

Standard Paper

The genus *Usnea* (Parmeliaceae, Ascomycota) in the southern Philippines: a first phylogenetic approach

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Abstract

A first integrative survey of the genus *Usnea* in the southern Philippines, taking into account morphological, anatomical, chemical and molecular characters, resulted in the recognition of 20 taxa, including three species new to science: *Usnea angulata* Ach., *U. baileyi* (Stirt.) Zahlbr., *U. bismolliuscula* Zahlbr., *U. brasiliensis* (Zahlbr.) Motyka, *U. confusa* Asah., *U. croceorubescens* Stirt., *U. dasaea* Stirt., *U. himalayana* C. Bab., *U. krogiana* P. Clerc, *U. longissima* Ach., *U. nidifica* Taylor, *U. norsticornuta* A. Gerlach & P. Clerc sp. nov. (characterized by a moderately thick cortex and by the presence of norstictic acid), *U. paleograndisora* A. Gerlach & P. Clerc sp. nov. (characterized by an orange subcortical pigmentation in the medulla, with enlarging soralia and a moderately thick and shiny cortex), *U. pectinata* Taylor, *U. pygmoidea* (Asahina) Y. Ohmura, *U. rubicunda* Stirt., *U. rubrotincta* (Stirt.) Zahlbr., *U. spinulifera* (Vain.) Motyka, *U. subscabrosa* Motyka and *U. yoshihitoi* P. Clerc & A. Gerlach sp. nov. (characterized by a lax medulla with non-conglutinated hyphae). *Usnea krogiana* is a new record for Asia; *Usnea brasiliensis*, *Usnea confusa* and *U. croceorubescens* are new records for the Philippines. This is the first phylogenetic study to include DNA sequences of *Usnea* from the Philippines. Molecular data from the ITS rDNA (76 newly generated sequences) are presented for most taxa except for *U. himalayana*, *U. longissima* and *U. subscabrosa*. At least six further taxa remain unidentified, awaiting the collection of additional specimens.

Keywords: anatomy; biodiversity; lichen; Mindanao; morphology; Negros; thin-layer chromatography

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Introduction

Usnea Adans. is a fruticose lichen genus of the family Parmeliaceae (*Lecanoromycetes*), comprising nearly 450 currently accepted species (Lücking *et al.* 2020), widely distributed in polar, temperate and tropical regions. The genus is readily distinguished by the shrubby to pendulous thallus, branches with an elastic central axis, and the presence of usnic acid in the cortex. The genus *Usnea* in the broad sense forms a strongly supported clade with groupings that have variously been recognized at the generic or infrageneric level (*Usnea* s. str., *Eumitria* Stirt., *Dolichousnea* (Y. Ohmura) Articus and *Neuropogon* Nees & Flot). The subclades *Usnea* s. str., *Eumitria* and *Dolichousnea* occur in the Philippines. *Eumitria* is characterized by the presence of a tubular central axis (with the exception of *U. pectinata* with a partially fistulose axis). It has a wide distribution, with taxa occurring in Africa (Swinscow & Krog 1974; Temu *et al.* 2019), Asia (Ohmura 2001, 2012), Australia (Stevens 1999) and South America (Truong &

Clerc 2013). Its morphological circumscription is diffuse since species without a central tubular axis (but with a partially fistulose axis) might cluster together in a molecular phylogeny (within a strongly supported clade) with species having a central tubular axis (Truong *et al.* 2013a). *Dolichousnea* is a smaller subclade with only three species, including *U. longissima*, reported for the Philippines by Herre (1946) but not found in this study. This subclade is characterized by annular pseudocyphellae and an amyloid central axis (Ohmura 2001). Given the fact that, in the molecular phylogeny, *Usnea* s. lat. forms a strongly supported monophyletic group and that morphological and anatomical features are not fully consistent with subclades recognized within it, here we follow previous workers (Ohmura 2002; Ohmura & Kanda 2004; Wirtz *et al.* 2006; Truong & Clerc 2013; Truong *et al.* 2013a; Ohmura & Kashiwadani 2018; Temu *et al.* 2019) in considering these subgroups at the infrageneric level in our taxonomic treatment of the species found in the Philippines.

The two most comprehensive taxonomic treatments of *Usnea* for the Philippines were published by E. A. Vainio (Vainio 1909), with 11 species and six varieties or forms, among them six new species (*Eumitria endochroa* Vain., *E. endorhodina* Vain., *Usnea furcata* Vain., *U. philippina* Vain., *U. pycnoclada* Vain. and *U. squarrosa* Vain.) and five new varieties (*Eumitria endochroa*

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var. *farinosa* Vain., *E. endochroa* var. *papillata* Vain., *Usnea furcata* var. *marivelensis* Vain., *U. longissima* var. *misamensis* Vain. and *U. philippina* var. *mearnsii* Vain.), and by Herre (1963), with 25 taxa described, among them three new species (*Usnea elmeri* Herre, *U. humilis* Herre and *U. ramosi* Herre), with a key for their identification. Further taxonomic studies were carried out by Asahina (1967, 1968, 1969a, b) who reported six taxa from the region including five new taxa (*U. neoguineensis* var. *gracilior* Asahina, *Usnea neoguineensis* Asahina var. *neoguineensis*, *U. ogatae* Asahina, *U. pseudorientalis* Asahina, and *U. pseudorubescens* Asahina var. *anaemica* Asahina).

The studies more recently published on the genus *Usnea* in the country were made in the northern Philippines, with a strong focus on chemistry (Sevilla-Santos & Mondragon 1972; Santiago *et al.* 2010, 2013; Timbreza *et al.* 2017). Galinato *et al.* (2018), in their review of *Usnea* in the Philippines, recorded 81 species, highlighting that the genus is poorly known in the country despite its high diversity.

A recently published checklist (Paguirigan *et al.* 2020) recorded 71 accepted names. However, some of these occur only in continental-temperate areas of the Northern Hemisphere and their superficial similarity with species that occur in the Philippines may have led to incorrect identifications. These include taxa such as *Usnea barbata* (L.) F. H. Wigg., *U. cavernosa* Tuck., *U. hirta* (L.) F. H. Wigg., *U. intermedia* (A. Massal.) Jatta, *U. perplexans* Stirt., *U. substerilis* Motyka and *U. trichodea* Ach. If we consider names treated as accepted taxa in the checklist but actually considered synonyms of other species, such as *U. ciliata* (Müll. Arg.) Vain., *U. himantodes* Stirt. and *U. lapponica* Vain., we are closer to 55–60 species of *Usnea* in this large, biodiversity-rich archipelago.

The Philippines is considered one of the 25 global biodiversity hotspots designated for priority conservation, based on their high endemicity and richness of flora and fauna (Myers *et al.* 2000). Despite this rich endemism, only 3% of the original vegetation is preserved. The Philippines is subdivided into four major groups of islands, corresponding roughly to the western island of Palawan, the northern island of Luzon, the central islands of the Visayas and the southern island of Mindanao. The latter two areas, as defined here, encompass the southern Philippines. This region lies fully in the tropical zone between 5°22'–12°40'N latitude, and 121°47'–126°36'E longitude. The major islands of the Visayas, from more or less west to east, are Panay, Negros, Cebu, Masbate, Bohol, Leyte and Samar, with numerous smaller islands interspersed throughout. Mindanao dominates the extreme south and is fringed by smaller islands such as Basilan, Camiguin and Dinagat.

This study is part of the NSF-funded Project 'Plant discovery in the southern Philippines' led by the Fort Worth Botanic Garden (the Botanical Research Institute of Texas, BRIT) and it reports the first results of lichens from the expedition made to Mindanao and Negros in 2019. This is the first study on the genus *Usnea* in the Philippines that takes into account molecular, morphological, anatomical and chemical data for the majority of the species analyzed.

Materials and Methods

Fieldwork

Two expeditions were conducted in the southern Philippines during June and December 2019, on three islands: Mindanao

(Bukidnon Province (Mt Malambo and Mt Limbawon), Davao del Sul (Marilog Forest Reserve) and Davao Oriental (Mt Hamiguitan Range Wildlife Sanctuary)); Camiguin Island (Mt Timboong, Mt Ilihan, Manabajao); Negros (Negros Oriental: Balinsasayao Twin Lakes Natural Park and Cuernos de Negros) (Fig. 1). To our knowledge, this is the first study on the genus *Usnea* to include samples from Negros (Balinsasayao Twin Lakes Natural Park).

