10 (as *U. madeirensis*).
**Thallus:** erect-shrubby to ±pendulous, 2 to 25 cm long, stiff; **branching:** isotomic-(basal part) to anisotomic dichotomous (extremities), generally divergent; **basal part:** distinctly black pigmented that sometimes reaches the basal part of the main branches, with numerous and conspicuous annular cracks extending upwards; **branches:** cylindrical or tapering; lateral branches: not narrowed at attachment points; **segments:** terete and cylindrical; **papillae:** verrucous to sometimes cylindrical, irregularly distributed, mainly on main branches; **tubercles and fiberles:** absent; **fibrils:** long (3-5 mm), sometimes numerous and giving fishbone-like aspect to the branches; **soralia and isidiomorphs:** absent; **cortex:** thick (9-14 %), dull, distinctly cracked at the base of main branches; **medulla:** thin and compact, not pigmented; **axis:** thick, not pigmented; **Apothecia:** not seen; **Spot tests:** K+ yellow turning red, C-, KC-, P+ orangish yellow; **Secondary metabolites:** salazinic acid (major), and ±protocetraric acid (minor).

**Substrate and ecology:** on bark; **World distribution:** Europe, Macaronesia, eastern and western North America; **Sonoran distribution:** Santa Cruz Island in southern California.

**Notes:** The combination of the following characters makes this species distinct: basal part with black pigmentation extending to the lower parts of the main branches, with numerous and conspicuous annular cracks, thick cortex (9-14%), very thin medulla (7-12%), soralia larger than half the diameter of the branch and the presence of salazinic acid. Sometimes, however, the black pigmentation may almost be absent, or the annular cracks may not be so numerous or the soralia may be badly developed. In these cases, the chemistry is the only distinct character that separates *U. silesiaca* from *U. subfloridana.*


**Thallus:** erect-shrubby, 2 to 5 cm long; **branching:** anisotomic dichotomous, divergent; **basal part:** concolorous with the branches, not distinctly annulate; **branches:** cylindrical to tapering, not distinctly segmented; lateral branches: not narrowed at attachment points; **segments:** terete to distinctly ridged, cylindrical; **papillae and tubercles:** absent; **fibrils:** short (1-2 mm), conspicuous, spinulous, not easily broken away, usually densely and regularly disposed all along the branches, giving a spinulous appearance to the whole thallus; **soralia and isidiomorphs:** absent; **cortex:** shiny, not distinctly cracked, moderately thick (6-8%); **medulla:** dense to compact, not pigmented; **axis:** moderately thick, not pigmented; **Apothecia:** numerous, up to 5 mm in diam., mainly terminal; **ascospores:** broadly ellipsoid, 9-10 x 5-6 µm; **Spot tests:** medulla K-, C-, KC-, P-; **Secondary metabolites:** diffractaic (major).

**Substrate and ecology:** on bark in thorn forest with Acacia, Lysiloma and Jatropha. **World distribution:** mainly eastern and southeastern North America, rare in Mexico; **Sonoran distribution:** southern Baja California.

**Notes:** *Usnea strigosa* has many different chemotypes and needs a modern and thorough revision of its taxonomy. It is characterized by its tufted habit with numerous terminal apothecia, its densely and regularly disposed fibrils that are short and spinulose, its ridged branches that are not narrowed at the point of attachment, the absence of papillae and its basal part that is not black pigmented. All the Mexican specimens studied have an unpigmented medulla. This diffractaic acid chemotype is so far the only chemotype that has been found in Mexico. *Usnea parvula* is morphologically very close to *U. strigosa* but the former species has shorter spores, a thinner cortex, typical foveoles, as well as a lax medulla without diffractaic acid.


Fig. 12: *Usnea subelegans*, photo by P. Clerc

**Thallus:** shrubby-erect, 2-8 cm long; branching: isotoomic- to anisotomic-dichotomous; basal part: paler or of the same color as main branches, without conspicuous cracks; branches: tapering or irregular; lateral branches: not or only slightly narrowed at attachment points; segments: terete and cylindrical; papillae: absent; tubercles and fibercles: generally absent; fibrils: slender and ±long (≥3 mm when mature), few to numerous especially on main branches, ±regular; soralia and isidiomorphs: short and spinulous, numerous especially on young soralia but present on mature soralia as well; pseudocyphellae: absent; cortex: thin (5-9%), glossy, not conspicuously cracked; medulla: large, compact to dense, often peripherally pale pink; axis: moderately thick, often peripherally pale pink; Apothecia: 2-15 mm in diam., mainly lateral, less commonly terminal; ascospores: ellipsoid, 8-10 x 5-6 μm long; Spot tests: medulla K+ yellow turning red, C-, KC-, P+ orangish yellow; Secondary metabolites: cortex with usnic acid; medulla with norstictic (major), galbinic (major) and salazinic (major) acids.

