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Eumitrioid *Usnea* species (*Parmeliaceae*, lichenized Ascomycota) in tropical South America and the Galapagos

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Abstract: Eumitrioid *Usnea* species are characterized by a tubular central axis throughout the entire thallus. Four species were identified in South America: *Usnea baileyi* is a (sub-) tropical species occurring both in continental South America and the Galapagos; *U. perplectata* has a scattered distribution worldwide and occurs in continental South America, mainly on the eastern range; *U. flaveola* and the newly described species *U. subflaveola* are both so far endemic to the Neotropical Andes. Distinct chemotypes, as well as anatomical characters, such as the thickness ratio of the medulla or the presence of medullar pigmentation, are diagnostic in delimiting these species. A detailed description of the species is provided together with an identification key.

Key words: chemistry, endemism, lichens, morphology, Neotropics, taxonomy

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Introduction

Usnea Adans. is a fruticose lichen genus from the family *Parmeliaceae* (Lecanoromycetes), comprising more than 350 species (Clerc 1998) widely distributed in polar, temperate and tropical regions. The genus is readily distinguished by the shrubby to pendulous thallus, branches holding a central axis and the presence of usnic acid in the cortex. At the species level, the extreme plasticity of morphological characters, in response to environmental parameters, considerably challenges the delimitation of species (Clerc 1998).

Eumitrioid *Usnea* species are characterized by a tubular central axis throughout the entire thallus, sometimes filled with loose internal hyphae. These species were circumscribed as the genus *Eumitria* (Stirton 1882), then under the genus *Usnea* subgenus *Eumitria* (Motyka 1936; Ohmura 2001, 2002). Articus (2004) attempted to re-elevate *Eumitria* to the genus level based on phylogenetic lineages, but other authors agreed to keep *Eumitria* as a subgenus (Ohmura & Kanda 2004; Wirtz *et al.* 2006), since the backbone of the phylogeny of *Usnea s. lat.* remained unresolved and phenotypic characters used to circumscribe the lineages were ambiguous. For example, only one species with a tubular central axis (*U. baileyi*) was included in the phylogeny and it clustered in a highly supported clade with a species with a solid central axis (*U. pectinata*). More eumitrioid species need to be added to the phylogeny to understand the circumscription and phylogenetic significance of *Eumitria*. Until that time, we prefer to use the term 'eumitrioid' for these species with a tubular central axis throughout the whole thallus, until the monophyly of these species is tested.

Motyka (1936) described several eumitrioid species that are now recognized as morphological variants of the same species, and the diversity of eumitrioid species has been drastically reduced over the years (Swinscow & Krog 1974; Rogers & Stevens 1988; Ohmura 2001). Comprehensive revisions of *Eumitria* species have been completed in Central and East Africa (Swinscow & Krog 1974, 1986; Krog 1994), Australia

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TABLE 1. *Distribution per country and altitudinal ranges of the species in tropical South America and the Galapagos.*

Species	*n*	BOL*	BRA	COL	ECU	GAL	PAR	PER	VEN	Altitude† (SAM)	Altitude† (GAL)
U. baileyi	125	+	+	+	–	+	–	+	+	0–2300	150–1100
U. flaveola	9	+	–	–	–	–	–	+	–	1100–2500	–
U. perplectata	21	+	+	–	–	–	+	–	+	0–1500	–
*U. subflaveola***	16	–	–	–	–	–	–	+	+	2000–3100	–

* BOL, Bolivia; BRA, Brazil; COL, Colombia; ECU, Ecuador (continental); GAL, Galapagos; PAR, Paraguay; PER, Peru; VEN, Venezuela; SAM, continental South America; *n*, number of specimens studied; +, presence; ** newly described species; †altitudes in [m].

(Rogers & Stevens 1988; Stevens 1999, 2004) and East Asia (Ohmura 2001, 2012). Today, *c.* 8 species are known to occur in East Africa (Swinscow & Krog 1974), one also occurring in Japan (Ohmura 2001, 2012), and two in Australia (Rogers & Stevens 1988) and in North America (Brodo *et al.* 2001; Clerc 2008). South America exhibits a high diversity of *Usnea* species and ongoing taxonomical investigations have been started recently in continental South America and the Galapagos (Rodriguez *et al.* 2011; Truong *et al.* 2011; Truong & Clerc 2012). This study is a further step towards the complete revision of *Usnea* in tropical South America, treating the species with a tubular central axis.

Materials & Methods

This study is based mainly on material collected by the authors in Bolivia, Ecuador (including the Galapagos) and Peru. For a detailed description of the collection sites see Truong *et al.* (2011). In addition, herbarium specimens from the collections of A. Spielmann (SP) and K. Kalb (private hb.) in Brazil, H. Sipman (B) in Colombia and M. E. Hale, Jr. (US) in Venezuela were examined, as well as the Galapagos collections from CDS and COLO. Specimens and types from the following herbaria were included: BM, G, LBL, S and TUR. Table 1 indicates the number of specimens studied for each species, their distribution per country and their altitudinal range. The complete list of specimens examined, including geographical coordinates and ecology, is available upon request to the author.

Morphology of specimens was examined using a stereomicroscope Leica MS5. For a description of characters used in the taxonomy of *Usnea*, see Clerc (1987*a*, 1998, 2011), Herrera-Campos *et al.* (1998) and Ohmura (2001). The shape of branches and branch segments in longitudinal and cross-section is a difficult character to understand and illustrations to clarify this are available in Clerc (2011, figs 1–5). Thickness of cortex/medulla/axis was measured in longitudinal sections of branches at ×40 magnification (on the largest branch above the trunk). The percentage ratio of cortex/medulla/axis of the total branch diameter (CMA) was calculated according to Clerc (1987*b*). The tubular part of the axis had been used to characterize species (Motyka 1936), but it was not expressed numerically in a formula to enable comparisons among species. Therefore we measured the tubular part of the axis (TBA) and developed a formula to calculate its percentage over the total axis diameter (Fig. 1).

In the description of species, CMA and TBA values are given with their standard deviations and CMA values follow the categories described by Clerc (2011). A synthesis of CMA and TBA values for each species is presented in Fig. 2. Spores were observed under a Leica DM 2000 microscope and at least 10 spores per specimen were measured at ×1000 magnification.