In 2019, AG and MDF collected a total of 1728 specimens of lichenized fungi (belonging to c. 36 families and 88 genera), more than 300 of which belong to the genus *Usnea* s. lat. This first paper is the result of the study of 107 specimens now collected for the genus within this project. Specimens not yet studied are housed in FWBG (part of the herbarium in the Botanical Research Institute of Texas, BRIT) and will be analyzed in a forthcoming paper.

Field trips were conducted in tropical rainforest and in low to upper montane forest in collaboration with Central Mindanao University (CMU). All specimens were corticolous (growing on tree bark or branches) and were collected above 700 m altitude (782–1582 m above sea level). The specimens analyzed here were largely collected in open areas, mainly in secondary forest or anthropized environments with crops or planted trees (e.g. coconut palms), more rarely on the ground on fallen branches in mossy forest. We did not find any *Usnea* growing on rocks. Approximately 29 additional specimens previously collected in the Philippines and housed in ZE Botanischer Garten und Botanisches Museum, Freie Universität Berlin (B) were integrated in this study. All analyzed specimens are detailed in Supplementary Material File S1 (available online) in order to avoid long lists of citations. Voucher specimens will be deposited according to the following priority order: Philippine National Herbarium (PNH) and/or Central Mindanao University (CMUH) (as required by Philippine national law), with duplicates in BRIT, and the Conservatoire et Jardin botaniques de la Ville de Genève (G).

DNA extraction, PCR and sequencing

The DNA extraction and PCR were performed at the Sumner Laboratory at the Botanical Research Institute of Texas. The procedures outlined in Dal Forno *et al.* (2013) were followed, except that the ITS primers used were *Usnea*-specific as proposed by Truong *et al.* (2013a), namely USITS3-F (50-GTA GGT GAA CCT GCG GAA G-30) and USITS4-R (50-CGC TTC ACT CGC CGT TAC T-30). Three additional sequences were obtained at the Botanic Garden of Berlin, using the Sigma REDExtract-N-Amp Plant PCR Kit (St Louis, Missouri, USA) for DNA isolation following the manufacturer's instructions, except that 30 µl of extraction buffer and 30 µl dilution buffer were used. DNA dilutions 1:10 were used in PCR reactions. PCR reactions contained 14.4 µl of NuFree H₂O, 2.5 µl 10× Standard Taq Reaction Buffer, 1 µl 25 mM MgCl₂, 3 µl dNTP (1.25 mM), 1 µl of each primer (10 pm/µl) and 2 µl (dilution 1:10) genomic DNA extract for a total of 25 µl. Thermal cycling parameters were: initial denaturation for 5 min at 94 °C, followed by 39 cycles of 30 s at 94 °C, 30 s at 48 °C, 1 min 30 s at 72 °C, and a final elongation for 5 min at 72 °C. PCR samples were visualized on a 1.5% agarose gel under UV light and PCR products of homogeneous size were treated enzymatically using ExoSAP-IT Express PCR Product Cleanup Reagent, following the manufacturer's instructions (Thermo Fisher Scientific). DNA concentrations



Figure 1. Study sites in the Philippines (marked with yellow filled circles) where collections were made during the two expeditions in 2019. Source: <http://qgis.osgeo.org>. In colour online.

were measured with Qubit™ dsDNA Broad Range Assay Kit (values available in Supplementary Material File S2, available online). Samples were sent to Psomagen/Macrogen (USA) for sequencing.

Sequence alignment and phylogenetic reconstructions

The DNA sequences obtained were aligned using MAFFT v. 7 (Katoh & Standley 2013) with the G-INS-I alignment algorithm, a scoring matrix of 20 PAM/K = 2, 0.1 as offset value and the remaining parameters set to default. To reconstruct the phylogeny, we used a total of 178 ITS sequences (see Supplementary Material File S2), 102 of which were obtained from GenBank, plus 76 newly generated sequences (54 from the Philippines (Table 1), 21 from Japan and Taiwan and one from Portugal) obtained for this study (Supplementary Material File S2). Almost all available sequences from Asia were added (Lücking *et al.* 2020), except those not identified or with dubious identification (*U. nidifica*_Li207c and *U. nidifica*_Li190c). Since we putatively found *Usnea dasaea* in the Philippine material, we also added a sequence for this species obtained from Portugal (type country). *Usnea longissima* was chosen as outgroup following Lücking *et al.* (2020).

To build the data matrix, we first added all newly obtained sequences (Table 1 and Supplementary Material File S2) to the global ITS dataset generated by Lücking *et al.* (2020; see their supplementary information S1). A best-scoring maximum likelihood (ML) tree was reconstructed in RAxML v. 8.2.12 (Stamatakis 2014), with RAxML-HPC Blackbox v. 8.2.12 on

the CIPRES Science Gateway (Miller *et al.* 2010). We used the universal GTR-Gamma model with 1000 bootstrap replicates (locally) using a saturation criterion (CIPRES). After reconstructing an initial tree, we subsequently removed terminals of less interest as they were only distantly related to the Philippine species. *Usnea (Dolichousnea) longissima* was chosen as outgroup due to its close relationship with *Usnea* s. str. and its occurrence in the archipelago (Paguirigan *et al.* 2020). Partitions above 70% are considered well supported (ML bootstrap (BS) >70%). The final data matrix contained 178 total sequences representing 62 *Usnea* taxa (Supplementary Material File S2) (Fig. 2).

Morphological, anatomical and chemical studies

The following account is based on field studies and on specimens deposited in herbaria B and G. Type material of the majority of species discussed here (except *U. baileyi*) was studied; types housed at the University of Turku (TUR-V) were specifically examined for this study in November 2021.

The morphology of specimens was examined using a Leica MS5 stereomicroscope, with measurements taken using a Leica DM2000 microscope (Switzerland). The phenotypic species concept used in this study follows Clerc (1998) and Ohmura (2001). Anatomical measurements of cortex, medulla and central axis were carried out in longitudinal sections of branches at $\times 40$ magnification. The percentage thickness of cortex/medulla/axis of the total branch diameter (%C/M/A) and the ratio of axis/medulla (A/M) of all the cited specimens were calculated according to

Table 1. Voucher information and GenBank Accession numbers for the 54 Philippine samples of the genus *Usnea* used for this study. Newly proposed species are in bold. Voucher number: AG = A. Gerlach; MDF = M. Dal Forno. Main chemistry column: BAR = barbatic acid; CST = constictic acid; DIF = difractaic acid; GAL = galbinic acid; LOB = lobaric acid; NOR = norstictic acid; PRO = protocetraric acid; PSO = psoromic acid; SAL = salazinic acid; STI = stictic acid; ZEO = zeorin.

