

New species and new records in the genus *Usnea* (Parmeliaceae, lichenized Ascomycota) from tropical South America

Camille TRUONG and Philippe CLERC

Abstract: *Usnea* is a cosmopolitan genus of lichen-forming Ascomycota (Parmeliaceae, Lecanorales). This hyperdiverse genus remains poorly known, especially in tropical regions, and recent efforts have been made to clarify the species concepts and describe the diversity of species. We describe five new species from tropical South America based on morphological and chemical features supported by molecular data from the ITS rDNA, nuLSU, *RPB1* and *Mcm7* markers. *Usnea cleriana* is a Galapagos endemic characterized by inflated branches holding elongated tubercles, excavate soralia and/or apothecia. *Usnea aranea* and *U. subaranea* share inflated branches with numerous papillae and a loose arachnoid medulla, but differ in the minute and irregular soralia in *U. aranea*, that are circular and excavate in *U. subaranea*. *Usnea rubriglabrata* and *U. subglabrata* are characterized by inflated branches with excavate soralia, with a reddish cortex pigmentation in *U. rubriglabrata* that is lacking in *U. subglabrata*. *Usnea aranea*, *U. rubriglabrata*, *U. subaranea* and *U. subglabrata* are so far endemic to continental South America; the three former species are closely related and cluster in a highly supported clade, characterized by species distributed in the tropical Andes. New records for the region are provided and *U. moreliana* is resurrected, corresponding to the valid name for *U. rubricornuta*.

Key words: macrolichens, Neotropics, phylogenetics, taxonomy, thin-layer chromatography

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Introduction

Usnea is a lichen-forming genus from the family Parmeliaceae (Lecanorales, Ascomycota), in which it forms a monophyletic lineage (Crespo *et al.* 2007) with the following synapomorphic characters: a fruticose thallus, branches with a cartilaginous central axis, and the presence of usnic acid in the cortex. This hyperdiverse genus comprises more than 350 species (Clerc 1998) that are widely distributed in polar, temperate and tropical regions. Since Motyka's world monograph (1936, 1938), taxonomic revisions of the genus *Usnea* have been ongoing in Europe (Clerc 1987b, 2011; Halonen *et al.* 1999), Macaronesia (Clerc 2006), North America (Halonen *et al.* 1998; Herrera-Campos *et al.* 1998, 2001; Clerc 2008), East Africa (Swinscow & Krog 1978,

1979), Asia (Awasthi 1986; Ohmura 2001, 2012; Ohmura *et al.* 2010), Australia (Stevens 1999, 2004), and polar regions (Walker 1985; Seymour *et al.* 2007; Wirtz *et al.* 2008, 2012). Tropical regions harbour a rich diversity of species but remain particularly unexplored, yet being a potential source of new species to be discovered. Recently, taxonomic investigations have been taking place in South America (Rodriguez *et al.* 2011; Truong *et al.* 2011, 2013b; Truong & Clerc 2012, 2013), contributing to a better understanding of this genus worldwide.

Many *Usnea* species show an extremely plastic morphology in response to environmental factors (Clerc 1998), which causes their circumscription to be particularly complex. Recent phylogenetic studies usually support the delimitation of *Usnea* species described from morphological and chemical characters (Ohmura 2002, 2008; Ohmura & Kanda 2004; Kelly *et al.* 2011; Saag *et al.* 2011; Truong *et al.* 2013a), but the presence of species complexes has also been detected

C. Truong and P. Clerc: Conservatoire et Jardin botaniques de la Ville de Genève, CP 60, 1292 Chambésy, Switzerland. Email: camille.truong@ville-ge.ch

(Seymour *et al.* 2007; Wirtz *et al.* 2008, 2012; Lumbsch & Wirtz 2011; Truong *et al.* 2013a). Various species have wide distributions over several continents and most clades within the phylogeny of *Usnea* tend to show low geographic structuration (Truong *et al.* 2013a). In addition, phenotypic characters used to characterize species are often homoplasious in the phylogeny of *Usnea* and therefore inadequate to describe generic subdivisions (Truong *et al.* 2013a). As a result, *Usnea* species with a similar morphology or geographical distribution are not necessarily closely related.

The present work aims to complement the ongoing investigation of the genus *Usnea* in tropical South America by formally describing five new species previously delimited in our recent phylogenetic study (Truong *et al.* 2013a), using morphological, chemical and ecological features combined with molecular data from the ITS rDNA, nuLSU, *RPB1* and *Mcm7* markers. In addition, one lectotypification is made and we report several new species records for the region.

Materials and Methods

Taxonomic studies

Herbarium specimens from B, CDS, COLO, G, H, LBL, SP and US were studied, in addition to material collected by the authors in Bolivia, Ecuador (including the Galapagos) and Peru. Collection sites are described in Truong *et al.* (2011). Morphology of specimens was examined using a Leica MS5 stereomicroscope. Critical morphological characters commonly used in the taxonomy of *Usnea* include, among others: shape of branch and branch segments, shape of lateral branches at ramification, cortex surface such as foveoles, maculae, or pseudocyphellae, and morphology of vegetative reproductive structures (i.e. soralia and isidiomorphs) (Clerc 1987a, 1998, 2011; Herrera-Campos *et al.* 1998; Ohmura 2001). The cortex, medulla and central axis were measured in longitudinal sections of the largest branch above the trunk at $\times 40$ magnification. The percentage thickness of the cortex, medulla, and axis compared to the total branch diameter (CMA) as well as the thickness ratio axis: medulla (A:M) were calculated according to Clerc (1987b) and Truong *et al.* (2011). In the description of species, CMA values are given with their standard deviations and follow the categories described in Clerc (2011). Chemical analyses were performed by thin-layer chromatography (TLC) following the method of Culberson & Ammann (1979), with solvent B modified according to Culberson & Johnson (1982).

Phylogenetic studies

The internal transcribed spacer (ITS) is widely used for successfully delimiting fungal species in phylogenetic studies (Kelly *et al.* 2011; Schoch *et al.* 2012), including in *Usnea* (Ohmura 2002, 2008; Ohmura & Kanda 2004; Wirtz *et al.* 2008; Lumbsch & Wirtz 2011; Truong *et al.* 2013a). Sequences from the nuclear ribosomal regions ITS and nuLSU, as well as portions of the protein-coding genes *Mcm7* and *RPB1* were assembled in a data matrix of 40 specimens from 26 *Usnea* species (Table 1) from the *Usnea* clade described in Truong *et al.* (2013a). Three species from the *Neuropogon* clade served as outgroup (Truong *et al.* 2013a). The dataset mainly includes sequences used in Truong *et al.* (2013a), in addition to new ITS and nuLSU sequences obtained from the newly described species *U. aranea*, *U. rubriglabrata*, *U. subaranea* and *U. cleriana*, following the procedure described in Truong *et al.* (2013a). Material from newly recorded species in South America was not included within the phylogeny, since these specimens mainly originate from herbarium collections and were not freshly collected by the authors.

Methods of alignment and tests for topological incongruence among markers are detailed in Truong *et al.* (2013a). Partition and substitution model selection were optimized using PartitionFinder 1.1.1 (Lanfear *et al.* 2012) with the following parameters: branch lengths = linked; models = raxML (GTR+G, GTR+I+G); model selection = BIC; search = greedy. Two partitions and models were selected (GTR+G: ITS1, ITS2, MCM7–position3, RPB1–position3; GTR+I+G: 5.8S, LSU, MCM7–position1, MCM7–position2, RPB1–position1, RPB1–position2) and subjected to a Bayesian inference with a Monte Carlo Markov chain (B/MCMC) in MrBayes 3.2.3 (Ronquist *et al.* 2012). We conducted three independent runs of 5 million generations, starting from a random tree. Parameters were estimated independently for each partition but sharing the same overall rate. Four chains were sampled every 1000 generations and temperature was set to 0.1 to improve mixing among chains. Convergence among runs was confirmed by 1) verifying that the average standard deviation of split frequencies was <0.01 ; and 2) plotting likelihood per generation for each run and identifying the effective sample size (ESS) for each parameter in Tracer v1.6 (Rambaut *et al.* 2014). The majority-rule consensus tree was constructed by pooling trees sampled from all runs after discarding 25% as burn-in, with posterior probabilities (PP) as branch support. The data matrix with the same partition was analyzed using the GTRGAMMA model for maximum likelihood (ML) inference with 1000 bootstrap pseudoreplicates in RAxML 8.0.24 (Stamatakis 2014) on the CIPRES web portal (Miller *et al.* 2010).

Results and Discussion

Taxonomic studies

Table 2 indicates the number of specimens studied for each species, their distribution

TABLE 1. Specimen location, major chemotype and GenBank accession numbers for the species referred to in this study. Newly described species and sequences are in bold.