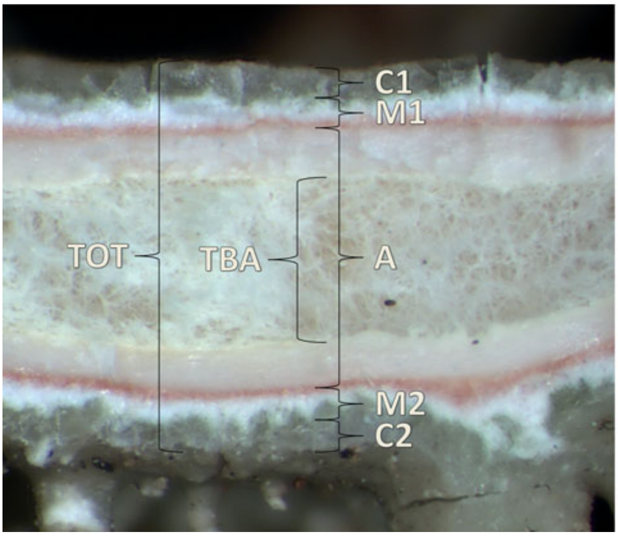
Chemical analyses were performed by thin-layer chromatography (TLC) in solvents A, B and C, following the method of Culberson & Ammann (1979), with solvent B modified according to Culberson & Johnson (1982). A summary of chemotypes detected for each species is presented in Table 2, with major metabolites highlighted. Metabolites were considered major if their presence was constant within the specimens studied of a given species.

The Species

Usnea baileyi (Stirt.) Zahlbr.

Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **83:** 182 (1909).—*Eumitria baileyi* Stirt., *Scott. Natur.* **6:** 100 (1882); type: Australia, Queensland, near Brisbane, *Bailey* 164 (BM!—lectotype). % C/M/A/TBA: 3.5/3/87/85. Chemistry: usnic, eumitrins A_2 and B, zeorin, salazinic and norstictic acids (Ohmura 2001).

Usnea antillarum (Vain.) Zahlbr., *Cat. Lich. Univ.* **6:** 536 (1930).—*Eumitria antillarum* Vain., *Ann. Acad. Sci. Fenn., Ser. A* **6** (7)**:** 9 (1915); type: Antilles, Ins. St. Thomas, Signalhill, 1876, *Eggers* (TUR V00328!—holotype, LBL!—isotype). % C/M/A/TBA: 3.5/1.5/90/68. Chemistry: usnic, norstictic and salazinic acids and eumitrins (Rogers & Stevens 1988).



$$\% \text{ cortex} = 100 \times \frac{(C1 + C2) \times 0{\cdot}5}{TOT}$$

$$\% \text{ medulla} = 100 \times \frac{(M1 + M2) \times 0{\cdot}5}{TOT}$$

$$\% \text{ axis} = 100 \times \frac{A}{TOT}$$

$$\text{ratio A/M} = \frac{\% \text{ axis}}{\% \text{ medulla}}$$

$$\% \text{ tubular axis (TBA)} = 100 \times \frac{TBA}{A}$$

FIG. 1. Measurements and calculations of % cortex/medulla/axis (CMA), ratio A/M and % tubular axis (TBA) in longitudinal section of branch (at the widest branch diameter above first ramification). In colour online.

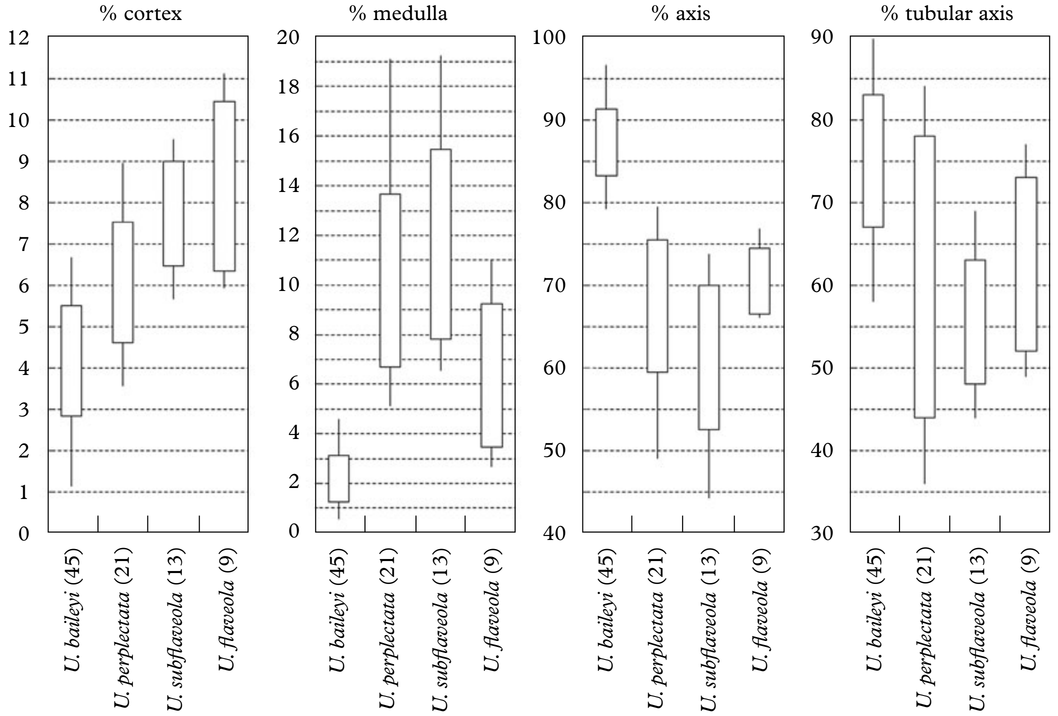


FIG. 2. % cortex/medulla/axis of total branch diameter and % tubular axis of total axis diameter. Standard deviations as wide bars; extreme values as lines; numbers in parentheses = number of specimens measured.