Taxon	Voucher number	DNA-code	Main chemistry	ITS Accession number
<i>U. angulata</i>	AG 954	PU04	NOR	QQ591810
<i>U. baileyi-1</i>	AG 897a	PU01	ZEO	QQ591799
<i>U. baileyi-1</i>	MDF 3493	PU26	NOR; SAL; ZEO	QQ591801
<i>U. baileyi-1</i>	AG 893a	PU37	NOR; ZEO	QQ591802
<i>U. baileyi-2</i>	AG 981b	PU24	NOR; ZEO	QQ591800
<i>U. baileyi-2</i>	AG 1012a	PU44	NOR; SAL	QQ591803
<i>U. bismolliuscula</i>	AG 897b	PU02	NOR; STI	QQ591814
<i>U. bismolliuscula</i>	AG 957a	PU12	NOR; STI	QQ591815
<i>U. bismolliuscula</i>	AG951	PU22	NOR; STI	QQ591816
<i>U. bismolliuscula</i>	AG 950d	PU50	NOR; STI	QQ591817
<i>U. bismolliuscula</i>	AG1007e	PU67	DIF; STI	QQ591818
<i>U. bismolliuscula</i>	AG950d	PU68	LOB; STI	QQ591819
<i>U. brasiliensis-1</i>	AG 950C	PU52	PRO	QQ591839
<i>U. confusa</i>	AG 897c	PU03	CST; SAL	QQ591840
<i>U. confusa</i>	AG 995c	PU10	CST; SAL	QQ591841
<i>U. confusa</i>	AG 996b	PU18	CST; SAL	QQ591842
<i>U. confusa</i>	AG 893b	PU38	CST; SAL	QQ591843
<i>U. croceorubescens</i>	AG 992b	PU23	BAR; NOR; SAL	QQ591844
<i>U. croceorubescens</i>	MDF 3471b	PU31	BAR; NOR; SAL	QQ591845
<i>U. croceorubescens</i>	AG 852a	PU34	BAR; NOR; SAL	QQ591846
<i>U. croceorubescens</i>	AG 850a	PU46	BAR; NOR; SAL	QQ591847
<i>U. dasaea</i>	AG 969c	PU09	GAL	QQ591849
<i>U. dasaea</i>	AG 980b	PU21	GAL	QQ591850
<i>U. krogiana</i>	MDF 3635a	PU35	NOR; PRO; SAL	QQ591851
<i>U. nidifica</i>	MDF 3496	PU28	NOR; PRO; SAL	QQ591852
<i>U. nidifica</i>	MDF 3554	PU30	NOR; PRO; SAL	QQ591853
<i>U. nidifica</i>	MDF 3483	PU33	NOR; PRO; SAL	QQ591854
<i>U. nidifica</i>	AG 636c	PU54	NOR; SAL	QQ591855
<i>U. norsticornuta</i>	AG 1005	PU11	NOR; SAL	QQ591858
<i>U. paleograndisora</i>	AG 1008b	PU42	GAL	QQ591859
<i>U. paleograndisora</i>	AG 998b	PU47	GAL	QQ591860
<i>U. paleograndisora</i>	AG 1018b	PU48	GAL	QQ591861
<i>U. pectinata</i>	AG 979	PU15	DIF; SAL	QQ591804
<i>U. pectinata</i>	AG 996c	PU17	STI	QQ591798
<i>U. pectinata</i>	MDF 3497	PU29	PRO	QQ591805
<i>U. pectinata</i>	MDF 3482	PU32	DIF; PRO	QQ591806
<i>U. pectinata</i>	AG 636a	PU49	PRO	QQ591807
<i>U. rubicunda-1</i>	MDF 3494	PU27	STI	QQ591862
<i>U. rubicunda-1</i>	AG 847	PU51	STI	QQ591863
<i>U. rubicunda-2</i>	AG 950b	PU53	STI	QQ591864
<i>U. rubrotincta</i>	AG 891b	PU06	NOR; SAL	QQ591865
<i>U. spinulifera</i>	AG 891a	PU05	GAL	QQ591866

(Continued)

Table 1. (Continued)

Taxon	Voucher number	DNA-code	Main chemistry	ITS Accession number
<i>U. spinulifera</i>	AG 969a	PU08	GAL	Q591867
<i>U. spinulifera</i>	AG 1003	PU20	GAL	Q591868
<i>U. spinulifera</i>	AG 893c	PU39	GAL	Q591869
<i>U. yoshihitoi</i>	AG 891c	PU07	STI	Q591870
<i>U. yoshihitoi</i>	AG 957c	PU14	STI	Q591871
<i>U. yoshihitoi</i>	AG 931	PU16	STI	Q591872
<i>U. yoshihitoi</i>	AG 908a	PU25	STI	Q591873
<i>U. yoshihitoi</i>	AG 992a	PU45	STI	Q591874
<i>U. aff. bismolliuscula</i>	AG852c	PU66	NOR: SAL	Q591811
<i>U. aff. brasiliensis</i>	AG 995b	PU41	PRO; PSO	Q591808
<i>U. aff. pygmoidea</i>	AG 909	PU40	STI	Q591809
<i>U. aff. subflammaea</i>	AG 1008c	PU43	STI	Q591812

Clerc (1984, 1987) and Clerc & Naciri (2021). Additionally, for the eumitrioid species (*Usnea baileyi*), the tubular part of the axis (%TBA) was measured according to Truong & Clerc (2013). The measurement ranges for each layer are indicated as follows: (min–mean–max), or (min–)sd *mean* +sd(–max). %C/M/A categories follow Clerc (2011). Analyses of the anatomical structure of the cortex were made according to Ohmura (2001), on thin hand-cut sections and observed at $\times 400$ magnification with a Leica DM2000 microscope.

Chemical analyses were performed on all cited specimens using thin-layer chromatography (TLC) following Culberson & Ammann (1979), with solvent B modified according to Culberson & Johnson (1982). K, C and P spot tests, according to Hale (1979), were directly applied to the medulla in longitudinal sections of branches. The unidentified substances US1 and US2 found in some of the species treated here were characterized by Ohmura (2001). Short descriptions are given for previously described species based on all the above information from a given number of samples (*n*).

Results

This study revealed 20 species or species complexes among the investigated material: *Usnea angulata* s. lat., *U. baileyi* s. lat., *U. bismolliuscula*, *U. brasiliensis* s. lat., *U. confusa*, *U. croceorubescens*, *U. dasaea*, *U. himalayana*, *U. krogiana*, *U. longissima*, *U. nidifica*, *U. norsticornuta* sp. nov., *U. paleograndisora* sp. nov., *U. pectinata* s. lat., *U. pygmoidea* s. lat., *U. rubicunda* s. lat., *U. rubrotincta*, *U. spinulifera*, *U. subscabrosa* and *U. yoshihitoi* sp. nov. *Usnea brasiliensis*, *U. confusa*, *U. croceorubescens* and *U. krogiana* are new records for the Philippines. *Usnea baileyi*, *U. bismolliuscula*, *U. confusa* and *U. rubicunda* are new records for Negros.

Molecular data and analysis

Fifty-one ITS sequences out of 54 samples of *Usnea* from the Philippines (Table 1) were generated for this study. The final ITS alignment comprised 178 sequences with 554 columns, 331 distinct patterns, 188 parsimony-informative, 102 singleton sites and 264 constant sites.

A modified ITS tree from Lücking *et al.* (2020) is presented here distributed in two supported clades (BS \geq 70, *Eumitria* and *Usnea* s. str.; Fig. 2 and 2A–E). The relationships among lineages within the *Usnea* s. str. clade (BS = 81) remain mostly unresolved (Fig. 2), with the exception of two subclades: one subclade (BS = 99) with two species, *U. glabrescens* and *U. fulvoreagens*, and another one (BS = 100) containing Asian specimens of *U. himalayana*, *U. nidifica* and *U. norsticornuta*. The specimens from the Philippines fall inside the *Eumitria* clade (Fig. 2A) and *Usnea* s. str. (18 clades). Most taxa from the Philippines clustered into well-supported clades: *U. bismolliuscula* (BS = 99), *U. croceorubescens* (BS = 99), *U. krogiana* (BS = 100), *U. nidifica* (BS = 99), *U. norsticornuta* (BS = 100), *U. paleograndisora* (BS = 100), *U. rubicunda* (BS = 94), *U. rubrotincta* (BS = 98), *U. spinulifera* (BS = 99) and *U. yoshihitoi* (BS = 100). Five specimens appear in the phylogeny as singletons (PU04 and PU43 in Fig. 2B; PU40, PU41 and PU52 in Fig. 2E) and their species identity is not conclusive.

Taxa recently described by Ohmura & Clerc (2019) and Gerlach *et al.* (2020) from the *Usnea cornuta* and *U. brasiliensis* aggregates appear across the tree in multiples lineages and are indicated by triangles (Figs 2A–C & E). From these, we found only two species belonging to the *U. cornuta* aggr., namely, *U. confusa* and the newly proposed species *U. norsticornuta*. Furthermore, two undescribed taxa belonging to the *U. brasiliensis* aggr. were detected; however, there is not enough material to describe them at this time.

Taxonomy

Usnea angulata Ach.

Synops. *Lich.*: 307 (1814); type: America septentrionalis, Muhlenberg 22-2 (H-ACH 1880A—lectotype). %C/M/A: 8/45/74. Chemistry: usnic and norstictic acids (Herrera-Campos *et al.* 1998).

For a detailed description of this taxon, see Herrera-Campos *et al.* (1998), Ohmura (2001) and Truong *et al.* (2013b).