Species	Isolate	Location	Chemotype	Source	GenBank Accession Numbers			
					ITS	LSU	<i>Mcm7</i>	<i>RPB1</i>
<i>U. acanthella</i> 1	NW289	Peru	—	Wirtz <i>et al.</i> 2006	DQ235482	—	—	JF283499
<i>U. acanthella</i> 2	NW169	Ecuador	—	Wirtz <i>et al.</i> 2006	DQ235483	—	—	JF283498
<i>U. angulata</i>	85	Peru	norstictic	Truong <i>et al.</i> 2013a	JQ837291	JQ837376	JQ837336	—
<i>U. araneal</i>1	121	Ecuador	stictic	Truong <i>et al.</i> 2013a	JQ837293	JQ837378	—	—
<i>U. araneal</i>2	120	Peru	stictic		KP668964	KP668969	—	—
<i>U. brasiliensis</i>	44	Madeira	protocetraric	Truong <i>et al.</i> 2013a	JQ837294	JQ837379	JQ837338	—
<i>U. clercianal</i>1 (non-sorediate)	125	Galapagos	salazinic	Truong <i>et al.</i> 2013a	JQ837311	JQ837395	JQ837354	—
<i>U. clercianal</i>2 (sorediate)	124	Galapagos	salazinic		KP668966	KP668971	—	—
<i>U. clercianal</i>3 (non-sorediate)	127	Galapagos	salazinic		KP668965	KP668970	—	—
<i>U. clercianal</i>4 (sorediate)	126	Galapagos	salazinic		KP668967	KP668972	—	—
<i>U. cornuta</i> s.l.1/1	27	Ecuador	norstictic	Truong <i>et al.</i> 2013a	JQ837297	JQ837382	JQ837340	—
<i>U. cornuta</i> s.l.1/2	24	Peru	stictic	Truong <i>et al.</i> 2013a	JQ837296	JQ837381	JQ837339	—
<i>U. cornuta</i> 1	29	Peru	salazinic	Truong <i>et al.</i> 2013a	JQ837299	JQ837384	JQ837342	—
<i>U. cornuta</i> 2	32	USA	salazinic	Truong <i>et al.</i> 2013a	JQ837300	JQ837385	JQ837343	—
<i>U. cornuta</i> 3	42	France	stictic	Truong <i>et al.</i> 2013a	JQ837301	JQ837386	JQ837344	—
<i>U. cornuta</i> 4	43	Madeira	salazinic	Truong <i>et al.</i> 2013a	JQ837302	JQ837387	JQ837345	—
<i>U. crocata</i>	35	Peru	protocetraric	Truong <i>et al.</i> 2013a	JQ837303	JQ837388	JQ837346	—
<i>U. dasaea</i>	81	Ecuador	galbinic	Truong <i>et al.</i> 2013a	JQ837306	JQ837391	JQ837349	—
<i>U. filipendula</i>	6	Scotland	salazinic	Kelly <i>et al.</i> 2011	JN943557	JN939691	—	JN992600
<i>U. flavocardia</i>	42	Ireland	psoromic	Kelly <i>et al.</i> 2011	JN943552	JN939717	—	—
<i>U. florida</i>	26	England	thamnolic	Kelly <i>et al.</i> 2011	JN943538	JN939703	—	JN992584
<i>U. fragilesceus</i> 1	40	Scotland	stictic	Kelly <i>et al.</i> 2011	JN943525	JN939715	—	JN992571
<i>U. fragilesceus</i> 2	119	Bolivia	salazinic	Truong <i>et al.</i> 2013a	JQ837309	JQ837393	JQ837352	—
<i>U. glabrata</i> 1	113	Switzerland	stictic	Truong <i>et al.</i> 2013a	JQ837313	JQ837397	JQ837356	—
<i>U. glabrata</i> 2	56	Scotland	protocetraric	Kelly <i>et al.</i> 2011	JN943512	JN939724	—	JN992561
<i>U. lambii</i>	NW42	Ecuador	—	Seymour <i>et al.</i> 2007	EF179800	—	—	EF179787
<i>U. patagonica</i>	NW63	Ecuador	—	Wirtz <i>et al.</i> 2006	DQ235487	—	—	JF283495
<i>U. perhispidella</i>	137	Peru	stictic	Truong <i>et al.</i> 2013a	JQ837290	JQ837375	JQ837335	—
<i>U. rubicunda</i> 1	38	Bolivia	salazinic	Truong <i>et al.</i> 2013a	JQ837316	JQ837399	JQ837358	—
<i>U. rubicunda</i> 2	75	Madeira	stictic	Truong <i>et al.</i> 2013a	JQ837319	JQ837402	JQ837361	—
<i>U. rubriglabrata</i> 1	135	Peru	protocetraric		KP668968	—	—	—
<i>U. rubriglabrata</i> 2	2	Peru	protocetraric	Truong <i>et al.</i> 2013a	JQ837320	JQ837403	—	—
<i>U. silesiaca</i>	88	Ecuador	salazinic	Truong <i>et al.</i> 2013a	JQ837331	JQ837412	JQ837370	—
<i>U. subaraneal</i>1	123	Ecuador	usnic only	Truong <i>et al.</i> 2013a	JQ837292	JQ837377	JQ837337	JQ837416
<i>U. subaranea</i> 12	122	Peru	salazinic		KP668963	—	—	—
<i>U. subdasaea</i>	22	Galapagos	galbinic	Truong <i>et al.</i> 2013a	JQ837329	JQ837410	JQ837368	—
<i>U. subglabrata</i>	25	Bolivia	stictic	Truong <i>et al.</i> 2013a	JQ837312	JQ837396	JQ837355	—
<i>U. subrubicunda</i>	76	USA	protocetraric	Truong <i>et al.</i> 2013a	JQ837332	JQ837413	JQ837371	—
<i>U. trachycarpa</i>	NW173	Argentina	—	Seymour <i>et al.</i> 2007	DQ235496	EF116570	—	EF179793
<i>U. wasmuthii</i>	28	Wales	barbatic	Kelly <i>et al.</i> 2011	JN943536	JN939705	—	JN992582

TABLE 2. Distribution of new species and newly recorded species of *Usnea* in South America.

Species	<i>n</i>	ARG	BOL	BRA	COL	ECU	GAL	PER	VEN	Altitude (m) (SAM)	Altitude (m) (GAL)
<i>U. aranea</i>	135		+		+	+		+	+	2350–4100	
<i>U. cleriana</i>	63						+				75–1300
<i>U. dorogawensis</i>	6				+		+	+		2300–2550	900–950
<i>U. grandisora</i>	9						+		+	1950	300–600
<i>U. moreliana</i>	84	+	+	+	+	+		+	+	(50) 500–3950	
<i>U. rubriglabrata</i>	3							+		2200–3000	
<i>U. subaranea</i>	146		+		+	+		+	+	1500–4150	
<i>U. subcornuta</i>	8		+	+		+		+	+	800–2400	
<i>U. subdasaea</i>	38		+	+	+	+	+	+	+	1275–2700	200–1300
<i>U. subglabrata</i>	60		+	+	+	+		+	+	1500–3500	

Abbreviations for countries: ARG = Argentina, BOL = Bolivia, BRA = Brazil, COL = Colombia, ECU = Ecuador (continental), GAL = Galapagos, PER = Peru, VEN = Venezuela, SAM = continental South America; *n* = number of specimens studied; + = presence of species; newly described species are indicated in bold font.

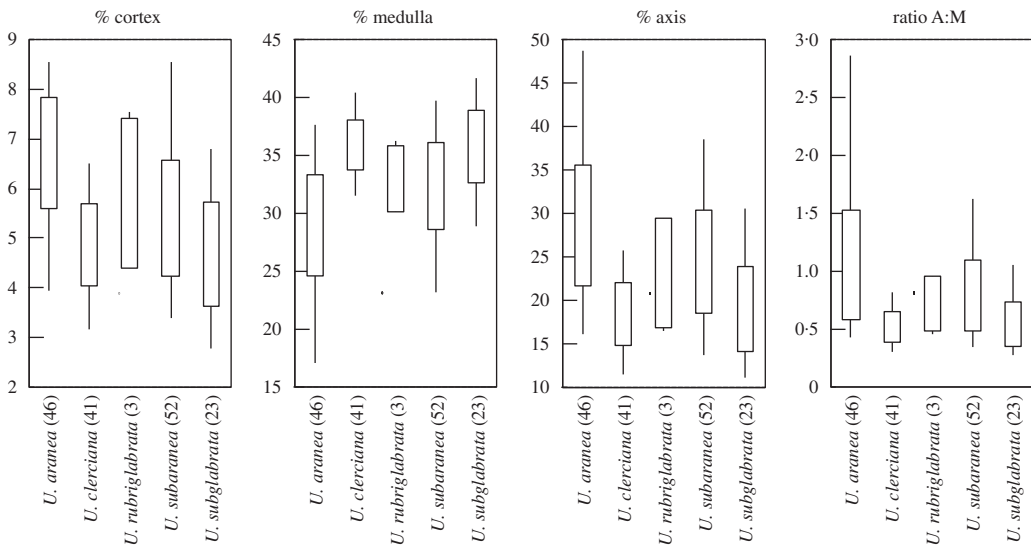


FIG. 1. The thickness of the cortex, medulla, and axis compared to the total branch diameter (CMA) expressed as a percentage and the thickness ratio axis:medulla (A:M) of the newly described species of *Usnea*. Standard deviations are shown as wide bars and range by vertical lines. The number of specimens measured is shown in parentheses.

per country and their altitudinal range. The newly described species *U. aranea*, *U. rubriglabrata*, *U. subaranea* and *U. subglabrata* are so far endemic to continental South America, whereas *U. cleriana* is endemic to the Galapagos. The distributions of *U. dorogawensis* and *U. grandisora* are extended to continental South America and new records from eastern South America (Argentina, Brazil

or Venezuela) are reported for *U. moreliana* and *U. subdasaea*. CMA values and chemotypes of the newly described species are illustrated in Figure 1 and Table 3, respectively.

Phylogenetic studies

The best ML tree (LnL = -7027.71) inferred from the multi-locus dataset is

TABLE 3. Major secondary metabolites and chemotypes detected in the medulla of new species of *Usnea* described in this study.

Species	n	Secondary Metabolites										K reaction	P reaction		
		BAR	PRO	PSO	NOR	SAL	STI	UU	USN	USN	USN				
<i>U. aranea</i> chemotype 1	30						+					±		yellow slowly turning orange	deep orange
<i>U. aranea</i> chemotype 2	9											±	+	none	none
<i>U. aranea</i> chemotype 3	7			+								±		dull yellow	deep yellow
<i>U. aranea</i> chemotype 4	1											+		none	none
<i>U. cleriana</i>	48							+						yellow turning red	yellow-orange
<i>U. rubriglabrata</i>	3		+											none	yellow-orange
<i>U. subaranea</i> chemotype 1	22					+								yellow turning red	yellow-orange
<i>U. subaranea</i> chemotype 2	14				±									yellow slowly turning orange	yellow-orange
<i>U. subaranea</i> chemotype 3	12			+								±		yellow slowly turning orange	deep orange
<i>U. subaranea</i> chemotype 4	5											±		dull yellow	deep yellow
<i>U. subaranea</i> chemotype 5	3											+		none	none
<i>U. subglabrata</i>	26	±									+			yellow slowly turning orange	deep orange

Abbreviations for secondary metabolites: BAR = barbatic acid, PRO = protoceraric acid, PSO = psoromic acid, NOR = norstictic acid, SAL = salazinic acid, STI = stictic acid group (incl. constictic and menegazziac acids), UU = unknown depside with RF classes A/B/C/D: 3/5-6/3-4/7, USN = usnic acid alone (detected in the cortex); n = number of specimens studied; + = presence constant within species; ± = presence variable among specimens within species.

illustrated in Figure 2. It contains 22 highly supported internodes (bootstrap support BS > 0.70). The B/MCMC majority-rule consensus tree (LnL = -7073.70) was almost identical to the ML tree, with 25 highly supported internodes (PP > 0.95). Posterior probabilities are reported on the ML tree adjacent to BS values.

As previously reported in *Truong et al.* (2013a), the *Usnea* clade is segregated into four highly supported clades USNEA-1 to USNEA-4 (shaded in light grey in Fig. 2). The placement of the newly described *Usnea* species within these clades has been discussed extensively in *Truong et al.* (2013a). *Usnea aranea* *Truong & P. Clerc*, *U. rubriglabrata* *Truong & P. Clerc* and *U. subaranea* *Truong & P. Clerc* cluster together with *U. acanthella* (I. M. Lamb) F. J. Walker within a small highly supported clade (USNEA-2, shaded in dark grey in Fig. 2), sister to the species from the section *Usnea* (i.e. *U. florida* (L.) F. H. Wigg. and relatives). All the species within this clade are endemic to the tropical Andes, in contrast to most clades within the phylogeny of *Usnea* that tend to show low geographic structuration, with several species occurring over different continents (*Truong et al.* 2013a). Concomitant patterns have been observed within the family *Parmeliaceae*, with truly widespread taxa but also lineages characterized by restricted geographical distributions (Fernández-Mendoza *et al.* 2011; Amo de Paz *et al.* 2012; Leavitt *et al.* 2013). *Usnea acanthella* shares the morphology and habitat of neuropogonoid species (i.e. black cortical pigmentation and saxicolous substratum) but clusters outside of the *Neuropogon* clade (*Truong et al.* 2013a). It is the only neuropogonoid species that is absent from polar regions, and its phylogenetic placement correlates with its distribution as a tropical Andean endemic, together with the non-neuropogonoid *U. aranea*, *U. rubriglabrata* and *U. subaranea*. In addition, *U. aranea* and *U. subaranea* share similar ecological preferences with *U. acanthella*, often growing close by in exposed habitats, for example at high altitudes above the tree limit.