TABLE 2. *Secondary metabolites (columns) detected by TLC in the medulla of eumitrioid species.*

Species	*n*	DIF*	EUM	NOR	SAL	ZEO	UT8
U. baileyi	62	–	+	±	±	+	–
U. flaveola	9	–	–	–	–	–	+
U. perplectata	20	+	–	–	–	–	–
U. subflaveola	16	–	–	±	–	–	+

*DIF, diffractaic; EUM, eumitrins; NOR, norstictic; SAL, salazinic acid; ZEO, zeorin; UT8, unidentified triterpenoid UT8 (RF classes A/B/C: 1-2/4-5/2, UV+ white after charring); *n*, number of specimens studied; +, presence constant within species; ±, presence variable among specimens within a species; grey boxes indicate major metabolites, in which presence was constant within the specimens studied of a given species.

Usnea implicita (Stirt.) Zahlbr., *Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl.* **83:** 182 (1909).—*Eumitria implicita* Stirt., *Scott. Natur.* **6:** 100 (1882); type: Madeira, W. Funchal, *Payne* (BM!—lectotype). % C/M/A/TBA: 5.5/2.5/84/63. Chemistry: usnic and norstictic acids, eumitrins A_1, A_2 and B, zeorin (Ohmura 2001).

Usnea inanis Motyka syn. nov., *Lich. Gen. Usnea Stud. Monogr. Pars Syst.* **1:** 58 (1936); type: Brazil, Matto Grosso, Serra da Chapada, Buriti, 1894, *Malme* (S!—holotype, LBL!—isotype). % C/M/A/TBA: 4.5/3.5/85/77. Chemistry: usnic, eumitrin A, zeorin and norstictic acid.

(Figs 3A & B, 4A–C)

Nomenclatural notes. Three specimens are represented on the herbarium sheet containing the holotype specimen of *U. inanis* Motyka: we marked them as (a), (b) and (c). Thallus (a) was designated by Motyka's handwriting as the holotype and corresponds well morphologically and chemically to *U. baileyi* (eumitrins), whereas thallus (c) corresponds to *U. perplectata* (diffractaic acid). An isotype specimen found in LBL also corresponds to *U. baileyi*.

Only names that have been cited for South America are included in the above list of synonyms. For a complete list of synonyms, see former publications (Swinscow & Krog 1974; Rogers & Stevens 1988; Ohmura 2001).

Diagnostic notes. For a detailed description of this taxon, see Ohmura (2001). *Usnea baileyi* is a sorediate species characterized by a stiff, erect-shrubby to subpendulous thallus, branches ± irregular, often sinuous towards the apices, with slightly to strongly flattened segments (Fig. 4B). The base is concolorous or blackish on the first mm below the first ramification (Fig. 4A). Branches are abundantly covered by minute soralia growing from the cortex *ad initio* or from low tubercles (Fig. 3A). Soralia are slightly raised, remaining plane, crowded on terminal branches, usually without fusing, with numerous short isidiomorphs (Fig. 3B). The cortex is very thin (3·0–5·5%), matt on the thallus surface but sometimes shinier in section. The medulla is extremely thin (1·5–3·0%), almost invisible except for the pink-red pigmentation throughout (Fig. 4C). The axis is extremely large (83·0–91·5%), with a large tubular section (67–83%) filled with loose hyphae. *Usnea baileyi* is characterized by the presence of eumitrins and zeorin detected by TLC in the medulla.

Variation. The density of ramifications, fibrils and isidiomorphs varies among individuals. Rarely, soralia may fuse in an irregular 'soralium' on terminal branches, from the aggregation of several minute soralia. In addition to eumitrins and zeorin, norstictic acid (*n* = 44) and rarely salazinic acid (*n* = 5) were also detected by TLC in the medulla of South American specimens and, as a consequence, the K reaction in the medulla is variable.

Differentiation. Usnea perplectata differs in the branch anatomy in longitudinal section (Fig. 2): it has a thinner axis than *U. baileyi* and a larger medulla, with a distinctly periaxial pigmentation. In addition, it has a somewhat thicker cortex and a thinner tubu-