Thallus pendulous; *trunk* single, concolorous; *lateral branches* cylindrical at ramification point; *cracks* irregular, numerous,

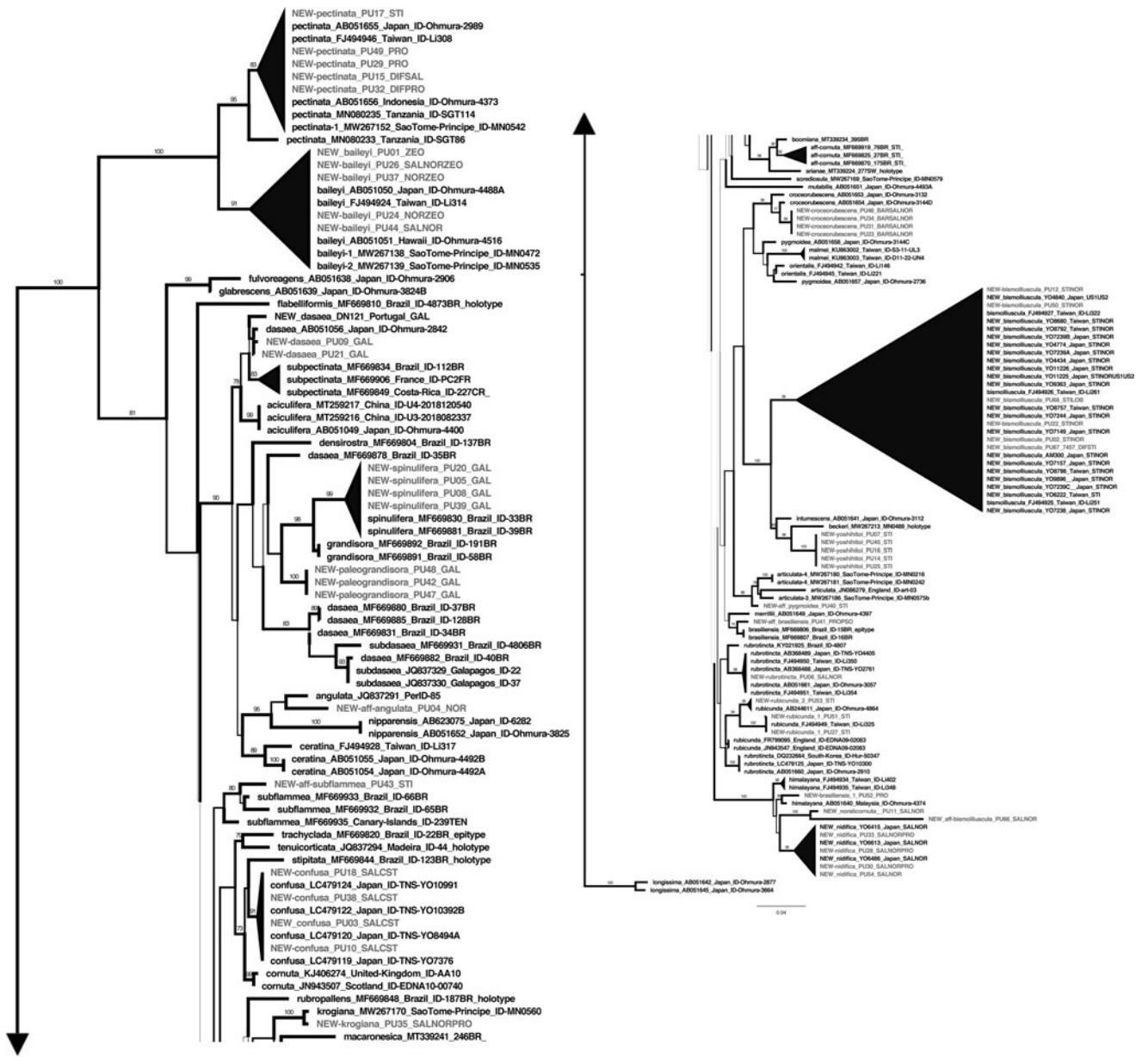


Figure 2. Molecular phylogeny of *Usnea* focusing on the species from the Philippines. The phylogeny is based on ITS rDNA sequence data and analyzed using maximum likelihood (RAxML) inference. The thickest bold branches represent ML bootstrap values > 75%, with branch values only shown of >70%. ‘NEW’ indicates sequences newly acquired for this study. Specimens collected in the Philippines are in grey; the species name is given with the DNA-code and concatenated codes for the main chemistry (BAR = barbatic acid; CST = constictic acid; DIF = difractaic acid; GAL = galbinic acid; LOB = lobaric acid; NOR = norstictic acid; PRO = proto-cetraric acid; PSO = psoromic acid; SAL = salazinic acid; STI = stictic acid; ZEO = zeorin) (see Table 1). *Usnea (Dolichousnea) longissima* is the outgroup. Details of branching, represented in this tree by filled triangles, are given in Figs 2A–E.

flaking off areolae with schizidia; *depressions*, *maculae*, *pseudocyphellae* absent; *fibrils* slender, numerous; *papillae* inconspicuous; *tuberles* absent; *soralia* minute circular, present mainly on fibrils; *idiomorphs* present; *cortex* moderately thin and shiny; *medulla* moderately thin and compact; *central axis* moderately thick (%C/M/A = 7.5/22/41, with an A/M = 1.8); *irregular cracks* numerous; (n = 1).

Chemistry. Medulla K+ yellow turning red. TLC: norstictic acid (n = 1).

Taxonomic notes. The specimen considered here does not present the typical alate branches of *U. angulata* with trapezoidal segments. Instead, we observed the upper areolate surface splitting

off as scale-like propagules (schizidia) (Fig. 8F). According to Truong *et al.* (2013b), *U. angulata* presents a wide range of variability regarding the shape of the branches (alate, ridged or squamulose). The sequenced specimen (Truong id-85) is similar to the specimen analyzed here; both share the pendulous thallus with ridged branches and the presence of norstictic acid in the medulla, but they differ in geographic distribution (Peru vs the Philippines) and their ITS sequences (see under Phylogenetic notes). The specimen from Peru corresponds to a young thallus without schizidia. More sequenced specimens of *U. angulata* need to be analyzed to better understand its variability.

Regarding the chemistry, although caperatic acid is reported for this species (Ohmura 2012, 2020), we did not find that