**Notes:** *Usnea subelegans* is very close to *U. dasaea*, from which it differs by its reproduction strategy and the fibrils that are not easily broken away, and hence densely cover the whole thallus.


**Thallus:** erect-shrubby, up to 5-7 cm long, compact and densely branched; branching: isotoomic-dichotomous, divergent; basal part: distinctly jet black with few annular cracks (very rarely concolorous with the branches); branches: tapered; lateral branches: not narrowed at attachment points; segments: terete, cylindrical; papillae: absent; tubercles and fibercles: generally absent; fibrils: slender and ±long (≥3 mm when mature), few to numerous especially on main branches, ±regular; soralia: punctiform, irregular, smaller than half of the diameter of the branch, arising initially on the cortex, slightly stipitate, ±erumpent, sometimes fusing together and looking like a large soralia, generally numerous, covering the terminal branches; isidiomorphs: short and spinulous, numerous especially on young soralia but present on mature soralia as well; pseudocyphellae: absent; cortex: thick (8-12%), dull to shiny; medulla: usually thin, dense to compact, not pigmented; axis: moderately thick, not pigmented; Apothecia: not seen; Spot tests: medulla K+ intensely yellow turning slowly orange, C-, KC-, P+ orangish yellow; Secondary metabolites: cortex with thamnolic acid (major), ±squamatic acid (minor) or squamic acid (major) alone.

**Substrate and ecology:** on bark (especially *Quercus* spp.), rarely on wood, coastal, mainly on in small oak forests or on diverse shrubs in the chaparral between 200 and 500 m or inland in the mountains on *Quercus* spp. and *Pinus* spp. between 1500 and 2800 m; World distribution: Eurasia, Macaronesia, and North America; Sonoran distribution: Mexico; *Sonoran distribution*.
coastal, southern California (frequent in the Channel Islands) and Baja California; rare in the mountains of SE Arizona and Chihuahua.

Notes: Its black pigmented basal part, its isotomic-dichotomous ramification pattern, its terete and cylindrical branch segments, its minute soralia with numerous isidiomorphs and the production of thamnolic ±squamatic acid or squamatic acid alone in the medulla are diagnostic characters for *U. subfloridana*. For differences from *U. praetervisa*, see under this species. There is a rare morphotype collected on Santa Catalina Island with nearly concave and enlarged soralia.


**Thallus:** erect-shrubby, 2 to 10 cm long, stiff and shiny; **branching:** anisotomic- to isotomic-dichotomous, divergent; **basal part:** concolorous with the branches, frequently red-brown pigmented at the very base, rarely partially black; **branches:** tapered, cylindrical; lateral branches: not narrowed at point of attachment; **segments:** terete, cylindrical; **papillae:** absent to abundant, mainly verrucose; **tubercles:** present; **fibrils:** absent to numerous, short (2-3 mm) to long (5-10 mm), irregularly distributed; **soralia:** punctiform to half width of branch bearing them, arising from cortex and/or tops of tubercles, plane to convex or capitate, rarely slightly concave, ±circular to irregular, transversally or longitudinally oblong, discrete or fusing together; **isidiomorphs:** nearly absent to abundant, on young and mature soralia; **pseudocypellae:** inconspicuous, ellipsoid to linear; **cortex:** thick (11-19%), vitreous, smooth and hard, occasionally with longitudinal cracks, seldom red-spotted; **medulla:** thin, compact, not pigmented; **axis:** thick, not pigmented; **Apothecia:** not seen; **Spot tests:** K-, C-, KC-, P+ yellow turning reddish orange or K-, C-, KC-, P-; **Secondary metabolites:** protocetraric acid (major), ±fumarprotocetraric acid (minor), or rarely none detected.