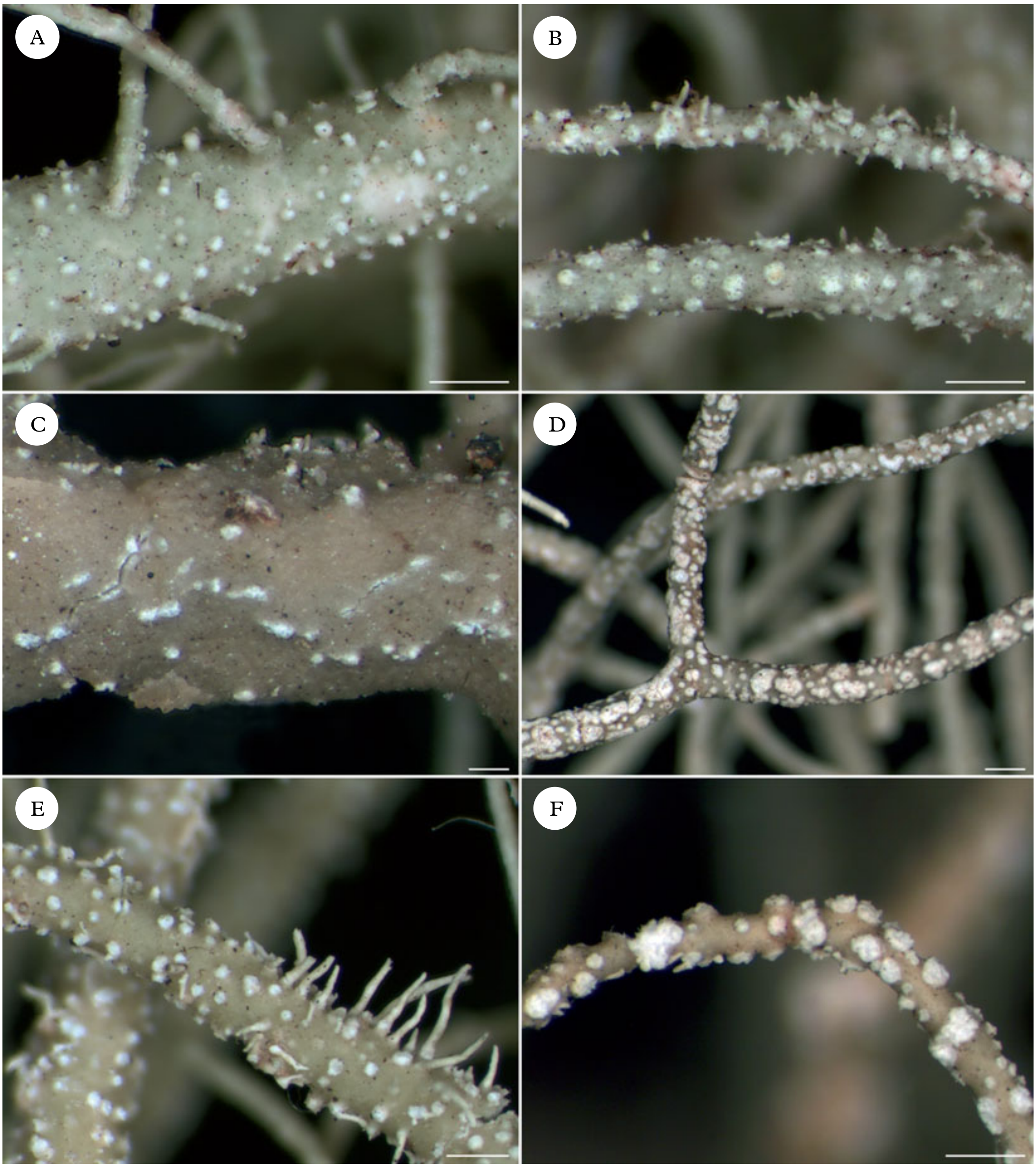


FIG. 3. A & B, *Usnea baileyi* (*Truong* 1446); A, tubercles turning into minute and slightly raised soralia; B, soralia circular and plane, without a cortical margin, crowded on terminal branches but without fusing. C & D, *Usnea perplectata*; C, minute to slightly elongated soralia bursting along cracks and ridges of branches (*Ferrero* 1062); D, soralia of irregular outline, plane to slightly capitate, without a cortical margin, crowded and fusing on terminal branches (*Bach* 373). E & F, *Usnea subflaveola*; E, fibercles abundantly distributed on the branches (*Truong* 1783); F, soralia distinctly stipitate, circular and often capitate at maturity, with a distinct cortical margin, crowded on terminal branches but without fusing (*Truong* 1707). Scales: A–F = 500 µm. In colour online.

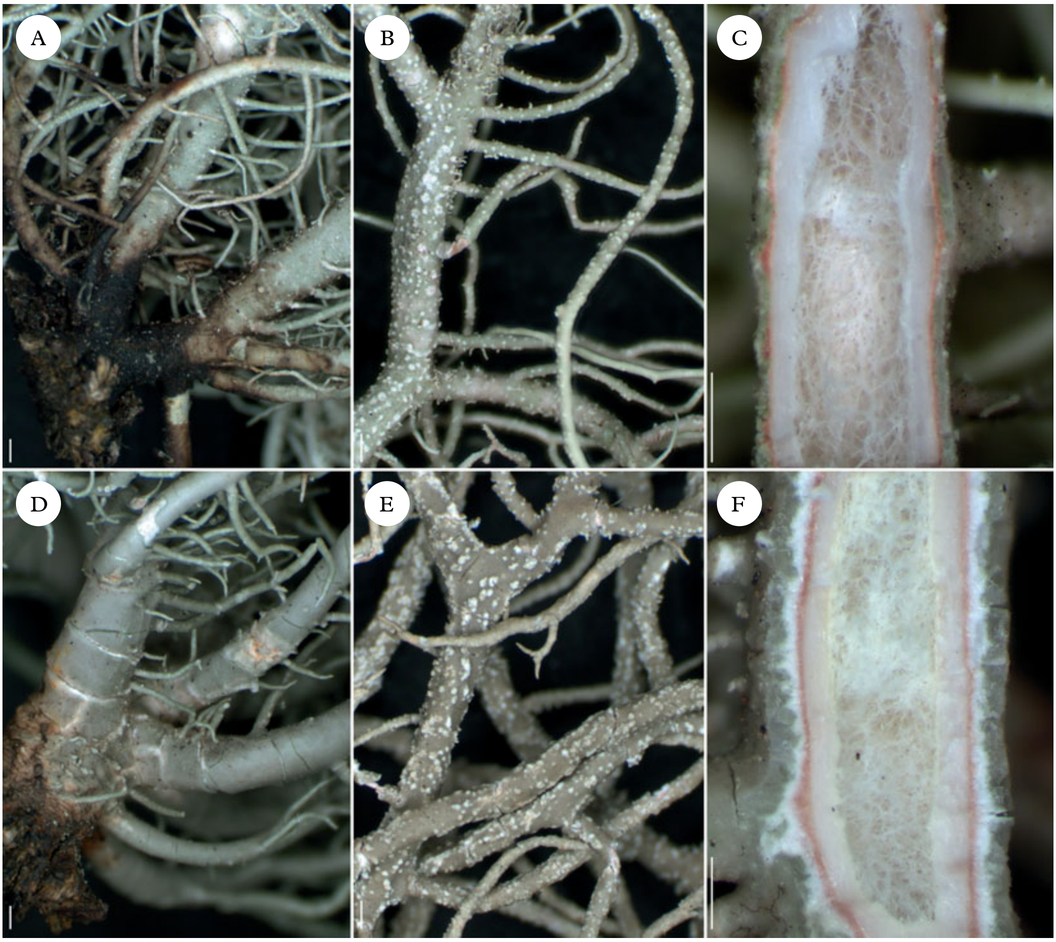


FIG. 4. A–C, *Usnea baileyi*; A, trunk blackish (*Truong* 1446); B, flattened branches abundantly covered by minute soralia (*Clerc* 08-319); C, thin cortex; extremely thin medulla, pigmented throughout; very large axis with large tubular section (*Clerc* 08-319). D–F, *Usnea perplectata*; D, trunk concolorous with thin annular cracks (*Rodriguez* 0261B); E, ridged branches abundantly covered by soralia of irregular outline (*Ferrero* 1062); F, cortex thicker than (C); medulla thicker than (C) with periaxial pigmentation; large axis with large tubular section (*Bach* 373). Scales: A–F = 500 µm. In colour online.

lar section of axis, although these values overlap in the two species. *Usnea perplectata* also has slightly ridged branches (flattened in *U. baileyi*), with few to numerous fibercles, especially visible on basal branches. Diffractaic acid is detected by TLC in the medulla instead of eumitrins in *U. baileyi*.