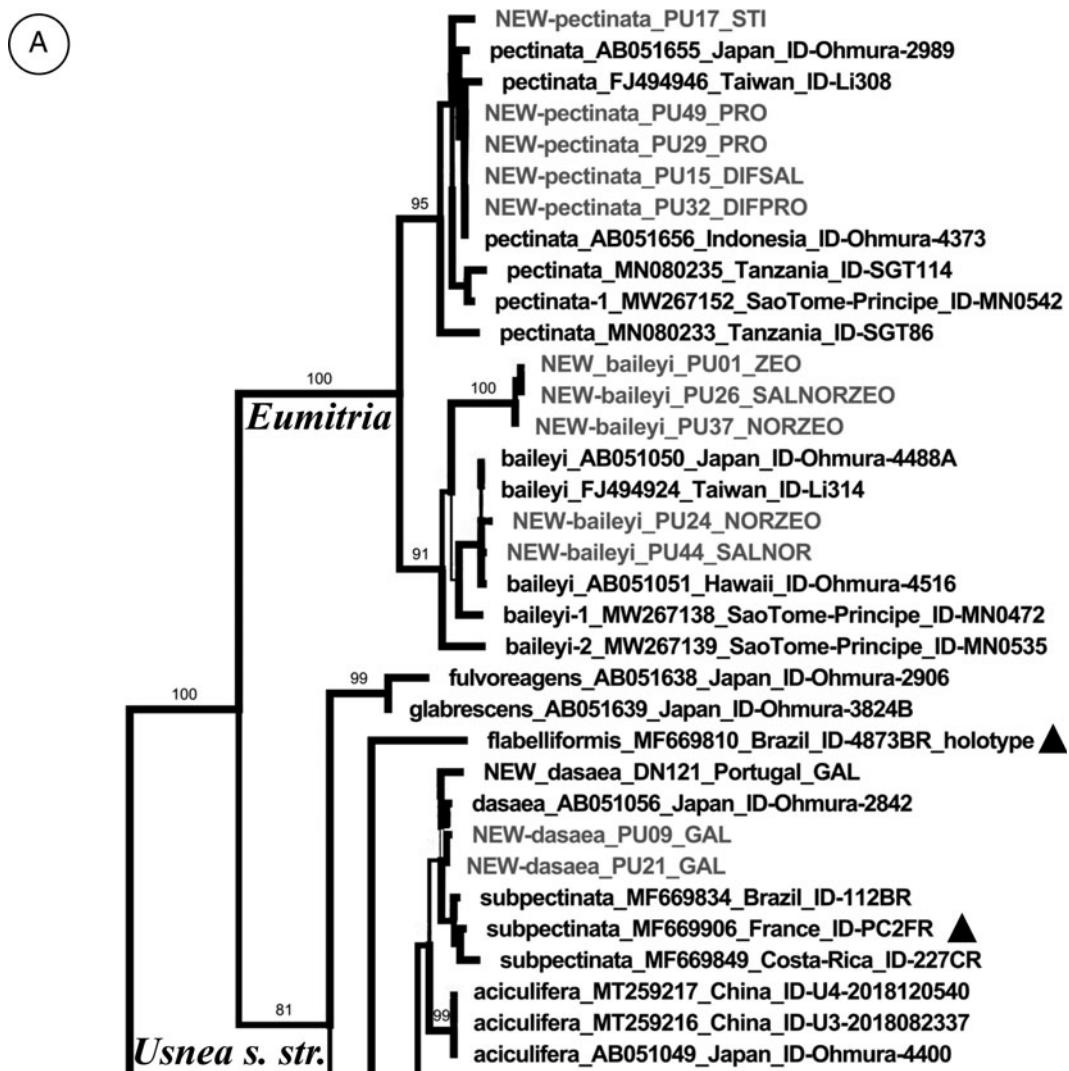


Figure 2A. Two clades *Eumitria* and *Usnea* s. str. The triangle symbols indicate taxa belonging to the *Usnea cornuta* aggregate. Taxa in grey are from the southern Philippines. Further details are given in the Fig. 2 caption.

compound in the specimen analyzed here. Ohmura (2020) suggested that this fatty acid is always present in this species (world-wide material, although the amount varies from major to trace) and recommended using a microcrystal test and TLC to detect its presence.

Usnea transitoria Motyka is a similar neotropical species, in having terete to slightly ridged segments and conspicuous bands of eroded cortex with areas of regeneration along main branches (Truong *et al.* 2013b). It differs from the specimen analyzed here mainly by the chemistry (norstictic acid instead of stictic acid found in *U. transitoria*). Other differences include the absence of tubercles (present in *U. transitoria*) and the geographical distribution, neotropical versus pantropical.

Phylogenetic notes. Despite being a relatively common and widespread species, there is only one ITS sequence for *U. angulata* published in GenBank (Truong id-85). The specimen PU04 is morphologically and phylogenetically close (but not supported and as a long branch, pairwise similarity = 0.95) to *Usnea angulata* from Peru (Truong id-85) (Fig. 2B). *Usnea angulata* is also closely related to *U. nippensis* Asahina, despite being morphologically very different (for more details see

Ohmura (2020)). Given the morphological, chemical and molecular differences, it is possible that the Philippine material is not *U. angulata* s. str. but represents a separate taxon; however, more material needs to be sequenced to test this hypothesis.

Distribution. *Usnea angulata* is widely distributed in temperate to subtropical regions in East Asia (Ohmura 2001). This is the first record for the Philippines.

Specimen examined. Philippines: Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1131 m, 7.45462°N, 125.23664°E, beginning of trail to Epol Waterfall, part way down, on fallen branch, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/954 (G), DNA-code: PU04.

Usnea baileyi (Stirt.) Zahlbr.

Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 83, 182 (1909); type: Australia, Queensland, near Brisbane, Bailey 164 (BM—lectotype). %C/M/A/TBA: 3.5/3/87/85 (Truong & Clerc

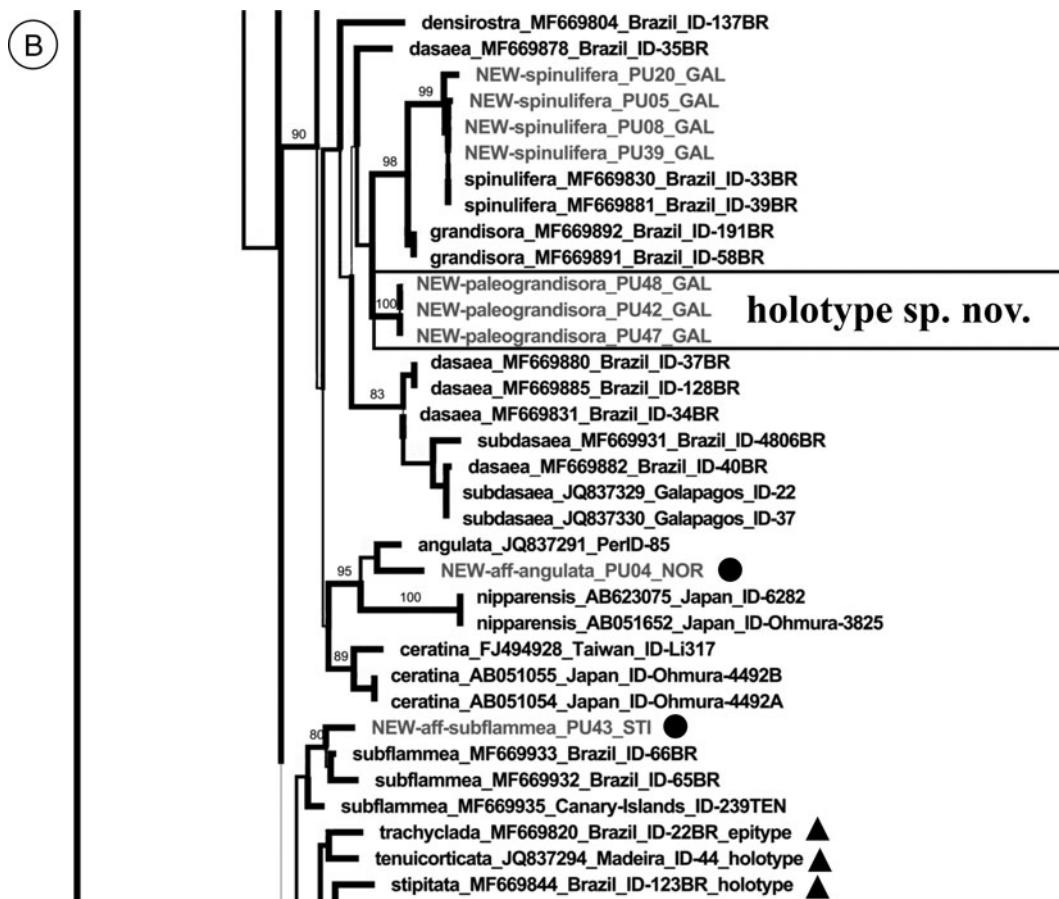


Figure 2B. Taxa belonging to the *Usnea* s. str. The triangle symbols indicate taxa belonging to the *Usnea cornuta* aggregate; the circle symbols indicate singletons. Taxa in grey are from the southern Philippines. A new species is indicated in the box. Further details are given in the Fig. 2 caption.

2013). Chemistry: usnic acid, eumitrins A2 and B, zeorin, salazinic and norstictic acids (Ohmura 2001).

Usnea chrysopoda Stein, *Abh. Schles. Ges. Vaterl. Kult., Abh. Naturw. Med.*, 4 (1882); type: Philippines, Mindanao, in ascensu ad Apo, in Lauraceis, c. 2000 m, 1882, Schadenberg (SLO).

Usnea endorhodina (Vain.) Zahlbr., *Cat. Lich. Univers.* 6, 564 (1930); type: Philippines, Luzon, Benguet Province, Pauai, Bur. Sci. 4543 p.p. Mearns, 2100 m, ad corticem Pini insularis Endl. Ster. (W).