Following the species-pair concept of Poelt (1970, 1972), *Usnea* taxa differing only in the

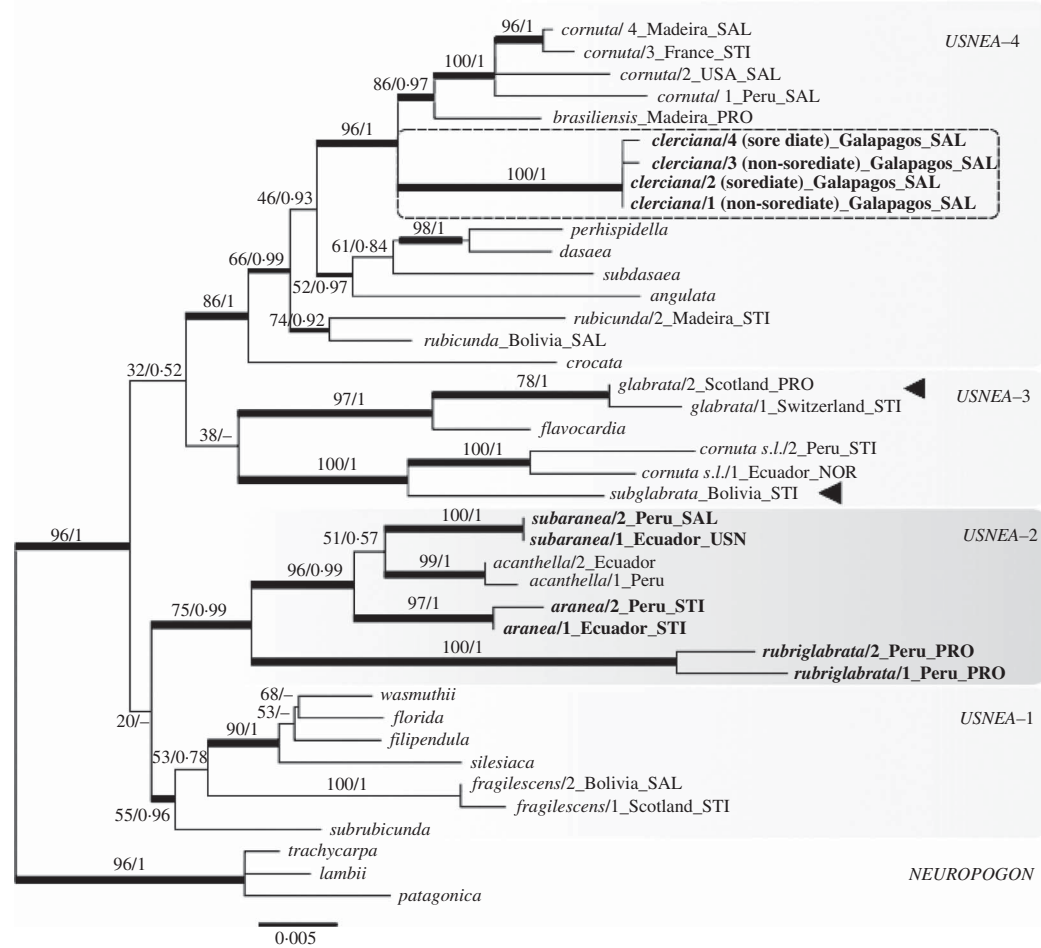


FIG. 2. Phylogram of the newly described species of *Usnea* based on maximum likelihood (ML) inference from the multi-locus dataset of ITS rDNA, nu LSU, *Mcm7* and *RPB1* genes revealing their position within the *Usnea* clade. Bootstrap supports (BS) are indicated above branches. Posterior probabilities (PP) from the Bayesian (B/MCMC) 50% majority-rule consensus tree are reported following the BS values. Thick branches indicate high support (BS ≥ 70 and/or PP ≥ 0.95). The *Usnea* clade is segregated into four clades USNEA-1 to USNEA-4 following Truong *et al.* (2013a) (shaded in light grey). The newly described species *U. aranea*, *U. rubriglabrata* and *U. subaranea* cluster together with *U. acanthella* within the USNEA-2 clade (shaded in dark grey). *Usnea glabrata* and *U. subglabrata* belong to distinct lineages (black arrow heads). Sorediate and non-sorediate specimens of *U. clerciana* cluster within the same lineage (delimited with dashes). Abbreviations for chemotypes: NOR = norstictic acid, PRO = protocetraric acid, SAL = salazinic acid, STI = stictic acid, USN = usnic acid only (cortical). Newly described species are indicated in bold font. The *Neurospogon* clade was used as the outgroup.

presence/absence of soralia are traditionally considered as distinct species, providing that they show dissimilarities in their distribution patterns (Clerc 1998). The evolutionary significance of reproductive traits may vary between lineages in lichen-forming fungi (Scherrer *et al.* 2005; Tehler *et al.* 2009) and assumptions need to be corroborated with molecular data for each particular case. Sorediate *Usnea* species often have a wider distribution than non-sorediate fertile taxa (Herrera-Campos *et al.* 1998), potentially correlated with increased dispersal abilities of vegetative propagules compared with ascospores. This does not necessarily mean that there isn't any gene flow occurring among populations of sorediate and non-sorediate specimens. Recently, several phylogenetic studies demonstrated that various species-pairs in *Usnea* did not represent distinct monophyletic lineages and should be considered conspecific (Articus *et al.* 2002; Seymour *et al.* 2007; Wirtz *et al.* 2012; Truong *et al.* 2013a). This seems to be the case for the newly described species *U. cleriana*, where sorediate and non-sorediate specimens belong to the same lineage based on their ITS and LSU sequences (delimited with dashed lines in Fig. 2).

New Species

Usnea aranea Truong & P. Clerc sp. nov.

MycoBank No.: MB 811375

Thallus stiff, branches inflated and constricted at ramification, papillae numerous, soralia minute and irregular, medulla loose and arachnoid.

Type: Bolivia, La Paz, Queara viejo, sendero hasta Muñamachay, 14.705556°S, 69.084306°W, 3379 m, bosque de neblina montano en transición con *matorral*, sobre ramas, 2007, *Truong* 2822 (LPB—holotype; G—isotype). % C/M/A: 6.5/34/19.5 Chemistry: usnic, stictic, constictic, menegazziaic acids, traces of norstictic acid.

(Fig. 3)

Thallus erect-shrubby, rarely sub-pendulous, very stiff, with a greyish and somewhat

translucid hue revealing clusters of algal cells visible in transparency, often abundantly infested by lichenicolous fungi typically forming a thin network on the branch surface (Fig. 3E); *ramifications* ± anisotomic-dichotomous; *trunk* blackish on the first mm below first ramification (Fig. 3B), rarely brownish to concolorous; *branches* ± tapering, segmented in slightly to strongly inflated segments, at least on basal branches (Fig. 3D); *branch segments* terete on terminal branches, slightly irregular or deformed on basal branches; *lateral branches* slightly to distinctly constricted at ramification, at least on basal branches (Fig. 3D); *foveoles* absent, rarely scarce on basal branches; *maculae* absent; *pseudocyphellae* minute, of irregular outline (young soralia?); *papillae* irregularly to abundantly distributed on basal and secondary branches (Fig. 3F), hemispherical, giving a coarse and rugulose aspect to the cortex surface; *tubercles* absent; *fibrils* slender, scattered to irregularly distributed; *fibercles* absent or scarce; *soralia* developing from the cortex *ad initio*, plane to slightly stipitate, becoming convex at maturity (Fig. 3F), remaining minute or slightly enlarged with irregular outline, aggregating in small clusters on terminal branches (Fig. 3G) and sometimes fusing in irregular 'soralium'; *isidiomorphs* often abundant, growing into isidiofibrils bursting solitary or in fasciculate clusters from soralia or pseudocyphellae (Fig. 3E); *cortex* thin to moderately thin (5.5–8.0%), very rigid, shiny to vitreous in section, surface of cortex often becoming necrotic with a dark blue to blackish pigmentation on small areas; *medulla* moderately thick to thick (24.5–33.5%), loose but thick-'arachnoid' (Fig. 3C), often forming bundles of tight hyphae connecting cortex and axis or forming a thin and compact layer applied to the cortex; *axis* thin to moderately thin (21.5–35.5%), often pale orange pigmented, with an A:M ratio of 0.5–1.5.

Apothecia rare ($n = 4$).

Pycnidia not seen.

Diagnostic notes. *Usnea aranea* is characterized by a stiff, erect-shrubby thallus with a

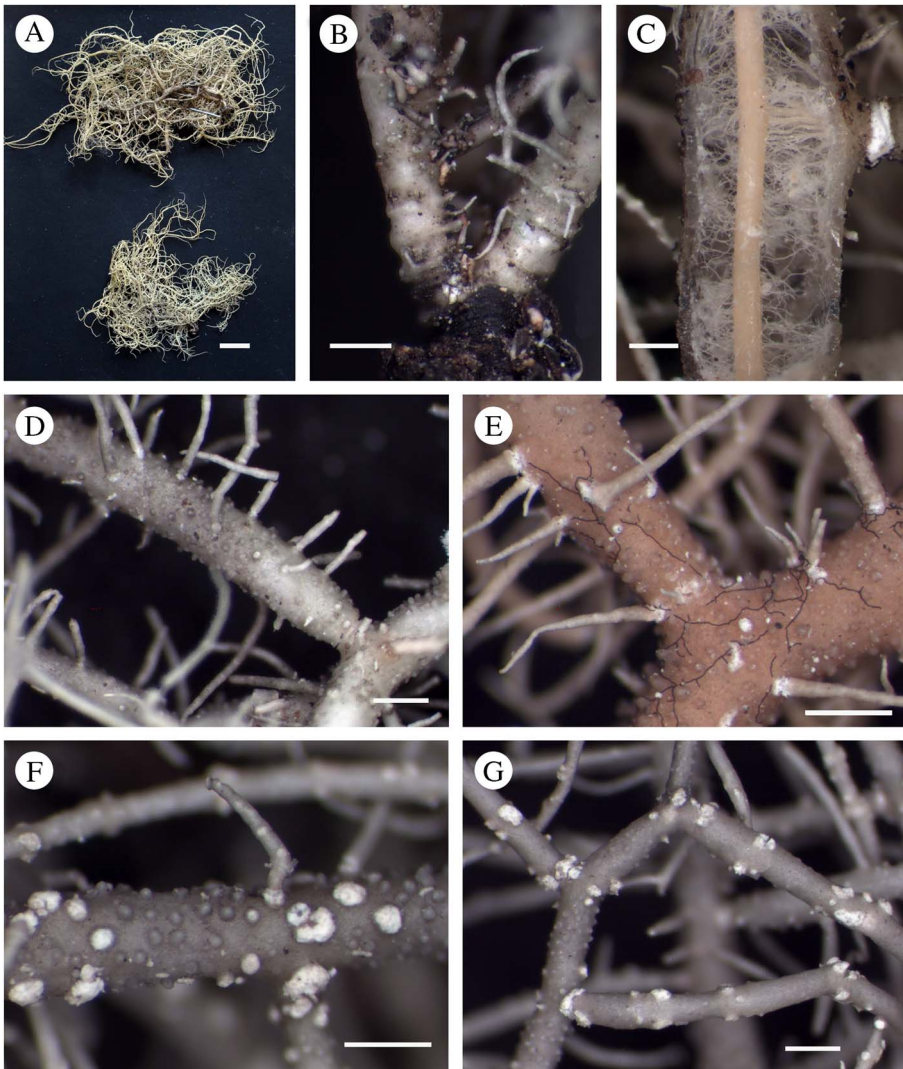


FIG. 3. *Usnea aranea*. A, holotype (above) and isotype (below); B, trunk blackish on the first mm below first ramification (Truong 286); C, section through branch (Truong 2822); D, branch slightly inflated and constricted at ramification (Truong 286); E, lichenicolous fungus forming a thin network on the surface of branches; fasciculate isidiofibrils bursting from pseudocyphellae (Cleef 3355); F, hemispherical papillae abundantly distributed on cortex surface; convex soralia (Truong 286); G, minute soralia aggregating in small clusters on terminal branches (Truong 286). Scales: A = 1 cm; B–G = 500 μ m. In colour online.

rough cortex surface harbouring numerous papillae. Basal branches are inflated and constricted at ramification. Minute soralia aggregate in irregular clusters on terminal branches, with numerous isidiomorphs growing into isidiofibrils. The cortex is relatively thin but very rigid, with a characteristic

greyish and somewhat translucent hue, and the medulla is loose and thick-‘arachnoid’.