Ecology and distribution. This is primarily a corticolous species, growing on a wide variety of trees and shrubs (including *Rhizophora* and cacti), occasionally also lignicolous (fencepost) or saxicolous. It is very frequent in the Galapagos, occurring from the arid to the humid zone (150–1100 m). In continental South America, it is one of the few *Usnea* species occurring at low altitudes (0–2300 m). It is found in open pastures, humid evergreen forests and mangroves, but also in the semi-arid climate of seasonally dry tropical forests and savannas of Brazil, Colombia and Venezuela. In Australia, this species was reported to be restricted to warm and moist places (Rogers & Stevens 1988). From these observations we can deduce that *U. baileyi* has a rather wide ecological range from humid to arid places. This species has a worldwide distribution in (sub-) tropical regions of Asia (Ohmura 2001), Australia (Rogers & Stevens 1988), East Africa (Swinscow & Krog 1974) and North and South America (Brodo *et al.* 2001; Clerc 2008).

Selected specimens examined. **Bolivia:** *Beni*: 20 km al SW del km 12 Yucumo – Rurrenabaque, 900 m, 1997, *Bach et al.* (B).—**Brazil:** *Minas Gerais*: Bei Lagoa Dourada etwa 50 km nordöstlich von São João del Rei, 1000 m, 1978, *Kalb & Plöbst* (private hb.). *Rio Grande do Sul*: Herveiras, 570 m, 2004, *Spielmann & Putzke* 6308 (SP). *São Paulo*: near Praia de Pernibe, near Itanhaéna, 0 m, 1979, *Sipman* 13501 (B).—**Colombia:** *Amazonas*: Araracuara, on S-side of river Caquetá, 350 m, 1988, *Sipman & Duivenvoorden* 27856 (B). *Cauca*: Los Robles, campus of Fundacion Universitária, 1750 m, 1986, *Sipman et al.* 32738 (B). *Cundinamarca*: Laguna de Pedro Palo, 2000 m, 1984, *Aguirre & Sipman* 5640 (B).—**Ecuador:** *Galapagos Islands*: Isabela, mirador el Mango, 161 m, 2008, *Truong* 1191 (G, CDS); Pinta, along the trail up to the summit from the S-coast, 369 m, 2007, *Bungartz* 5850 (CDS); Pinzón, on the W-slope of the highest mountain, 310 m, 2006, *Aptroot* 64105 (CDS); San Cristobal, Cerro Colorado summit, 159 m, 2008, *Truong* 1420 (G, CDS); Santa Cruz, dirt road to Mina Granillo, 547 m, 2008, *Truong* 1302 (G, CDS); Santiago, Cerro Gavilan, 680 m, 2006, *Bungartz* 4686 (CDS).—**Peru:** *Cusco*: Valle de Lacco, 1928, *Herrera* 2066 (US).—**Venezuela:** *Amazonas*: en la cumbre de la laja de Carestía, bajo Sanariapo, 150 m, 1942, *Williams* 16038 (US). *Aragua*: Arriba de Guanitas, parque nacional, 950 m, 1939, *Williams* 12213 (US). *Distrito Federal*: Silla de Caracas, 1700 m, 1951, *Vareschi* 57 (LBL). *Lara*: Morán, bordeando a las cabeceras del río Tocuyo, 1900 m, 1974, *Steyermark & Carreño Espinoza* 111081 (US). *Merida*: La Carbonera, sector San Rafael del Macho, 2200 m, 1976, *Hale* 46631 (US). *Miranda*: Los Guayabitos, 1400 m, 1955, *Vareschi* 3935 (LBL). *Sucre*: Peninsula de Paria, Cerro de Río Arriba, 700 m, 1966, *Steyermark y Rabe* 96276 (US).

Usnea flaveola Motyka

Lich. Gen. Usnea Stud. Monogr. Pars Syst. **1:** 52 (1936); type: Peru, Sandia, 2100 m, 1902, *Weberbauer* (LBL!—holotype, isotype). % C/M/A/TBA: 7/7.5/71.5/75. Chemistry: usnic acid and unknown triterpenoids UT8.

(Fig. 5D–F)

Nomenclatural note. Motyka (1936) mentions that the holotype specimen of *U. flaveola* was deposited in B, but we found it within his collections in LBL.

Thallus stiff, erect-shrubby to subpendulous (to *c.* 10 cm long); *ramifications* ± anisotomic-dichotomous; *trunk* concolorous with the branches, without annulations or rarely with very thin annular cracks (Fig. 5D); *branches* tapering to irregular; *branch segments* terete to flattened or ridged, sometimes almost angular; *lateral branches* not constricted at ramification; *foveoles and maculae* absent; *papillae and tubercles* absent or scarce (not to be confounded with young fibrils); *fibrils* slender (to 5 mm long), abundantly and regularly distributed on the branches, looking like cylindrical papillae crowded on the cortex surface at a juvenile stage; *fibercles* usually numerous (Fig. 5E), especially on basal branches; *soralia* absent; *cortex* shiny in section, moderately thin to moderately thick (6·5–10·5%); *medulla* white (Fig. 5F), compact and thin (3·5–9·0%); *axis* thick (66·5–74·5%) with a moderate tubular section (52–73%) loosely filled with thin hyphae and often also chondroid strands of hyphae, axis rarely solid (not tubular) on thin terminal branches.

Apothecia usually present and often numerous, (sub-) terminal, large at maturity (to *c.* 15 mm diam.), with few to numerous long cilia; *spores* hyaline, obovoid, 8·5–10·5 × 5–7 µm ($n = 45$).

Pycnidia rare, usually visible when apothecia are absent, appearing as small hemispherical protuberances on terminal branches.