(Fig. 3)

For a detailed description of this taxon, see Swinscow & Krog (1974), Stevens (1999), Ohmura (2001), Clerc (2007), Truong & Clerc (2013) and Temu *et al.* (2019).

Thallus erect-shrubby to mostly subpendulous; *trunk* usually concolorous, rarely irregularly blackened, rarely partially decorticated, single; *lateral branches* not constricted; *branches* tapering or cylindrical in longitudinal section and terete in transversal section; *fibrils* slender, irregularly distributed, sometimes as fish-bone pattern; *fiberles* often present; *soralia* minute, distinct; *isidiomorphs* few to numerous; *cortex* thin to moderately thin; *medulla* thin and compact; *axis* thick, tubular; *tubular section* often filled with loose hyphae, white, rarely with a yellow pigment to sometimes cottony and whitish, mostly with a thin pink layer just below the cortex, sometimes also

with a yellow pigment. %C/M/A/TBA = 3–5.8–8/2.5–4.5–8/68–79.5–86/29.5–50–68.5; (n = 18).

Chemistry. Medulla K+ yellow turning red. TLC (n = 15): norstictic and \pm salazinic acids, \pm zeorin, \pm protocetraric acid (trace).

Taxonomic notes. *Usnea baileyi* is easily recognized by the hollow and thick (>50%) central axis, by the pink-pigmented narrow medulla and by the punctiform soralia. The density of ramifications, fibrils and isidiomorphs varies among individuals, as also indicated in Truong & Clerc (2013).

Phylogenetic notes. *Usnea baileyi* most probably represents a complex of several species, as evidenced by the presence of a geographical signal and supported phylogenetic structure, even within a single area (Temu *et al.* 2019; Lücking *et al.* 2020). Although *U. baileyi* is reported as subcosmopolitan (<https://www.gbif.org/species/7247545>) and known from the Americas (e.g. Osorio 1992; Truong & Clerc 2013; Herrera-Campos 2016), sequenced specimens are available only from Africa (Temu *et al.* 2019; Nadel & Clerc 2022), Asia, Hawaii (Ohmura 2002) and now from the Philippines. Unfortunately, no sequence from the type region (Australia) is yet available. The sequenced specimens from the Philippines clustered into two different clades: one entirely with specimens from the Philippines (*baileyi*-1: PU01, PU26, PU37) and one (*baileyi*-2) with five Asian specimens (Ohmura 4488A, Id-Li 314, PU24, PU44)

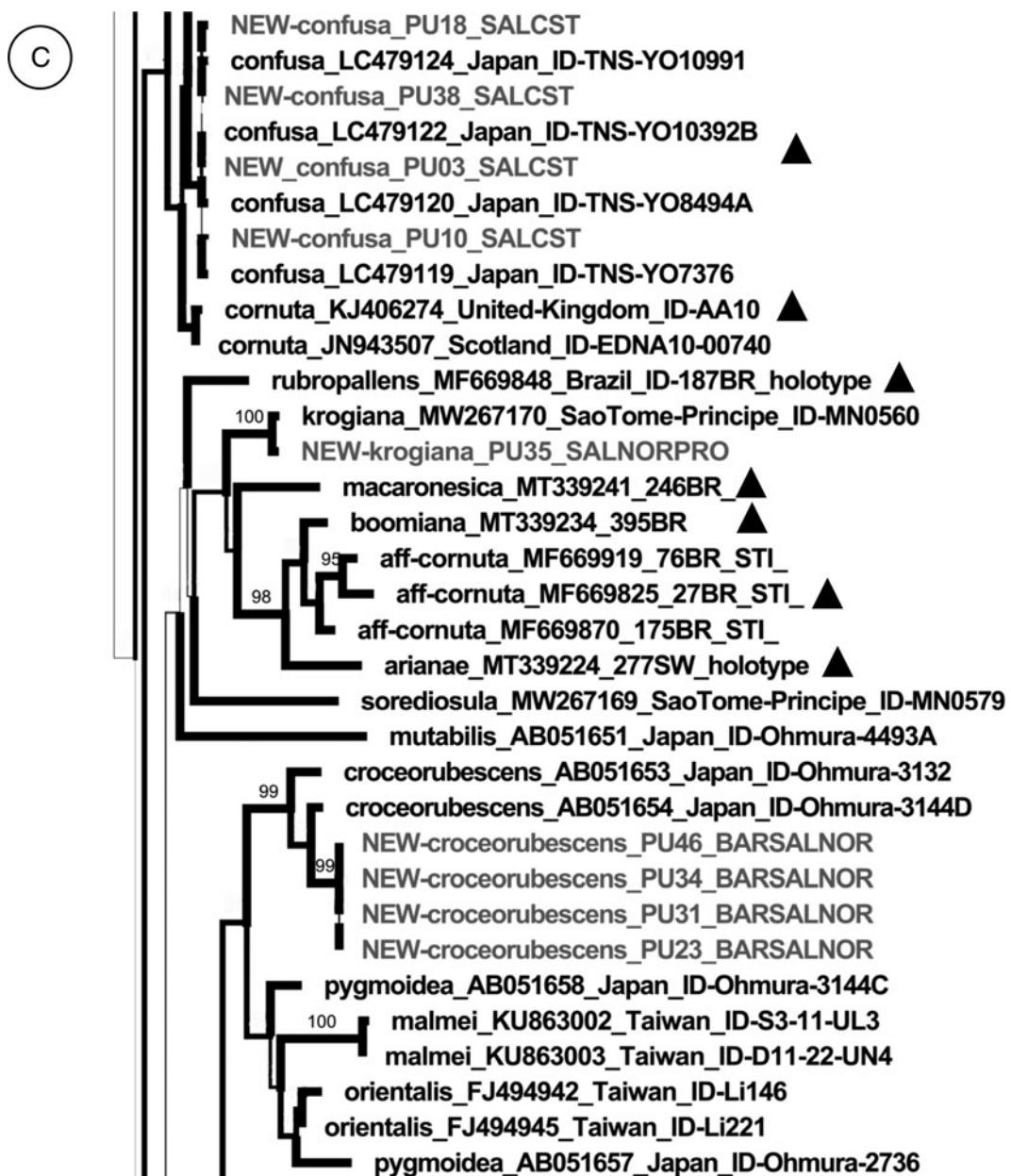


Figure 2C. Taxa belonging to the *Usnea* s. str. The triangle symbols indicate taxa belonging to the *Usnea cornuta* aggregate. Taxa in grey are from the southern Philippines. Further details are given in the Fig. 2 caption.

together with one from Hawaii as a long branch (Ohmura 4516) and with a different morphology (Fig. 2A).

In the 'baileyi-1' clade, the tubular section is filled with very loose, arachnoid, white or orange-yellow hyphae (the colour might vary in the same branch), and the subcortical/medullary pigment is salmon-coloured. In contrast, in the Philippines specimens of the 'baileyi-2' clade, the tubular part is denser and more spongy, white to pale yellow or cream-coloured, and the subcortical/medullary pigment is pale yellow-orange. However, the specimen Ohmura 4488a belonging to 'baileyi-2' has a 'baileyi-1' type of tubular section. The thin pigmented section of the medulla is often pink but sometimes also yellow to ochraceous. Only one specimen from the Philippines (PU44) does not have the pink pigment but a yellow pigmentation. The analysis of more specimens with molecular tools is necessary to

possibly find morphological differences between these two clades (Fig. 3).