Variation. Individuals with almost non-inflated and non-constricted branches may occur, for example in compact morphotypes growing at highly exposed sites. Basal part of

trunk may lack black pigmentation and appear brownish or concolorous. Soralia of various sizes are visible on the branches, minute to slightly enlarging with irregular outline, always becoming convex at maturity. Isidiomorphs and isidiofibrils vary in abundance but are usually numerous. Several chemotypes were detected (Table 3), including an unidentified yellowish brown depside with Rf classes A/B/C/D: 3/5–6/3–4/7, which do not correspond to either lecanoric or gyrophoric acid.

Differentiation. See under *U. subaranea*. *Usnea aranea* resembles *U. cornuta* Körb. with branches inflated and constricted at ramification, irregular soralia aggregating in clusters, and the chemotype of stictic acid. *Usnea cornuta* differs in having a denser medulla with thin hyphae and the somewhat thinner axis (ratio A:M < 1). In addition, the cortex is not as rigid as in *U. aranea*, resulting in a softer thallus, without a greyish translucent hue.

Ecology. Highlands of *puna* and *páramo* grasslands (i.e. shrubby *páramo*, *páramo de pajonal*, *páramo de Frailejones*, *Polylepis* stands or wooded ravines in *páramo*), transition between forest and *páramo*, primary and disturbed mountain cloud forests to the upper tree limit (*Ceja andina*), pastures or deforested zones of *matorral* in the vicinity of forest; corticolous on various trees and shrubs, occasionally saxicolous, rarely lignicolous on fence posts. This is a very common and abundant species on shrubs, at high altitudes or in exposed sites combining strong wind and high humidity from mist. It is closely related to the neuropogonoid species *U. acanthella* (I. M. Lamb.) F. J. Walker (Fig. 2). Both species are endemic to the tropical Andes and tend to grow in similarly exposed, high altitude habitats. They are often found close by in the same localities, where *U. aranea* is usually corticolous on shrubs but *U. acanthella* is saxicolous.

Distribution. So far endemic to the tropical Andes.

Selected specimens examined. **Bolivia:** Cochabamba: Prov. Ayopaya, comunidad de Saila Pata, 3350 m, 1997, *Bach & Jimenez* 911 (B). La Paz: Parque Nacional Alto Madidi, sendero hasta Muñamachay, 14-692306°S, 69-050111°W, 3008 m, 2007, *Truong* 2853 (G).—**Colombia:** Antioquia: 12 km al E de Sonsón hacia Nariño y Argelia, 2580 m, 1985, *Churchill & Sastre de Jesús* 12991 (B). Boyacá: páramos al NW de Belén, vereda San José de la Montaña, Alto de las Cruces y alrededores, 3800 m, 1972, *Cleef* 2302 (B). Caldas: Nevado del Ruiz, 3430 m, 1965, *Merill King et al.* 494 (US). Cauca: along road La Plata-Puracé, páramo 2 km W of Laguna de San Rafael, 3300 m, 1984, *Aguirre & Sipman* 5985 (B). Cundinamarca: páramo de Cruz Verde, km 16 of carretera Bogotá-Choachi, 3365 m, 1972, *Cleef* 2990 (B). Nariño: Munic. Pasto, páramo El Frailejonal, 8 km E de Mocondino, 3400 m, 1997, *Ramirez et al.* 10513 (B). Risaralda: Munic. Santa Rosa de Cabal, c. 500 m S of Finca La Sierra, 3750 m, 1984, *Aguirre & Sipman* 5478 (B).—**Ecuador:** Azuay: Parque Nacional Cajas, sector laguna Toreadora, sendero García Moreno, 2-783639°S, 79-209917°W, 3794 m, 2007, *Truong* 3188 (G). Imbabura: Reserva Ecológica Cotacachi-Cayapas, Laguna Piñán, 0-517611°N, 78-438333°W, 2786 m, 2007, *Truong* 3252 (G). Loja: Parque Nacional Podocarpus, sendero de las lagunas del Compadre, 4-115083°S, 79-165139°W, 3000 m, 2007, *Truong* 254 (G). Pichincha: Reserva de Vida Silvestre Pasochoa, sendero Los Pantzas, 0-443278°S, 78-494306°W, 3460 m, 2013, *Truong* 3943 (G). Tungurahua: Parque Nacional Llaganates, parte alta desde Pelileo, cerca de la entrada del parque, 1-082167°S, 78-411861°W, 3498 m, 2007, *Truong* 468 (G).—**Peru:** Cajamarca: Parque Nacional Cutervo, subiendo al cerro Tarros, 6-301389°S, 78-799778°W, 3075 m, 2007, *Truong* 1712 (G). Cusco: Santuario Histórico de Machu Picchu, Camino Inca, abra Runkuraquay, 13-226167°S, 72-508111°W, 3809 m, 2007, *Truong* 2006 (G). Huanuco: Lagunas Pichgacocha, bajando desde la primera laguna, 10-026833°S, 76-135611°W, 3751 m, 2007, *Truong* 761 (G). Pasco: Parque Nacional Yanachaga-Chemillén, trocha hasta la laguna San Alberto, 10-530833°S, 75-350556°W, 2835 m, 2007, *Truong* 2592 (G).—**Venezuela:** Mérida: Potrereros de San Rafael, páramo de Las Coloradas, 2950 m, 1975, *Hale & López-Figueiras* 44400 (US).

Usnea clerciana Truong sp. nov.

Mycobank No.: MB 811376

Thallus erect-shrubby, branches inflated and constricted at ramification, tubercles elongated and eroded, soralia large and excavate, apothecia usually present when soralia are absent, medulla loose, reacting K+ (salazinic acid).

Type: Ecuador, Galapagos, Santa Cruz, above Mina Granillo, 0-618750°S, 90-365416°W, 607 m, upper transition zone, branches of ferns at the top of a rock outcrop, 2008, *Truong* 1127 (CDS—holotype; G—isotype). % C/M/A: 6.5/36.0/15.0. Chemistry: usnic, salazinic, traces of protocetraric acids.

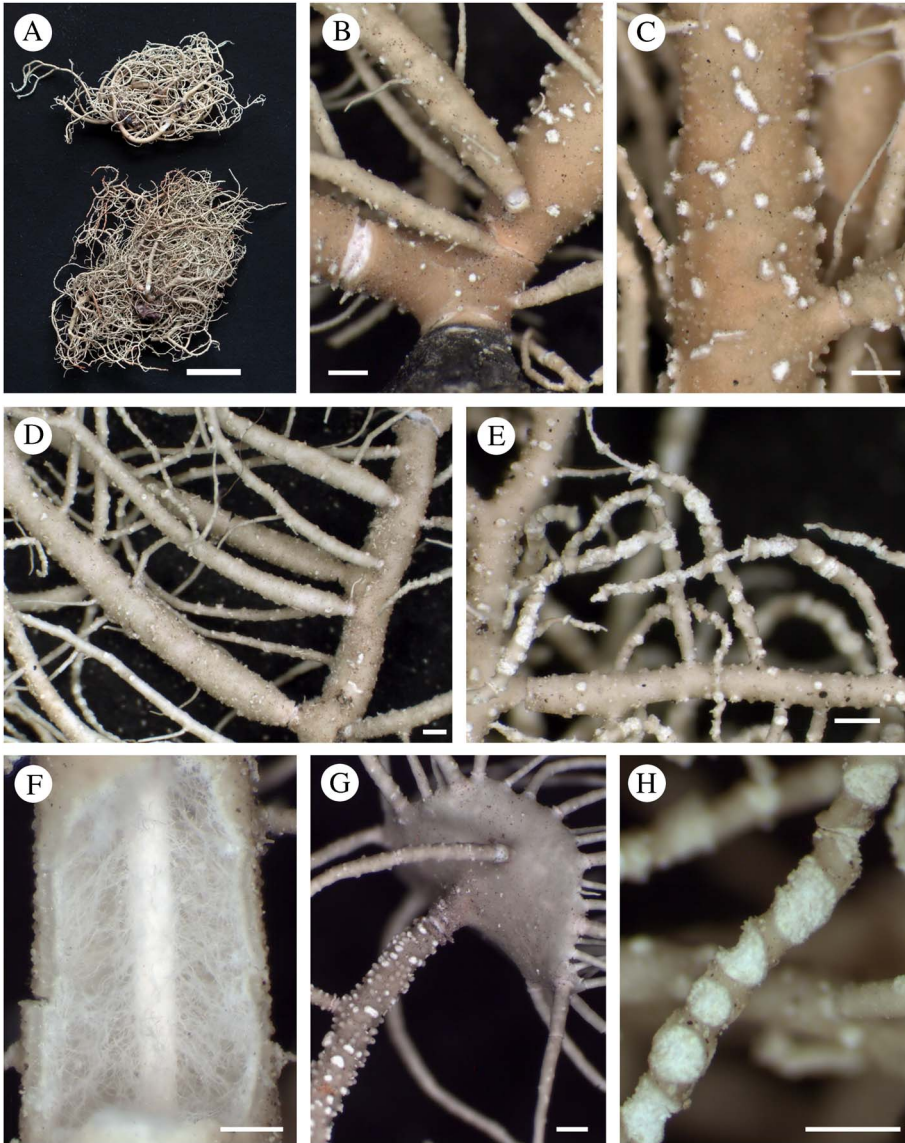


FIG. 4. *Usnea clericiana*. A, holotype (above) and isotype (below); B, trunk concolorous (*Bungartz* 7701C); C, elongated tubercles, eroded on top (*Bungartz* 7701C); D, branch inflated and constricted at ramification (*Truong* 1127); E, thin terminal branches with large and excavate soralia, eroding branch apices and exposing the central axis (*Truong* 1127); F, section through branch (*Truong* 1394); G, branch abundantly covered by tubercles and holding apothecia (*Clerc* 08-76); H, circular and excavate soralia delimited with a thin cortical margin (*Truong* 1127). Scales: A = 1 cm; B–H = 500 μ m. In colour online.

(Fig. 4)

Thallus erect-shrubby, relatively stiff; *ramifications* \pm anisotomic-dichotomous; *trunk* concolorous (Fig. 4B), rarely blackish or

brownish on the first mm below first ramification; *branches* tapering to \pm irregular, segmented into slightly to strongly inflated segments, at least on basal branches (Fig. 4D); *branch segments* \pm terete to slightly

flattened or deformed on basal branches; *lateral branches* slightly to strongly constricted at ramification towards base of thallus (Fig. 4D), terminal branches often thin (Fig. 4E) and not constricted; *foveoles* absent or scarce; *maculae* and *pseudocyphellae* absent; *papillae* scarce to abundantly distributed on basal and secondary branches; *tubercles* irregularly to abundantly distributed on basal and secondary branches, conical to verrucose, sometimes almost cylindrical, slightly elongated and usually eroding on top when fully developed (Fig. 4C & G); *fibrils* \pm thick and long, scattered to densely distributed; *fibercles* absent or scarce; *soralia* developing from the cortex *ad initio* or from tubercles, large and circular to elongated, delimited with a thin cortical margin, plane to strongly excavate (Fig. 4H), sometimes becoming slightly convex with age, often crowded on terminal branches and eroding the branch apices, exposing the central axis (Fig. 4E); *isidiomorphs* absent or scarce within soralia, sometimes few isidiomorphs bursting from tubercles on basal and secondary branches; *cortex* thin (4.0–5.5%), opaque and \pm shiny in section; *medulla* thick (33.5–38.0%), loose with thin hyphae (Fig. 4F), somewhat denser towards the cortex; *axis* thin (15.0–22.0%), unpigmented, with an A:M ratio > 0.75 .