Diagnostic notes. Usnea flaveola is a non-sorediate species (usually with apothecia) characterized by an erect to subpendulous thallus, with somewhat irregular branches abundantly covered by fibrils and fibercles. Clerc & Herrera-Campos (1997) described fibercles as stipitate scars left by the breaking away of fibrils, probably functioning as sterile propagules, sometimes exposing the central axis of the fallen fibril. The axis is large with a moderately large tubular section and the medulla is thin and white (without pigmentation), reacting K− (unidentified triterpenoids UT8: RF classes A/B/C: 1-2/4-5/2, UV+ white after charring). Triterpenoids seem to be frequent in Neotropical *Usnea* specimens and are useful for identifying several species, for example *U. rubricornuta*

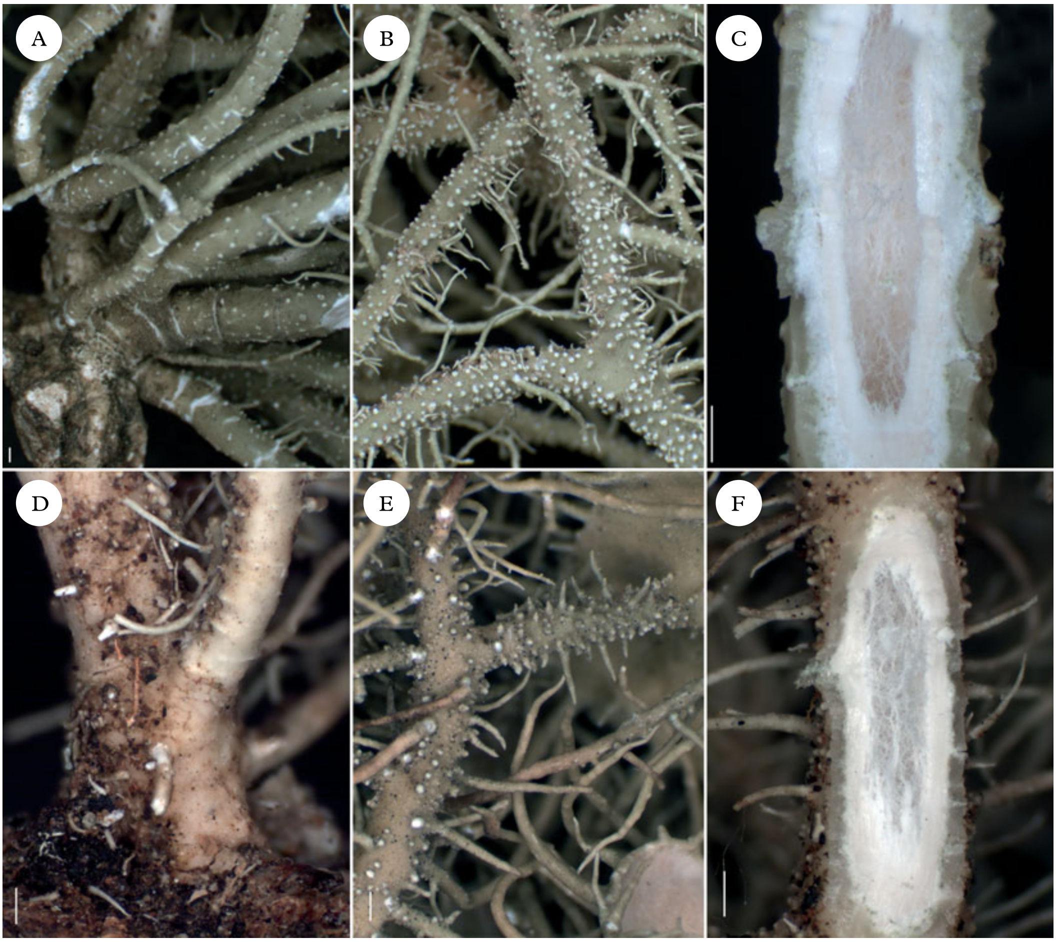


FIG. 5. A–C, *Usnea subflaveola*; A, trunk concolorous, sometimes with thin annular cracks; branch segments almost angular (*Truong* 2783); B, tapering branches abundantly covered by fibercles (*Truong* 1783); C, cortex moderately thin; medulla thin, without pigmentation; axis large, with a moderately large tubular section (*Truong* 1707). D–F, *Usnea flaveola*; D, trunk concolorous, without annular cracks (*Truong* 3140); E, branches covered by fibrils and fibercles, holding apothecia (*Bach* 325); F, cortex moderately thin; medulla thinner than (C), without pigmentation; axis large, with a moderately large tubular section (*Truong* 3140). Scales: A–F = 500 µm. In colour online.

Truong & P. Clerc and *U. steineri* Zahlbr. (Truong *et al.* 2011).

Variation. The irregularity of branch diameter, as well as the shape of branch segments (terete to flattened or ridged, sometimes even angulate) vary mostly with the development stage of the thallus. The abundance of fibrils and fibercles also vary among individuals; nevertheless, fibercles are always present and characteristic of this species.

Differentiation. The tubular axis, the absence of medullar pigmentation and the absence of soralia readily distinguish this species. It is the only non-sorediate eumitrioid species occurring in South America so far (see also *U. trullifera* Motyka in the paragraph treating doubtful species).

Ecology and distribution. This is mostly a corticolous species, occasionally also found on rocks. It occurs in humid and somewhat open places within evergreen forest, mountain cloud forest or in the vicinity of the forest. It is so far endemic to the Neotropical Andes, at moderate altitudes (1100–2500 m).

Selected specimens examined. **Bolivia:** *La Paz*: 15 km de Charazani hacia Apolo, 2400 m, 1997, *Bach et al.* 252 (B). *Cochabamba*: Parque Nacional Carrasco, Sehuencas hasta Monte Puncu, 2500 m, 2007, *Truong* 3140 (G).—**Peru:** *Junin*: Distrito de San Ramon, carretera arriba de la catarata Tirol, 1139 m, 2007, *Truong* 2676 (G).

Usnea perplectata Motyka

Lich. Gen. Usnea Stud. Monogr. Pars Syst. **1:** 55 (1936); type: Paraguay, Gran Chaco, ad Rio Negro e ad Capernicians, 1883, *Malme* (S!—holotype). % C/M/A/TBA: 6.5/16/55/41. Chemistry: usnic, diffractaic, traces of 4-*O*-demethylbarbatic acids and associated compounds.

Usnea elata Motyka *syn. nov.*, *Lich. Gen. Usnea Stud. Monogr. Pars Syst.* **1:** 57 (1936); type: [Congo], Mpala, ad litus occid. Lacus Tanganjika, 1898, *Guillemé* (TUR!—holotype). C/M/A/TBA: unknown (small fragment of branch). Chemistry: usnic and diffractaic acids (Rogers & Stevens 1988).