**Substrate and ecology:** on bark (*Quercus* spp., *Pinus* spp. and on shrubs in coastal shrubs communities), rarely on rock, between 0 and 300 m; **World distribution:** southwestern Europe, Macaronesia, eastern and western North America, South America; **Sonoran distribution:** coastal southern California, including the Channel Islands, and Baja California, and the Sierra Madre Occidental of Sinaloa.

Notes: *Usnea subscabrosa* is characterized by a thick, hard, and vitreous cortex, a compact medulla, a basal part that is frequently red pigmented, cylindrical branch segments, minute soralia and the presence of protocetraric acid in the medulla. *Usnea hesperina* differs by having a dull and soft cortex and *U. ceratina* by having stipitate soralia, a pink pigment in the medulla and a different chemistry.


**Thallus:** shrubby, forming rather dense erect tufts, 2 to 12 cm long; **branching:** anisotomic-dichotomous; **basal part:** concolorous with the branches to distinctly blackened; **branches:** irregular, inconspicuously segmented; lateral branches: not narrowed at point of attachment; **segments:** terete and ±cylindrical, sometimes slightly swollen; transversal furrows: often present; **papillae:** usually numerous especially on main branches, thick and verrucose; **tubercles** and **fibercles:** generally absent; **fibrils:** unevenly distributed; **soralia:** slightly tuberculate to slightly excavate but remaining superficial, as large as the branches when mature, sometimes ±encircling the end of branches, ±circular, ±widely spaced and usually not confluent, arising initially on cortex; soredia: generally granulose; **isidiomorphs:** rare, only on young soralia, never on mature ones; **Apothecia:** not seen; **cortex:** thin to moderately thick (4-7%), dull to slightly shiny; **medulla:** moderately thick, dense to compact; **axis:** moderately thick; **Spot tests:** medulla K±
yellow turning dark red, C-, KC-, P± orange; K-, C-, KC-, P-; **Secondary metabolites:** usnic, salazinic (major), ±barbatic (minor), ±4-O-demethylbarbatic (minor), ±caperatic (minor), ±lobaric (minor) acids or usnic acid alone.

**Substrate and ecology:** on bark (mainly *Quercus* spp., *Pseudotsuga* spp., *Pinus* spp., *Abies* spp., *Picea* spp.) mainly in montane forests between 1900 and 3300 m, rarely coastal in *Quercus* woodland between 600 and 800 m; **World distribution:** circumpolar, mainly in continental areas; **Sonoran distribution:** mountains of Arizona, southern California and Baja California.

**Notes:** *Usnea substerilis* is closely related to *U. lapponica* and is frequently mixed with this species, which has deeply excavate soralia often reaching the central axis and tearing off the cortex around the soralia and never produce isidiomorphs. *Usnea diplotypus* can also be confused with *U. substerilis*, but the former species has punctiform soralia and usually abundant isidiomorphs on young and mature soralia. However, in *U. diplotypus*, the punctiform soralia often fuse together and then appear like large soralia making it difficult to separate both species, especially when *U. diplotypus* has few isidiomorphs. For differences from *U. ammannii*, see under that species.


**Thallus:** pendulous, up to 250 cm long, stiff, poorly to moderately branched; **branching:** anisotomous-dichotomistic, parallel; **basal part:** concolorous with or paler than the branches, with distinct annulations, often with many points of attachment; **branches:** cylindrical; lateral branches: not narrowed at point of attachment; **segments:** cylindrical to slightly trapezoidal, weakly to strongly ridged, sometimes slightly alate, with small to extensive areas where cortex is erose; **papillae:** absent; **tubercles:** conspicuous, low and large, verrucous to truncate-conical, paler at top, sometimes eroded, frequent on secondary branches; **fibercles:** absent; **fibrils:** short (0.5-2 mm), up to long (3-10 mm), mostly spinulose, in a fishbone-like arrangement; **soralia:** punctiform, circular to irregular, smaller than half the diameter of the branch, slightly stipitate, arising on top of tubercles and on cracked ridges, often becoming confluent and thus looking like large convex to capitate soralia; **isidiomorphs:** on both young and mature soralia, conspicuous; **pseudocyphellae:** short and linear, inconspicuous on secondary and thin branches; **cortex:** thin to moderately thick (4-12%), often erose, especially on main branches; **medulla:** thin and compact, not pigmented; **axis:** thick, often fistulose at base of main branches; **Apothecia:** not seen; **Spot tests:** K+ yellow turning red, C-, KC-, P + orangish yellow, or K-, C-, KC-, P-; **Secondary metabolites:** salazinic (major) or caperatic (major) acids.