Apothecia often abundant, usually present when soralia are absent ($n = 38$), rarely both soralia and apothecia present ($n = 1$), pedicellate (Fig. 4G) or rarely sessile, with \pm thick and long cilia.

Pycnidia hemispherical on terminal branches, usually present only when apothecia or soralia are absent.

Etymology. This species is named in honour of Philippe Clerc for his major contribution to the study of the genus *Usnea* worldwide.

Diagnostic notes. *Usnea clerciana* is characterized by a stiff erect-shrubby thallus, basal branches inflated and constricted at ramification, and elongated eroded tubercles irregularly to densely distributed on branches. When present, large and circular soralia are often crowded on terminal branches, eroding the apices of branches. Numerous apothecia are

usually present when soralia are lacking. The medulla is relatively loose, reacting K⁺ yellow turning red (salazinic acid).

Variation. Branch segments are \pm terete to deformed, with various degrees of branch inflation and constriction at ramification. Papillae and tubercles vary in abundance and in some specimens, especially when apothecia are present, a majority of tubercles may not erode, appearing verrucose to almost cylindrical. When present, soralia of all sizes may be visible on branches, but large and excavate soralia are always present. Sorediate and non-sorediate thalli often grow side by side and specimens with both soralia and apothecia were rarely encountered ($n = 1$). Phylogenetic studies provided evidence that sorediate and non-sorediate specimens belong to the same lineage based on their ITS and LSU sequences (delimited with dashes in Fig. 2).

Differentiation. *Usnea cirrosa* Motyka, *U. cornuta* Körb. and *U. fragilescens* Lynge share with *U. clerciana* the inflated branches constricted at ramification, and the thick medulla with an A:M ratio < 1 . They differ from *U. clerciana* in the flaccid thallus, the terete branch segments, basal branches not irregular or deformed, and the absence or rarity of tubercles, remaining lower and never elongated. The non-sorediate *U. cirrosa* is distinguished by the denser medulla reacting K⁺ yellow (stictic) or K⁺ yellow turning red (salazinic acid) in South America. The sorediate *U. fragilescens* has circular to slightly excavate soralia that remain isolated (not crowded on terminal branches). *Usnea cirrosa* and *U. fragilescens* are abundant in continental South America but have not been encountered in the Galapagos so far. *Usnea cornuta* s. str. (according to Truong *et al.* 2013a) is present in the Galapagos and differs by the minute soralia aggregating in irregular clusters, not circular or excavate, and the denser medulla, reacting K⁺ yellow (stictic) or K⁺ yellow turning red (salazinic acid). Our phylogenetic results indicate that *U. clerciana* and *U. cornuta* s. str. are potentially closely related (Fig. 2).

Ecology. Wide altitudinal range from the arid to the high altitude dry zone, most common in the transition zone; primarily corticolous on various trees and shrubs, including on cacti, rarely saxicolous or lignicolous.

Distribution. So far endemic to the Galapagos, where it is relatively common.

Selected specimens examined. Ecuador: Galapagos Islands: Isabela, volcán Darwin, 0-203194°S, 91-311472°W, 1286 m, 2007, *Bungartz* 7505 (CDS); Pinta, along trail going up the south-western slope to Las Pampas, 0-570417°N, 90-760611°W, 316 m, 2008, *Nugra* 577 (CDS); Pinzón, along the trail going up from Playa Escondida, 0-602778°S, 90-666944°W, 254 m, 2006, *Aproot* 64129 (CDS); San Cristóbal, Cerro Colorado summit, 0-414556°S, 89-433194°W, 167 m, 2008, *Truong* 1413 (G); Santa Cruz, dirt road to Mina Granillo, 0-614611°S, 90-369944°W, 547 m, 2008, *Clerc* 08-174 (G); Santiago, along the trail from Bucanero to Jaboncillos, 0-176111°S, 90-815278°W, 225 m, 2006, *Aproot* 65364 (CDS).

***Usnea rubriglabrata* Truong & P. Clerc
sp. nov.**

Mycobank No.: MB 811377

Thallus erect-shrubby, basal branches inflated and constricted at ramification, soralia large and excavate, reddish and maculate pigmentation on the cortex surface, medulla dense and reacting K- (protocetraric acid).

Type: Peru, Cajamarca, carretera 8 de Chachapoyas a Celendin, cerca del distrito de Las Palmas, 6-717972°S, 77-844833°W, 2940 m, *matorral* arbóreo, sobre ramas, 2007, *Truong* 1877 (G—holotype). % C/M/A: 7.5/30.0/24.5. Chemistry: usnic and protocetraric acids.

(Fig. 5)

Thallus erect-shrubby; *ramifications* ± anisotomic-dichotomous; *trunk* concolorous (Fig. 5B), sometimes brownish on the first mm below first ramification; *branches* tapering to ± irregular, segmented in slightly to strongly inflated segments on basal branches (Fig. 5C), terminal branches relatively thin and non-inflated, sinuous at the apices (Fig. 5E); *branch segments* ± terete, rarely irregular on basal branches; *lateral branches* distinctly constricted at ramification on basal branches (Fig. 5C), terminal branches often not constricted; *foveoles* absent or scarce on

basal branches; *maculae* and *pseudocyphellae* absent, although reddish pigmentation may look maculate; *papillae* and *tubercles* scarce to irregularly distributed on basal branches (Fig. 5D); *fibrils* slender, scattered to irregularly distributed; *fibercles* absent or scarce; *soralia* arising on terminal branches from the cortex *ad initio*, large and strongly excavate (Fig. 5E), delimited with a thin cortical margin; *isidiomorphs* absent with granular soredia instead; *cortex* thin to moderately thin (4.5–7.5%), shiny in section, with a reddish and maculate pigmentation on the cortex surface (Fig. 5C); *medulla* thick (30.0–36.0%) and dense, looser towards the axis (Fig. 5F); *axis* thin (17.0–29.5%), with an A:M ratio < 1.0.

Apothecia and *pycnidia* not seen.

Diagnostic notes. *Usnea rubriglabrata* is characterized by the erect-shrubby thallus with reddish maculate pigmentation on the cortex surface. Basal branches are inflated and constricted at ramification, contrasting with the thin and sinuous terminal branches bearing large and excavate soralia. The medulla is dense, reacting K- (protocetraric acid). This species was described as a potential new species named *Usnea* sp. 1 in Truong *et al.* (2011), but the small number of specimens available prevented us from describing it formally. Later, phylogenetic studies gave additional evidence for the validity of this taxon as a distinct species (Fig. 2).

Variation. The abundance of papillae, tubercles, fibrils and fibercles may vary among individuals. Isidiomorphs are usually absent, but may occur abundantly when the thallus is infected by parasitic fungi.

Differentiation. The red-pigmented cortex surface and the large excavate soralia make *U. rubriglabrata* readily distinguishable from any other *Usnea* species. In the Galapagos, *U. dorogawensis* Asahina has reddish orange subcortical pigmentation visible in section in the medulla as well as, a thinner cortex with a smoother cortex surface without papillae, and a looser medulla reacting K+ (lobaric with stictic or norstictic acids).

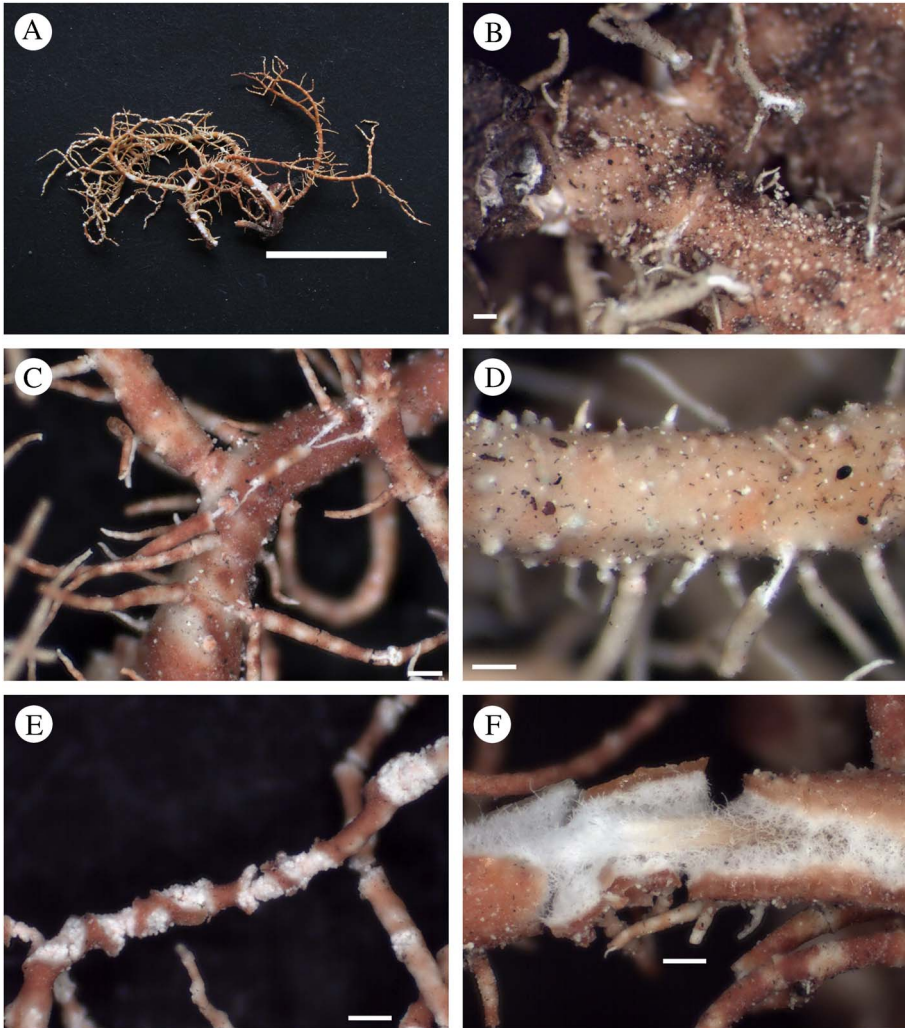


FIG. 5. *Usnea rubriglabrata*. A, holotype; B, trunk concolorous (*Truong* 1625); C, branch inflated and constricted at ramification; reddish and maculate cortex surface (*Truong* 1877); D, papillae on basal branches (*Truong* 1625); E, terminal branches thin and sinuous, with strongly excavate soralia (*Truong* 1877); F, section through branch (*Truong* 1877). Scales: A = 1 cm; B–F = 250 μ m. In colour online.

Ecology. Pastures or deforested zones of *matorral* in the vicinity of forest; corticolous.

Distribution. So far endemic to northern Peru; rare.

Selected specimens examined. **Peru:** *Cajamarca:* Parque Nacional Cutervo, cerca de San Andrés de Cutervo, sector alto pajonal, 6-221750°S, 78-742861°W, 2541 m, 2007, *Truong* 1625 (G); carretera 8 de Chachapoyas a Celendín, entre los distritos de Balsas y Celendín, 6-873917°S, 78-100889°W, 2254 m, 2007, *Truong* 1894 (G).

***Usnea subaranea* *Truong & P. Clerc* sp. nov.**

Mycobank No.: MB 811378

Similar to *U. aranea* but with large, circular and excavate soralia, without or with few isidiomorphs.