Usnea subcavata Motyka syn. nov., *Lich. Gen. Usnea Stud. Monogr. Pars Syst.* **1:** 57 (1936); type: Brazil, Sao Paulo, prope S. Amaro in circuito urbis S. Paulo, 800 m, 1901, *Schiffner* (W—holotype, LBL!—isotype). % C/M/A/TBA: 4.5/8.5/73.5/67. Chemistry: usnic, diffractaic, traces of barbatic, 4-*O*-demethylbarbatic acids and associated compounds.

(Figs 3C & D, 4D–F)

Nomenclatural note. Clerc (2008) synonymized *U. perplectata* into *U. baileyi*. However, the current study treats *U. perplectata* as a distinct species.

Thallus relatively stiff, subpendulous to pendulous (to *c.* 25 cm long); *ramifications* ± anisotomic-dichotomous; *trunk* concolorous with the branches or rarely blackish on the first mm (below first ramification), usually with thin annulations extending along the basal branches (Fig. 4D); *branches* of slightly to strongly irregular diameter; *branch segments* terete to slightly ridged (Fig. 4E); *lateral branches* not constricted at ramification; *foveoles and maculae* absent; *papillae* absent or scarce; *tubercles* few to abundant on main branches; *fibrils* slender (to 5 mm long), scattered on the thallus; *fibercles* few to abundant on basal branches; *soralia* growing from the cortex *ad initio* (cracks, along ridges of branches, Fig. 3C) or from tubercles, at once slightly raised, usually remaining minute to slightly enlarging (less than the branch half-diameter), often elongated (along ridges of branches) or of irregular outline, without a cortical margin, plane to slightly capitate at maturity, often crowded on terminal branches and aggregating in irregular 'soralium' (Fig. 3D), with few to numerous isidiomorphs, rarely growing into isidiofibrils; *cortex* shiny in section, thin to moderately thin (4·5–7·5%); *medulla* compact and thin (6·5–13·5%), with a pink to orange, periaxial pigmentation (Fig. 4F); axis large (59·5–75·5%), with a moderately large tubular section (44–78%) loosely filled with thin hyphae that are often yellow pigmented and reacting C+ yellow-orange.

Apothecia rare ($n = 1$), lateral.

Pycnidia not seen.

Diagnostic notes. This species is characterized by a stiff thallus with slightly ridged branches and minute to slightly elongated soralia, crowded and aggregating on terminal branches, with few to numerous isidiomorphs. The medulla is thin and compact, with a characteristic pink to orange pigmentation, located at the periphery of the axis. Diffractaic acid was detected by TLC in the medulla.

Variation. The density of tubercles, fibrils, fibercles and isidiomorphs varies among individuals. The trunk is usually concolorous and distinctly annulated, but it is rarely brownish to blackish (below first ramification) and without annulations.

Differentiation. See under *U. baileyi*.

Ecology and distribution. This is mostly a corticolous species, occasionally also found on rocks. It occurs in continental South America, mainly on the Eastern range. As *U. baileyi*, it is one of the few *Usnea* species occurring at low altitudes (0–1500 m). It is found in humid places, within evergreen forest, coastal forest (*restinga*) or in the vicinity of the forest, but also in drier places such as the Brazilian *cerrado*. It also occurs in North America (Brodo *et al.* 2001), East Africa and Australia (*sub U. elata*).

Selected specimens examined. **Argentina:** *Corrientes*: Capital San Cayetano, 1976, *Ferraro* 1062 (G). *Formosa*: Dpto. Lahisi, ruta nacional 11, 2007, *Rodriguez* 281B

(G). *Misiones*: Bei den Wasserfällen Victoria am Rio Iguazu, 1933, *Hosseus* (LBL).—**Bolivia:** *Beni*: 16 km al SW del km 12 Yucumo–Rurrenabaque, 750 m, 1997, *Bach et al.* 373 (B).—**Brazil:** *Mato Grosso*: Serra dos Coroados, Naturschutzgebiet der evangelischen Schule von Buriti, 600 m, 1980, *Kalb* (private hb.). *Santa Catarina*: Ilha de Santa Catarina, Praia do Forte, 3 m, 1980, *Kalb* (private hb.). *São Paulo*: Reserva biologica de Mogi-Guaçu, fazenda Campininha, 610 m, 2008, *Jungbluth* 1755 (SP).—**Tanzania:** Sud-Pale Gebirge, bei Vudu, 1800 m, 1958, *Schüz* (LBL).—**Paraguay:** In vicinity urbis Assuntion, *Aminsris* (LBL).—**USA:** *Florida*: Standford, 1924, *Rapp* (LBL).—**Venezuela:** *Aragua*: Choroni, Peñon Blanco, 1200 m, 1954, *Vareschi* 3603 (LBL). *Zulia*: Selva de Geonema, 1500 m, 1954, *Vareschi* 3172 (LBL).

Usnea subflaveola Truong & P. Clerc sp. nov.

MycoBank No.: MB 564913

Thallus sorediate, fibrils and fibercles abundant, medulla unpigmented, reacting K− (triterpenoids), axis tubular to the apices.

Type: Venezuela, Merida, La Carbonera, Merida–La Azulita road, 2200 m, remnants of forest in open pasture, fence post, 1976, *Hale* 47542 (USM—holotype; G—isotype). % C/M/A/TBA: 6.5/18.5/54. Chemistry: usnic and norstictic acids, unidentified triterpenoids UT8.