The chemistry of the Philippine specimens is rather uniform, with norstictic acid accompanied or not by salazinic acid and zeorin (see Chemistry above). Sequenced specimens from Tanzania and São Tomé also have salazinic and norstictic acids (Temu *et al.* 2019; Nadel & Clerc 2022) but apparently without zeorin. In addition to norstictic acid and zeorin, eumitrins (red pigment present in the medulla) were found in specimens from Japan and Taiwan (Ohmura 2001, 2012). Eumitrins and zeorin were also reported from South American specimens (Truong & Clerc 2013). The presence of many chemotypes, the large distribution area and the morphological variation are good indications that *U. baileyi* is a complex of species, as shown recently (Temu *et al.* 2019; Lücking *et al.* 2020). At least two names are

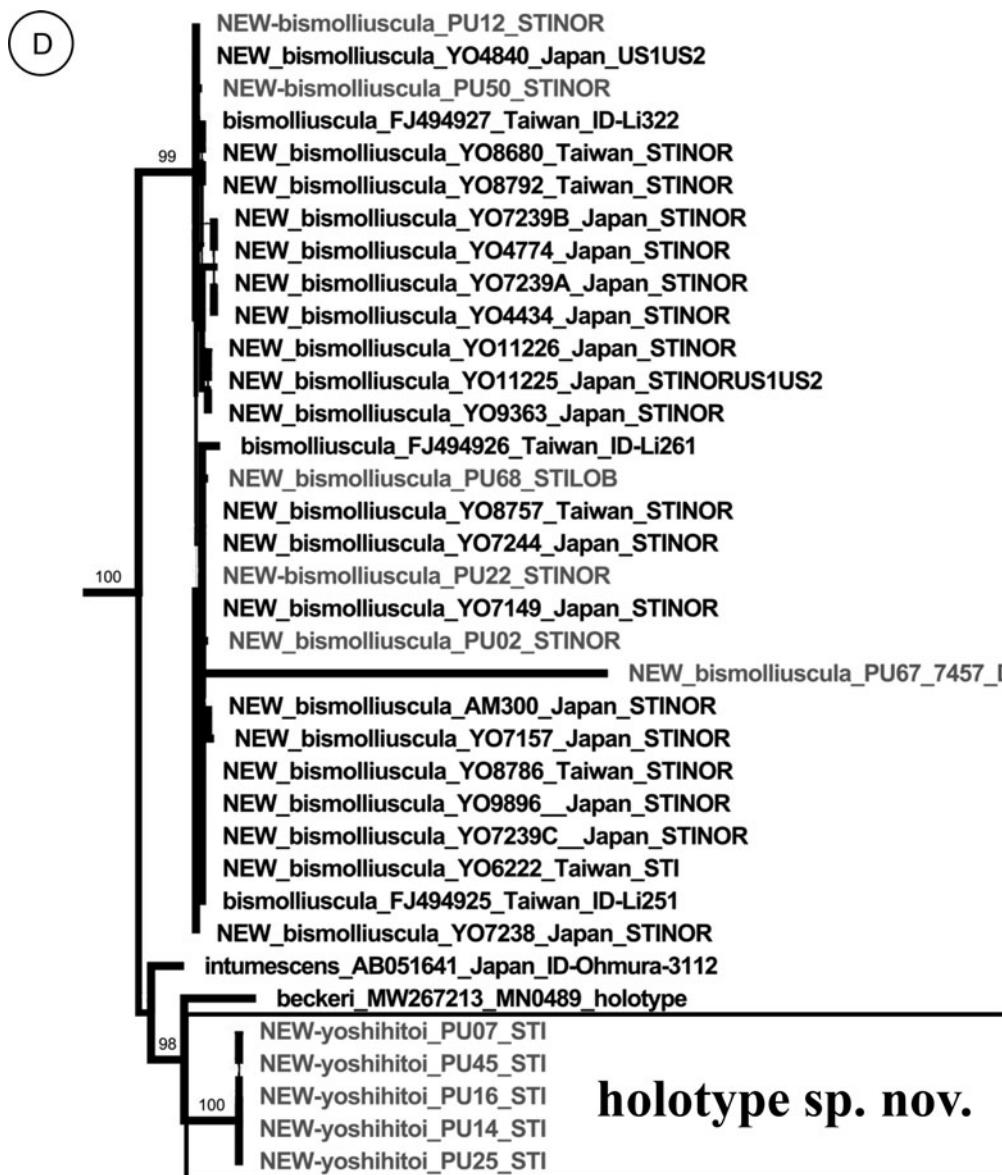


Figure 2D. Taxa belonging to the *Usnea* s. str. Taxa in grey are from the southern Philippines. A new species is indicated in the box. Further details are given in the Fig. 2 caption.

good candidates for one or both of these two clades found in the Philippines: *U. chrysopoda* and *U. endorhodina*. Further studies of these different types are necessary before reaching any taxonomic conclusion. A more in depth study, taking into account all the distribution range and chemistry variation, with the help of molecular tools is necessary to better understand this aggregate.

Distribution. *Usnea baileyi* has been reported from Luzon, Mindanao and Palawan Islands (Santiago *et al.* 2010, 2013; Sipman *et al.* 2013; Galinato *et al.* 2017, 2018; Timbreza *et al.* 2017). In the present study, it was also found in Mindanao (Marilog Forest Reserve) and Negros (Balinsasayao Twin Lakes Natural Park). This is the first record for Negros.

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1202 m, 7.45392°N, 125.24509°E, anthropized area, corticolous on *Pinus* sp., 2019, A. Gerlach (with *M. Dal Forno* & J. Nobleza).

Nobleza AG 2019/897a (BRIT), DNA-code: PU01; *ibid.*, 1227 m, 7.45938°N, 125.25106°E, 2019, A. Gerlach (with *M. Dal Forno* & J. Nobleza) AG 2019/893a (BRIT), DNA-code: PU37; *ibid.*, 1279 m, 7.48936°N, 125.25365°E, 2019, A. Gerlach (with *M. Dal Forno* & J. Nobleza) AG 2019/981b (G), DNA-code: PU24; *ibid.*, 1184 m, trail with native plants, 2019, A. Gerlach (with *M. Dal Forno* & J. Nobleza) AG 1012a (G), DNA-code: PU44. Negros: Negros Oriental, Dumaguete City, Tacloba, Larena Drive, Balinsasayao Twin Lakes Natural Park, fernery behind restaurant, 909 m, 9.36083°N, 123.17846°E, planted edible ferns and coconut palms, on coconut tree, 2019, *M. Dal Forno* (with A. Gerlach & A. D. Nietes) 3493 (BRIT), DNA-code: PU26.

Usnea bismolliuscula Zahlbr.

Cat. Lich. Univ. 6, 542 (1923); type: Japan, Prov. Harima, on *Pinus densiflora*, 19.11.1916, A. Yasuda 232 (TUR-V—holotype!). %C/M/A = 2.5/38/19; A/M = 0.5; A/C = 8.1; M/C = 16.3 (TUR-V