Type: Colombia, Cundinamarca, Parque Nacional Natural Chingaza, Munic. Fomeque, about halfway between Embalse de Chuza and Laguna Seca, 4-617°S, 74-733°W, 3200 m, subpáramo scrub on steep slope, epiphytic, 1988, *Sipman & Aguirre* 27435a (B—holotype;

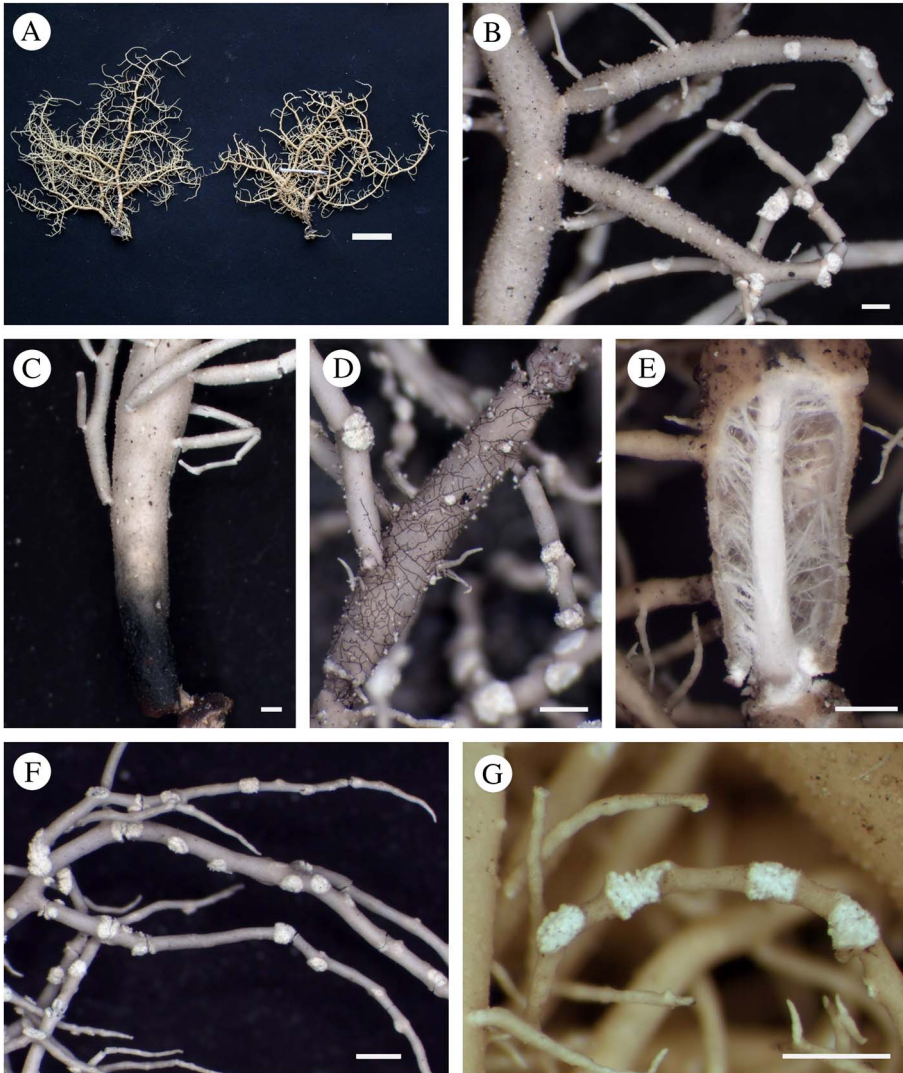


FIG. 6. *Usnea subaranea*. A, holotype (left) and isotype (right); B, branch slightly inflated and constricted at ramification; papillae abundant, giving a rugulose aspect to the cortex surface (Truong 2013); C, trunk blackish on the first mm below first ramification (Truong 2013); D, lichenicolous fungus forming a thin network on the branch surface (Truong 3229); E, section through branch (Sipman & Aguirre 27435a); F, terminal branches thin and sinuous, holding circular and isolated soralia (Truong 313); G, large and excavate soralia encircling thin terminal branches (Sipman & Aguirre 27435a). Scales: A = 1 cm; B–G = 500 μ m. In colour online.

G—isotype). % C/M/A: 4.5/30.0/30.0. Chemistry: usnic, salazinic and norstictic acids.

(Fig. 6)

Thallus erect-shrubby, rarely subpendulous, very stiff, with a greyish and somewhat translucent hue revealing clusters of algal cells visible

when transparent, often abundantly infested by lichenicolous fungi typically forming thin networks on the surface of branches (Fig. 6D); *ramifications* \pm anisotomic-dichotomous; *trunk* blackish on the first mm below first ramification (Fig. 6C), rarely brownish or concolorous; *branches* \pm tapering, basal branches

segmented in slightly to strongly inflated segments (Fig. 6B), terminal branches often thin and non-inflated, with long and sinuous apices (Fig. 6F); *branch segments* terete on terminal branches to slightly irregular or deformed on basal branches; *lateral branches* slightly to distinctly constricted at ramification at least on basal branches; *foveoles* sometimes present on basal branches; *maculae* absent; *pseudocyphellae* absent or scarce, minute, of irregular outline; *papillae* irregularly to abundantly distributed on basal and secondary branches, hemispherical, giving a coarse and rugulose aspect to the cortex surface (Fig. 6B); *tubercles* absent; *fibrils* slender, scattered to irregularly distributed; *fibercles* absent or scarce; *soralia* arising on terminal branches from the cortex *ad initio*, circular, remaining isolated (Fig. 6F) and delimited with a thin cortical margin, plane to excavate, sometimes encircling thin terminal branches (Fig. 6G); *isidiomorphs* absent or scarce within soralia with granular soredia instead, rarely few to numerous isidiomorphs bursting from pseudocyphellae or fibercles on basal and secondary branches, but not on terminal branches, and growing into isidiofibrils; *cortex* thin to moderately thin (4.0–6.5%), very rigid, shiny to vitreous in section; *medulla* thick (28.5–36.0%), loose but thick-‘arachnoid’ (Fig. 6E), often forming bundles of tight hyphae connecting cortex and axis or forming a thin and compact layer applied to the cortex; *axis* thin to moderately thin (18.5–30.5%), often pale orange pigmented, with an A:M ratio usually >1.0 (rarely to 1.5).

Apothecia rare ($n = 1$).

Pycnidia not seen.

Diagnostic notes. *Usnea subaranea* is characterized by a stiff, erect-shrubby thallus with a rough cortex surface harbouring numerous papillae. Basal branches are inflated and constricted at ramification. Circular and excavate soralia remain isolated and delimited with a thin cortical margin, with granular soredia instead of isidiomorphs. The cortex is relatively thin but very rigid, with a characteristic greyish and somewhat translucent hue, and the medulla is loose and thick-‘arachnoid’.

Variation. Individuals with almost non-inflated and non-constricted basal branches may occur, for example in compact morphotypes growing at highly exposed sites. Basal part of trunk may lack black pigmentation and appear brownish or concolorous. Several chemotypes were detected (Table 3), including an unidentified yellowish brown depside with Rf classes A/B/C/D: 3/5–6/3–4/7, which does not correspond to either lecanoric or gyrophoric acid.

Differentiation. See under *U. subglabrata*. Apart from soralia, *U. aranea* has a similar morphology and branch section. It differs in the non-enlarging soralia of irregular outline, capitate at maturity, not circular or excavate, often aggregating in clusters with numerous isidiomorphs. In *U. subaranea*, isidiomorphs are usually absent from soralia with granular soredia instead, but occasionally grow from pseudocyphellae on basal branches (i.e. in thalli infested by parasitic fungi). Both species share several chemotypes (Table 3), yet the most frequent chemotype in *U. subaranea* (salazinic acid) is absent in *U. aranea*. Phylogenetic studies provided evidence that these two species are closely related (Fig. 2). Intermediate morphs may occur between the two species and the presence of hybrids is not excluded.

Ecology. Highlands of *puna* and *páramo* grasslands (i.e. shrubby *páramo*, *páramo de pajonal*, *páramo de Frailejones*, *Polylepis* stands or wooded ravines in *páramo*), transition between forest and *páramo*, primary and disturbed mountain cloud forests to the upper tree limit (*Ceja andina*), *Pinus* plantations, pastures or deforested zones of *matorral* in the vicinity of forest; corticolous on various trees and shrubs, occasionally saxicolous, rarely lignicolous on fence posts. This is a very common and abundant species on shrubs, at high altitudes or in exposed sites combining strong wind and high humidity from mist. It is closely related to *U. aranea* and the neuropogonoid species *U. acanthella* (I. M. Lamb.) F. J. Walker (Fig. 2). The three species are endemic to the tropical Andes and share similar ecological

preferences, often growing close by in exposed habitats, for example at high altitudes.

Distribution. So far endemic to the tropical Andes.

Selected specimens examined. **Bolivia:** Cochabamba: Parque Nacional Carrasco, Sehuenacas, alrededores del puente sobre río Fuertemayu, 17-496528°S, 65-272500°W, 2183 m, 2007, *Truong* 3124 (G). La Paz: Reserva Faunística Ulla Ulla, saliendo de Pelechuco, 14-818750°S, 69-063722°W, 3499 m, 2007, *Truong* 2898 (G).—**Colombia:** Antioquia: c. 10 km NW of Medellín, hilltop with transmission tower along the road to San Félix, 3000 m, 1986, *Sipman et al.* 34273 (B). Boyaca: Páramo de la Rusia, along road Charala-Duitama, 3500 m, 1988, *Sipman & Aguirre* 27679 (B). Cauca: along road La Plata-Puracé, páramo 2 km W of Laguna de San Rafael, 3300 m, 1984, *Aguirre & Sipman* 5985 (B). Cundinamarca: Laguna Seca in páramo Alto between Cogua and San Cayetano, 3450 m, 1975, *Florschütz* 4467 (B). Risaralda: Pereira, Nevado de Santa Isabel, vertiente NW, 4150 m, 1980, *Boekhout* 159 (B).—**Ecuador:** Azuay: Cuenca, sendero hasta el cerro Cajas desde el puente de los Dos Chorreras, 2-740306°S, 79-153889°W, 3796 m, 2007, *Truong* 397 (G). Imbabura: Reserva Ecológica Cotacachi-Cayapas, laguna Cuicotcha, Isote Verovi, 0-301194°N, 78-362750°W, 3068 m, 2007, *Truong* 3304 (G). Loja: Parque Nacional Podocarpus, sendero de las lagunas del Compadre, 4-115083°S, 79-165139°W, 3000 m, 2007, *Truong* 257 (G). Pichincha: Reserva de Vida Silvestre Paschoa, sendero Los Pantzas, 0-443278°S, 78-494306°W, 3547 m, 2013, *Truong* 4197 (G). Tungurahua: Parque Nacional Llaganates, ruta desde Pelileo, a lo lado del río Talata, 1-081889°S, 78-410528°W, 3567 m, 2007, *Truong* 453 (G).—**Peru:** Cajamarca: Carretera 8 de Chachapoyas a Celendín, cerca del distrito Las Palmas, 6-717972°S, 77-844833°W, 2940 m, 2007, *Truong* 1878 (G). Cusco: Centro de Investigación Wayqecha, Trocha Picaflor, 13-173972°S, 71-587944°W, 2892 m, 2007, *Truong* 2119 (G). Huanuco: Bosque de Carpish, 9-715306°S, 76-094167°W, 2675 m, 2007, *Truong* 2794 (G). Pasco: Parque Nacional Yanachaga-Chemillén, trocha hasta la ambra Esperanza, 10-540250°S, 75-356250°W, 2482 m, 2007, *Truong* 2495 (G).—**Venezuela:** Bolívar: Cerro Guaiquinima, near west end of upper plateau, 1500 m, 1990, *Sipman* 27246b (B). Mérida: vers la laguna de Los Patos, 3700 m, 1989, *Grundler* (G).