(Figs 3E & F, 5A–C, 6)

Thallus subpendulous to pendulous (to *c.* 30 cm long), rarely erect-shrubby; *ramifications* mostly anisotomic-dichotomous; *trunk* concolorous with the branches, without annulations or rarely with thin annular cracks (Fig. 5A); *branches* tapering to slightly irregular; *branch segments* terete to slightly ridged or angular, sometimes slightly inflated; *lateral branches* not constricted at ramification; *foveoles and maculae* absent; *papillae and tubercles* absent or scarce (not to be confounded with young fibrils); *fibrils* slender (to 5 mm long), scattered (mainly on basal branches) to abundantly distributed on the branches; *fibercles* usually numerous (Fig. 3E & 5B), especially on basal branches; *soralia* developing at the top of fibercles thus being distinctly stipitate, minute to circular, circular, enlarging almost to the branch diameter on terminal branches, convex or rarely slightly excavate at maturity, often crowded on terminal branches but remaining well-delimited with a thin cortical margin (Fig. 3F), with numerous isidiomorphs, sometimes growing into isidiofibrils; *cortex* shiny in section, moderately thin to moderately thick (6·5–9·5%); *medulla* white (Fig. 5C), compact and thin (8·0–15·5%); axis large (52·0–69·5%) with a moderate tubular section (47–62%), loosely filled with thin hyphae and sometimes chondroid strands of hyphae, axis rarely solid (not tubular) on small terminal branches.

Apothecia and *pycnidia* not seen.

Diagnostic notes. This is a sorediate species characterized by a (sub)pendulous thallus, with tapering to slightly irregular branches abundantly covered by fibrils and fibercles, from which arise stipitate soralia, often crowded on terminal branches but remaining well-delimited with a distinct cortical margin. The medulla is thin and white (without pigmentation), reacting K− (unidentified triterpenoids UT8), rarely faintly K+ (norstictic acid).

Variation. The abundance of fibrils and fibercles may vary among individuals, but fibercles are conspicuously present, at least towards the basal branches. The development of soralia and isidiomorphs varies among individuals or in response to infestation by parasitic fungi, as is often the case in *Usnea*. In addition to UT8, norstictic acid ($n = 6$) was sometimes detected by TLC in the medulla.

Differentiation. The absence of medullar pigmentation and the presence of circular soralia growing from fibercles readily distinguish this species. Apart from the presence of soralia, it shares with *U. flaveola* a similar morphology (presence of fibercles, absence of medullar pigmentation) and the same chemotype. CMA values show slight differences between the two species, *U. subflaveola* having a thicker medulla and a thinner axis than *U. flaveola*, although these values overlap in the two species (Fig. 2). The corroboration of molecular tools will be needed to distinguish these two taxa.

In East Africa, *U. cristata* Motyka is another sorediate eumitrioid species without medullary pigmentation. The holotype specimen of *U. cristata* deposited in W is apparently missing (Swinscow & Krog 1974), but

FIG. 6. *Usnea subflaveola*; A, holotype; B, isotype. Scale = 1 cm. In colour online.

we found an isotype in Motyka's collections in LBL. It doesn't correspond to *U. subflaveola*: in *U. cristata*, branches are deformed, with strongly ridged segments and the presence of foveoles. Soralia arise irregularly along the ridges of branches or from thick fibercles. They remain minute to slightly elongated, with an irregular outline and numerous isidiomorphs.

Ecology and distribution. This is mostly a corticolous species, occasionally also found on dead wood (fence post). It occurs in humid places within mountain cloud forest or in open places in the vicinity of the forest, such as deforested zones of *matorral*, remnants of forest within pastures or isolated trees. It is so far endemic to the Neotropical Andes, at a moderately high altitude (2000–3100 m).

Selected specimens examined. **Peru:** *Cajamarca*: Ruinas de Kuelap, 3100 m, 2007, *Truong* 1870 (G). *Huanuco*: Bosque de Carpish, 2424 m, 2007, *Truong* 2738 (G). *Pasco*: Parque Nacional Yanachaga-Chemillén, camino hasta el refugio El Cedro, 2309 m, 2007, *Truong* 2444 (G).—**Venezuela:** *Merida*: La Carbonera, sector San Rafael del Macho, 2200 m, 1976, *Hale* 46603 (US). *Tachira*: Slopes of Pico Banberas, páramo de Tama, 2600 m, 1975, *Hale & Lopez-Figueiras* 45208 (US).

Doubtful Species

Usnea trullifera Nyl.

Lich. Gen. Usnea Stud. Monogr. Pars Syst. **1:** 65 (1936); type: Tahiti, 1875, *Moseley* (BM!—holotype). % C/M/A/TBA: 4/3.5/85/71. Chemistry: usnic, salazinic and norstictic acids, zeorin.

This is a non-sorediate species (usually with apothecia), characterized by the presence of high tubercles abundantly covering the branches and often eroded at the top. CMA values are similar to *U. baileyi*, with a very thin and pale pink to orange pigmented medulla. In his description, Motyka (1936) mentions specimens from Tahiti, East Africa and Brazil, most of which were hosted in B and are probably lost today. We found one Brazilian specimen identified by Motyka in LBL. It is composed of a small fragment of branch, holding apothecia (without soralia), but lacking the trunk and basal branches. Apart from the presence of apothecia, this specimen resembles *U. baileyi*, but it is too small to be accurately identified. Despite studying more than 100 South American specimens of *U. baileyi*, we have never observed apothecia in this species. In addition, protocetraric acid and zeorin were detected by TLC in the medulla of this Brazilian specimen. Protocetraric acid has been detected in Asiatic *U. baileyi* specimens (Ohmura 2001), but we have never found it in South American specimens.

Selected specimens examined. **Brazil:** *Mato Grosso*: Caracas, 1908, *Hoehne* (LBL).—**Cameroon:** Kamerunberg, 1800 m, 1958, *Knorr* (LBL).—**Tahiti:** 1847, *Vesco* (LBL).—**Uganda:** Kasatoro Forest Kigezi, 1800–2500 m, 1947, *Dale* 39 (LBL).

Key to eumitrioid *Usnea* species from tropical South America and the Galapagos

1 Medulla with a pink, orange or red pigmentation 2
Medulla white (not pigmented) 3

2(1) Medulla extremely thin ($<5\%$); pigmentation pink-red throughout the entire medulla; branch segments terete to flattened . . . . **U. baileyi**
Medulla thicker ($>5\%$); pigmentation pink to orange, distinctly periaxial; branch segments terete to ridged . . . . **U. perplectata**

3(1) Soralia present, developing at the top of fibercles, distinctly stipitate, often crowded on terminal branches, remaining well-delimited with a distinct cortical margin . . . . **U. subflaveola**
Soralia absent and apothecia usually present, if not pycnidia often visible as hemispherical protuberances on terminal branches; fibrils and fibercles abundantly distributed on the branches . . . . **U. flaveola**

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