![Fig. 13: Usnea transitoria. photo by P. Clerc](image)

**Substrate and ecology:** on bark; **World distribution:** southern North America and South America; **Sonoran distribution:** Baja California Sur and Chihuahua (Sierra Madre Occidental).

**Notes:** *Usnea transitoria* is characterized by a pendulous habitus, a thick central axis, ridged segments with an erose cortex, punctiform confluent soralia, conspicuous tubercles that are frequently eroded at top, and salazinic or caperatic acid as its main secondary product. This species is closely related to *U. goniodes* that has numerous apothecia and lacks soralia.

Illustration: Clerc (1987a), fig. 1D; Halonen et al. (1999), fig. 8; Ohmura and Kashiwadani (2000), fig. 2b.

Thallus: shrubby, compact, 2-5 cm long; branching: isotoomic- to anisotomic-dichotomous, divergent; basal part: usually distinctly jet black, sometimes concolorous or brownish black, often but not always with few to numerous longitudinal cracks; branches: tapered; lateral branches: not narrowed at attachment points; segments: terete, cylindrical; papillae: few to numerous and then dense on main branches, verrucous; tubercles: few to numerous, especially on main branches; fibers: generally absent; fibrils: usually slender and ±long (2-3 mm long when mature), few to numerous especially on main branches, irregularly distributed; soralia: conspicuous, even to ±excavate, as large as the branches or larger when mature, irregularly rounded to often oblong cylindrical when mature, often confluent, arising initially on the cortex and on top of tubercles; isidiomorphs: only present on young soralia (sometimes very few and difficult to find), always absent on mature soralia; cortex: dull to shiny, thin to thick (5-13%); medulla: in average thin, dense; axis: thick; Apothecia: not seen; Spot tests: K-, C-, KC+ yellow, P-; or K+ yellow turning red, C-, KC+ yellow, P+ orangish yellow; or K+ yellow intense turning slowly orange, C-, KC-, P+ orange; Secondary metabolites: barbatic acid (major), ±4-0-demethylbarbatic acid, ±salazinic acid (minor); or salazinic acid (major) alone; or thamnolic acid (major) and ±squamatic acid (minor).

Substrate and ecology: mainly on bark of Quercus spp. or on scrub in the chaparral between 200 and 500 m; World distribution: Eurasia and western North America; Sonoran distribution: rare on the Channel Islands (Santa Catalina, San Clemente, Santa Cruz and Santa Rosa) and more rarely on the mainland of southern California.

Notes: Usnea wasmuthii is a difficult species to identify in western North America. The thallus is generally small and its typical characters are badly developed. Therefore, TLC is often needed to confirm identifications. Although it is close to U. subfloridana, it differs from that species by its larger soralia that are usually concave and oblong longitudinally when optimally developed. Rare morphs of U. subfloridana with large and concave soralia have numerous isidiomorphs. In U. wasmuthii, isidiomorphs are always few in number and only on young soralia. Usnea fulvoreagens has deeply excavate soralia adjacent places where the cortex is torn off, no isidiomorphs and a different chemistry. Usnea wasmuthii might be sometimes difficult to separate from U. substerilis. The latter species has, however, irregular branches (often with foveoles or transversal furrows), a distinctive anisotomic-dichotomous branching pattern, a basal part without longitudinal cracks and has a continental type of distribution (mountains of Arizona).


Family: Verrucariaceae; Type: Verrucaria rupestris Schrader; No. species: c. 500 world-wide (estimated); Selected lit.: McCarthy (2001), Servit (1954), and Zschacke (1933).

Life habit: lichenized, few species lichenicolous.

Thallus: crustose endosubstratic or superficial, indistinct to rather thick, continuous or rimose to areolate, sometimes subsquamulose or granular (of goniocysts), when superficial fully attached with lower surface or with basally constricted areolae, rarely by stipe-like holdfasts; margin determinate or indeterminate, prothallus usually dark, entire or fimbriate, or not apparent; surface: white, gray, ochraceous, green, shades of brown to black, dull or shiny, even or variously rugose, very rarely isidiate-pseudosorediate; upper cortex: paraplectenchymatous of small roundish-