***Usnea subglabrata* Truong & P. Clerc sp. nov.**

Mycobank No.: MB 811379

Thallus small erect-shrubby, branches inflated and constricted at ramification, low papillae often abundant, soralia strongly excavate without isidiomorphs, medulla loose with thin hyphae, reacting K+ yellow-orange (stictic acid).

Type: Bolivia, La Paz, ruta nueva hasta Coroico, 1 km después de Unduavi, 16-291639°S, 67-860556°W, 3132 m, bosque de neblina montano en transición con matorral, sobre ramas de árboles pequeños, 2007, *Truong* 2978 (LBP—holotype; G—isotype). % C/M/A: 5.0/31.5/27.0. Chemistry: usnic, stictic, constrictic, menegazziac, barbatic, traces of norstictic acids.

(Fig. 7)

Thallus erect-shrubby, usually of small size (1–3 cm); *ramifications* ± anisotomic-dichotomous; *trunk* blackish on the first mm below first ramification (Fig. 7C), rarely brownish or concolorous; *branches* tapering to ± irregular, with thick apices, slightly to strongly inflated on basal branches (Fig. 7B); *branch segments* slightly to strongly irregular or deformed on basal branches, ± terete on terminal branches; *lateral branches* slightly to distinctly constricted at ramification at least on basal branches (Fig. 7B); *foveoles* often present on basal branches; *maculae* and *pseudocyphellae* absent; *papillae* irregularly to abundantly distributed on basal and secondary branches, hemispherical, giving a coarse and rugulose aspect to the cortex surface (Fig. 7D); *tubercles* absent; *fibrils* slender, scattered to irregularly distributed; *fibercles* absent or scarce; *soralia* arising on terminal branches from the cortex *ad initio*, circular, isolated and delimited with a thin cortical margin, strongly excavate at maturity, becoming larger than the branch diameter or encircling thin terminal branches and exposing the axis (Fig. 7F & G); *isidiomorphs* usually absent with granular soredia instead; *cortex* thin (3.5–5.5%), shiny to vitreous in section; *medulla* thick (32.5–39.0%), loose with thin hyphae (Fig. 7E); *axis* thin (14.0–24.0%) with an A:M ratio < 0.75.

Apothecia and *pycnidia* not seen.

Diagnostic notes. *Usnea subglabrata* is characterized by a small erect-shrubby thallus with basal branches inflated and constricted at ramification, and short terminal branches with thick apices, holding strongly excavate soralia, bearing granular soredia instead of isidiomorphs. The cortex is thin and shiny, with a rugose cortex surface irregularly covered by papillae. The medulla is loose

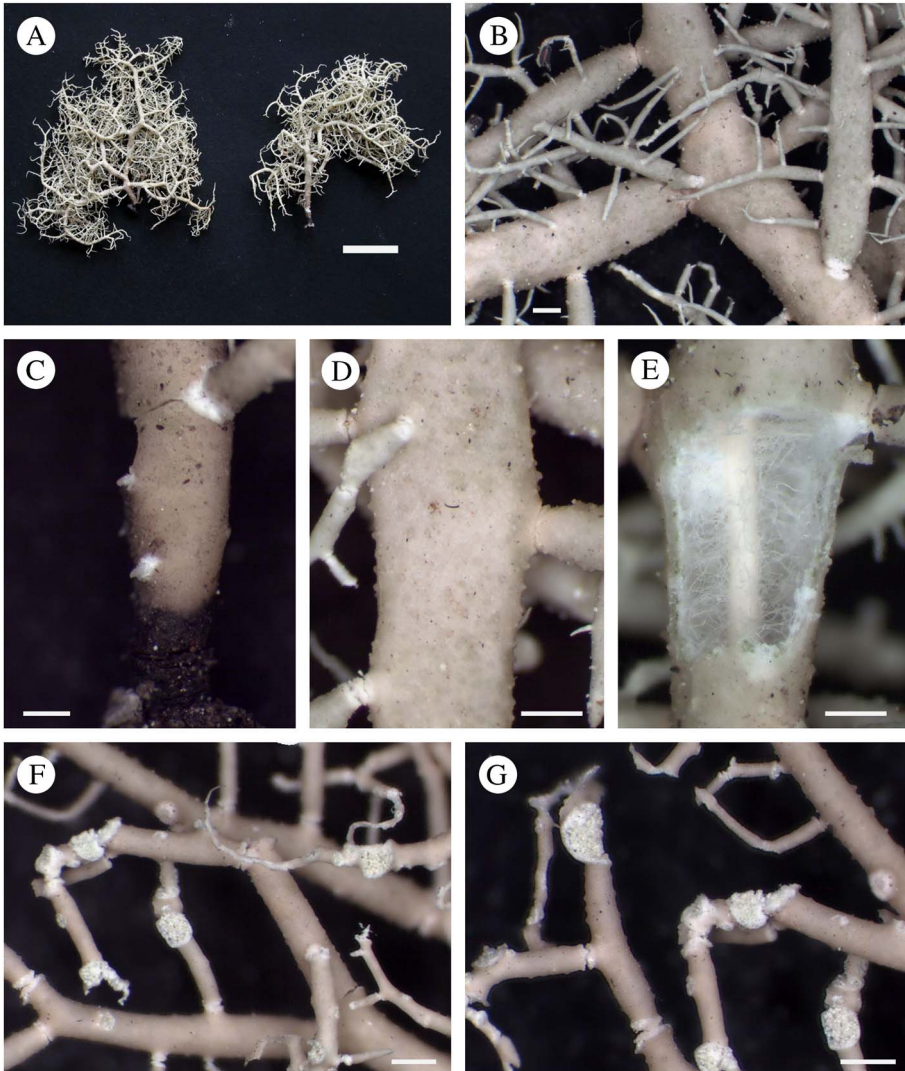


FIG. 7. *Usnea subglabrata*. A, holotype (left) and isotype (right); B, branch distinctly inflated and constricted at ramification (*Truong* 304); C, trunk blackish on the first mm below first ramification (*Truong* 2978); D, papillae abundant on basal branches, giving a rugulose aspect to the cortex surface (*Truong* 304); E, section through branch (*Truong* 304); F & G, strongly excavate soralia becoming larger than the branch diameter (*Truong* 2409). Scales: A = 1 cm; B–G = 500 μ m. In colour online.

with thin hyphae, reacting K⁺ yellow (stictic \pm barbatic acids), although the reaction is often faint and may take a few minutes to become visible.

Variation. The degree of inflation and constriction of branches at ramification may

vary among individuals, as well as the number of papillae on the cortex surface. Basal part of the trunk may lack black pigmentation and appear brownish or concolorous. Isidiomorphs are usually absent, but may occur abundantly when the thallus is infected by parasitic fungi.

Differentiation. *Usnea subaranea* has a similar morphology of soralia and specimens with short and compact thalli may be difficult to distinguish from *U. subglabrata*. In *U. subaranea* the thallus is usually stiffer from the rigid cortex, with a typically greyish shade. Terminal branches tend to be thin and sinuous towards the apices, while they are short and thick in *U. subglabrata*. Soralia usually remain circular, rarely exceeding the branch diameter in size or torn apart as in *U. subglabrata*. The medulla is loose with thick-‘arachnoid’ hyphae, which are thin in *U. subglabrata*. Both species share one chemotype (stictic acid), but with different accompanying substances; barbatic acid in *U. subglabrata* and an unidentified yellowish brown depside in *U. subaranea*. In the temperate zone, *U. glabrata* (Ach.) Vain. has a very similar morphology, with a short and shrubby thallus, inflated branches and strongly excavate soralia. It differs mainly in the smooth cortex surface without apparent papillae. The medulla of *U. glabrata* usually reacts K– (protocetraric acid), but the chemotypes of salazinic or stictic acids have also been detected, as in *U. subglabrata* (Herrera-Campos *et al.* 2001; Clerc 2011). Our phylogenetic study revealed that these two taxa belong to distinct lineages within the *Usnea* clade–3 (black triangles in Fig. 2).

Ecology. Relatively open sites within primary or disturbed mountain cloud forests to the upper tree limit (*Ceja andina*), highlands of *puna* and *páramo* grasslands (i.e. shrubby *páramo*, *páramo de pajonal*, *Polylepis* stands or wooded ravines in *páramo*), *Pinus* and *Eucalyptus* plantations, pastures with forest relics or deforested zones of *matorral* in the vicinity of forest; primarily corticolous on various trees and shrubs, rarely saxicolous or lignicolous on fence posts. This is a small but often abundant species, with a wide ecological and altitudinal range.

Distribution. So far endemic to continental South America.

Selected specimens examined. **Bolivia:** Cochabamba: Cerca de Corani, alrededores de la laguna, 17-227278°S, 65-889528°W, 3173 m, 2007, *Truong* 587 (G). *La Paz:* Parque Nacional Cotapata, ruta antigua hasta Coroico,

16-288194°S, 67-808417°W, 2664 m, 2007, *Truong* 3907 (G).—**Brazil:** *Rio de Janeiro:* Parque Nacional do Itatiaia, km 11–12 on Planalto road to Agulhas Negras, 22-383°S, 44-683°W, 2400 m, 1993, *Marcelli et al.* 25155 (H).—**Colombia:** *Antioquia:* Munic. Guarne, Piedras Blancas, along the road to Santa Helena, 2300 m, 1986, *Sipman et al.* 33946 (B). *Boyaca:* Munic. Cucaita, c. 10 km W of Tunja along road to Villa de Leiva, 2950 m, 1986, *Sipman & Reyes* 34467 (B). *Cundinamarca:* Mosquera, Alto de Mondoñedo, 4-675833°N, 74-289333°W 2903 m, 1998, *Pinzón & Linares* 912 (B). *Huila:* Munic. La Plata, Vereda La Candelaria, volcán Merenberg, 2600 m, 1984, *Aguirre & Sipman* 5842 (B). *Nariño:* Munic. Piedrancha, along road from San Isidro to Reserva Natural La Planada, 1700 m, 1986, *Sipman et al.* 33482 (B).—**Ecuador:** *Imbabura:* Reserva Ecológica Cotacachi-Cayapas, laguna Cuicotcha, islote Veroti, 0-301194°N, 78-362750°W, 3068 m, *Truong* 3296 (G). *Loja:* Loja, antenna militar arriba de San Lucas, 3-679361°S, 79-237889°W, 3217 m, 2007, *Truong* 222 (G). *Pichincha:* Quito, comunidad de Llano Grande, 2585 m, 2007, *Araguillín* (G). *Tungurahua:* Parque Nacional Llaganates, ruta desde Pelileo, cerca de la entrada, 1-082167°S, 78-411861°W, 3498 m, 2007, *Truong* 470 (G).—**Peru:** *Cajamarca:* Parque Nacional Cutervo, cerro Tarros, 6-295083°S, 78-796111°W, 3207 m, 2007, *Truong* 1721 (G). *Cusco:* Santuario Histórico de Machu Picchu, km 82 cerca de Wayllabambabajo, 13-242444°S, 72-428083°W, 2700 m, 2007, *Truong* 1919 (G). *Huanuco:* Bosque de Carpish, 9-698917°S, 76-086472°W, 2473 m, 2007, *Truong* 2765 (G).—**Venezuela:** *Bolívar:* Auyan Tepui, 1996, *Schultz* 24026b (private hb.). *Mérida:* Potrerros de San Rafael, páramo de Las Coloradas, 2950 m, 1976, *Hale* 46782 (US).

New Records

Usnea dorogawensis Asahina

Journal of Japanese Botany 28: 228 (1953); type: Japan, Honshu, Yamato Prov., Dorogawa, Amakawa-mura, Yoshino-gun, 1952, *Togashi* (TNS!—lectotype). % C/M/A: 4.0/37.5/16.0. Chemistry: usnic, lobaric, norstictic, stictic and constictic acids, unidentified US6 (Ohmura 2001).

Detailed descriptions and illustrations are available in Ohmura (2001) and *Truong et al.* (2011). This species is characterized by a short erect-shrubby thallus, branches inflated and constricted at ramification, large and excavate soralia without isidiomorphs, a smooth cortex surface without papillae, and a loose medulla with orange subcortical pigmentation. Lobaric acid was detected in the medulla of all specimens, together with norstictic acid (major) in the Galapagos, or with stictic (major) and norstictic (traces) acids in the tropical Andes.

Distribution. Newly reported for continental South America in the tropical Andes, occurring in the upper part of the montane cloud forest (*Ceja andina*) or in deforested zones of *matorral* in the vicinity of forest; previously reported from Japan (Ohmura 2001) and the Galapagos (Truong *et al.* 2011). This species has been rarely reported but could be overlooked in the field.

Selected specimens examined. **Colombia:** Antioquia: Piedras Blancas, c. 10 km S of Medellín, along the road to Santa Helena, 2300 m, 1986, Sipman *et al.* 33945 (B).—**Peru:** Huamaco: Bosque de Carpish, 9-703333°S, 76-088944°W, 2557 m, 2007, Truong 3913 (G).

Usnea grandisora Truong & P. Clerc

Bryologist 114: 490 (2011); type: Ecuador, Galapagos, Santa Cruz, above Mina Granillo, 607 m, Truong 1122 (CDS!—holotype; G! UPS!—isotypes). % C/M/A: 11.0/20.5/38.0. Chemistry: usnic, salazinic, galbinic and norstictic acids (Truong *et al.* 2011).

Detailed description and illustrations are available in Truong *et al.* (2011). This species is characterized by an erect-shrubby thallus, branches irregularly covered by fibrils and isidiofibrils, large and excavate soralia crowded on terminal branches, a relatively thick and shiny cortex in section, and a dense medulla with orange subcortical pigmentation.

Distribution. Newly reported for continental South America in Venezuela, where it is possibly rare and overlooked; previously reported from the Galapagos (Truong *et al.* 2011).

Selected specimen examined. **Venezuela:** Mérida: La Carbonera, El Pedregal, 1950 m, 1989, Grundlehner 51281E (G).

Usnea moreliana Motyka

Lich. Gen. Usnea Stud. Monogr. Pars Syst 2: 584 (1938); type: Mexico, Morelia, Cerro San Miguel, 1910, Brouard 137 (LBL!—lectotype and isolectotype selected here). % C/M/A: 6.0/32.0/24.5. Chemistry: usnic acid and unidentified triterpenoids UT6.

Usnea rubricornuta Truong & P. Clerc *syn. nov.*, *Bryologist* 114: 494 (2011); type: Bolivia, Cochabamba, Parque Nacional Carrasco, Sehuencas, ruta hasta Monte Puncu, 2500 m, 2007, Truong 3132 (LPB!—holotype; G! UPS!—isotypes). % C/M/A: 8.0/32.0/20.5.

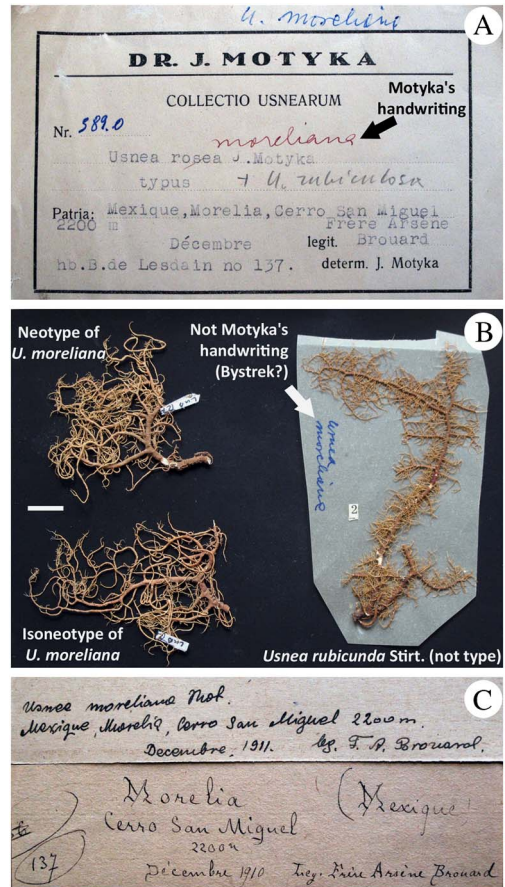


FIG. 8. Lectotypification of *U. moreliana* based on a paratype specimen found in LBL. A, identification of *U. moreliana* by Motyka; B, three specimens inside the packet, two of them corresponding to *U. moreliana* and one corresponding to *U. rubicunda* (right); C, original label. Scale = 1 cm. In colour online.

Chemistry: usnic acid and unidentified triterpenoids UT6 (Truong *et al.* 2011).

(Fig. 8)

Lectotypification. Motyka (1938) indicated that the holotype of *U. moreliana* was deposited in B, but this specimen appears to be missing. In LBL, we found a paratype of *U. moreliana* that was cited in Motyka's description. This paratype included heterogeneous material from three specimens

(Fig. 8B): one specimen corresponded to *U. rubicunda* Stirt., with the reddish cortex and the compact medulla reacting K+ red (salazinic and norstictic acids), with an A:M ratio > 2.0. The two other specimens represented fragments of thalli lacking trunk, that we identified as *U. rubricornuta* from the reddish cortex and the dense medulla reacting K- (unidentified triterpenoids UT6), with a ratio A:M < 2.0 (see in Truong *et al.* 2011 for a detailed description of this species). These two specimens have almost non-inflated and non-constricted branches, characters that appear to be variable in this species (Truong *et al.* 2011). Motyka's description mentioned the reddish cortex of *U. moreliana*, but for unknown reasons he didn't place this species in subsection *Rubiginiae* of his monograph, together with other species with a reddish cortex. Because of this, the name was overlooked when describing *U. rubricornuta* and it was only when we discovered the paratype of *U. moreliana* in LBL that we realized it corresponded to the same taxon. These two specimens fit perfectly with Motyka's description that mentions the reddish cortex, branches slightly constricted at ramification, the minute soralia and the dense medulla reacting K-, corresponding to the presence of triterpenoids. We therefore selected one of the two individuals (LUB127) as the lectotype of *U. moreliana* and the second fragment (LUB128) was considered as an isolectotype.

Distribution. Newly reported here for eastern South America in Brazil and Argentina, in relatively open sites within primary forest or in *Pinus* plantations; previously reported from Mexico and the tropical Andes (Motyka 1936; Truong *et al.* 2011). It is a common and often abundant species in tropical South America.

Selected specimens examined. **Argentina:** Misiones: San Ignacio, Gisela, 50 m, 1953, *Montes* (LBL).—**Brazil:** Parana: Res. Biológica de Sapitanduva, 50 m, 1991, *Hatschbach* 55396B (B). São Paulo: Serra de Paranapiacaba, 80 km südwestlich von São Paulo, am rio Juquiá, 700 m, 1978, *Kalb & Plöbst* (G); Serra da Mantiqueira, Campos do Jordão, 150 km nordöstlich von São Paulo, 1700 m, 1978, *Kalb & Plöbst* (G); zwischen Guapira und Apiaí, 800 m, 1980, *Kalb* (G).

***Usnea subcornuta* Stirt.**

Scott. Nat. 6: 107 (1881); type: Portugal, Madeira, near Funchal, *Payne* (BM!—holotype). % C/M/A: 8.5/23.0/37.0. Chemistry: usnic acid and unknown yellow substances (Clerc 1987b).

Detailed description and illustrations are available in Truong *et al.* (2011). This species is characterized by an erect-shrubby thallus, branches inflated and constricted at ramification, slender fibrils scattered on branches, minute soralia aggregating in irregular clusters on terminal branches, and a dense medulla with orange subcortical pigmentation. Recent studies demonstrated that specimens identified as *U. subcornuta* were clearly polyphyletic in the phylogeny of *Usnea* (Truong *et al.* 2013a). Morphological delimitation will need careful re-examination in the light of molecular data, but the paucity of material available makes it a difficult task.

Distribution. Newly reported here for eastern South America in Venezuela and Brazil; previously reported from south-western Europe, North Africa, Western Asia (Clerc 1987b; Fos & Clerc 2000) and the tropical Andes (Truong *et al.* 2011). It is a rare but possibly overlooked species with a scattered distribution.

Selected specimens examined. **Brazil:** São Paulo: Ilha de São Sebastião, 130 km östlich von São Paulo, 780 m, 1978, *Kalb & Plöbst* (G).—**Venezuela:** Bolívar: Auyan Tepui, 1996, *Schultz* 24026a (private hb.).

***Usnea subdasaea* Truong & P. Clerc**

Bryologist 114: 499 (2011); type: Ecuador, Galapagos, Isabela, road to Sierra Negra crater, close to la Esperanza, 306 m, *Truong* 1194 (CDS!—holotype; G! UPS!—isotypes). % C/M/A: 5.0/30.0/30.0. Chemistry: usnic, salazinic, galbinic and norstictic acids (Truong *et al.* 2011).

Detailed description and illustrations are available in Truong *et al.* (2011). This species is characterized by an erect-shrubby thallus, irregular branches ± inflated and constricted at ramification, spinulose fibrils and isidiofibrils irregularly distributed on branches, minute soralia aggregating in irregular clusters on terminal branches, a thin and shiny cortex in section, and a dense medulla with orange subcortical pigmentation.

Distribution. Newly reported here for Venezuela and Brazil; it is a South American endemic previously reported from the tropical Andes and the Galapagos (Truong *et al.* 2011).

Selected specimens examined. **Brazil:** Minas Gerais: Munic. de Catas Altas, Parque natural do Caraça, Tanque Grande, 20°102806'S, 43°494000'W, 1275 m, 2006, Spielmann *et al.* 2358 (SP).—**Venezuela:** Mérida: La Carbonera, El Pedregal, 1950 m, 1989, Grundlehner 73281F (G).

Fieldwork was supported by the Conservatoire et Jardin botaniques de la Ville de Genève (G), an 'Augustin Lombard' grant from the Société de Physique et d'Histoire Naturelle de Genève and a grant from the Amazon Conservation Association. The authors collaborated with the herbaria CDS, LPB, QCNE, USM and the Wayqecha Biological Station (Peru). F. Bungartz, M. Herrera-Campos, C. Aldana Munguia, M. F. Collaguazo, A. Cuba Villena, Y. Manami, A. Ramirez-Ordaza, P. Rodriguez, L. Salcedo Valdez and A. X. Shuguli participated in the field work. Curators of the cited herbaria kindly sent specimens on loan. Laboratory work was supported by a grant from the Basler Stiftung für Biologische Forschung and was carried out in G and in the Facultad de Farmacia of the Universidad Complutense of Madrid. Sequences generated in Madrid were supported by the Spanish Ministerio de Ciencia e Innovación funds (CGL2010-21646) and a Ramón y Cajal start-up grant (RYC02007-01576). P. K. Divakar supervised laboratory work in Madrid and gave valuable advice on the analysis of data.

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