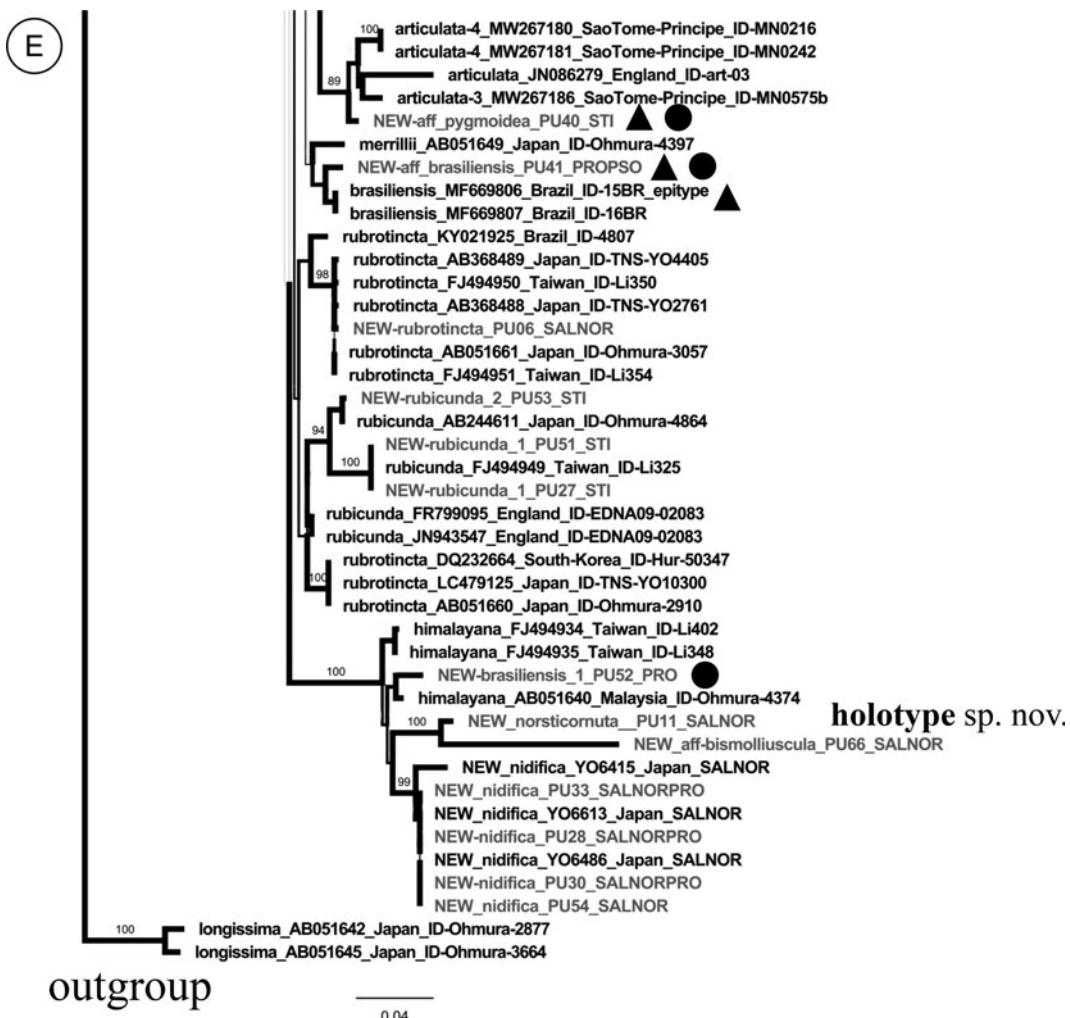


Figure 2E. Taxa belonging to the *Usnea* s. str. The triangle symbols indicate taxa belonging to the *Usnea cornuta* aggregate; the circle symbols indicate singletons. Taxa in grey are from the southern Philippines. A new species is indicated. Further details are given in the Fig. 2 caption.

879—isotype!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids (Ohmura 2001).

For a detailed description and figures of this taxon, see Ohmura (2001, 2012).

Thallus erect-shrubby to subpendulous; *trunk* concolorous; *lateral branches* constricted; *annular cracks* absent to few, rarely with medulla in between; *branches* irregular in longitudinal section, terete in transversal section; *foveolae* and *transversal furrow* absent to sometimes present; *cortical perforation* always present, few to numerous; *maculae* often present; *fibrils* slender, irregularly distributed; *papillae* inconspicuous; *tuberles* absent; *soralia* minute to large, circular to becoming irregular when confluent, often even to the cortex, (AG 1007e) sometimes slightly stipitate, plane, cortical margin thin to indistinct, few to numerous, often forming consoralia (?) to sometimes aggregating and becoming large at terminal branches; *isidiomorphs* few to numerous. *Cortex* thin to moderately thin, shiny; *medulla* thick, lax heterogeneous with conglutinated hyphae; *central axis* thin. $\%C/M/A = 2.5-4.5-8/31-35.5-41/12-19.5-30$ with an $A/M = 0.3-0.5-0.7$, $M/C = 12.5-7.5-5$, $A/C = 3.5-4.5-5$; ($n = 29$).

Apothecia often absent.

Chemistry. Medulla K+ yellow. TLC: 1) stictic, constictic (trace), \pm menegazziaic (trace), \pm cryptostictic (trace), \pm norstictic (trace) and \pm lobaric acids ($n = 18$); 2) barbatic, \pm stictic and \pm salazinic acids, \pm US1, US2 ($n = 4$); 3) stictic and salazinic acids, \pm US1, US2 ($n = 2$); 4) norstictic, \pm salazinic and \pm protocetraric acids (trace) ($n = 2$).

Taxonomic notes. *Usnea bismolliuscula* is easily recognized by the erect to subpendent thallus with constricted lateral branches, ±inflated segments, a glossy and smooth cortex surface with perforations, soralia that are circular to irregular in shape and even with the cortex surface, a thick and lax medulla and by the presence of stictic acid as the main medullary compound. The lax medulla with conglutinated hyphae and the large soralia at terminal branches (Fig. 9F & G) are good characters to separate this species from *U. yoshiihitoi*. In the southern Philippines, *U. bismolliuscula* displays four chemotypes. In addition to the stictic acid chemotype ($n = 18$), we found four specimens with barbatic acid, two specimens with stictic and salazinic acids and two specimens with norstictic acid as the main medullary substance. Ohmura (2001) mentioned the presence of only two chemotypes

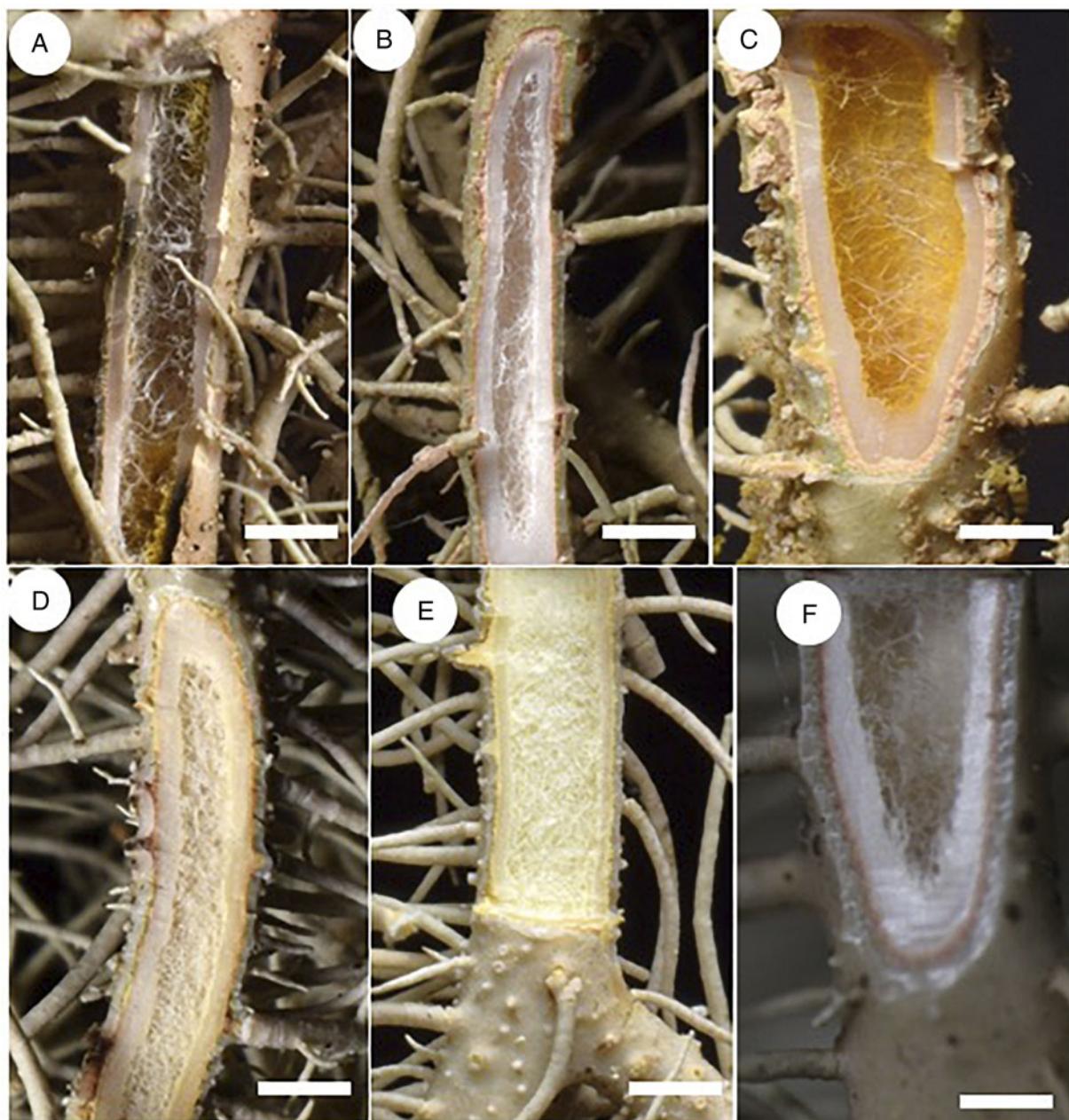


Figure 3. Variation found in the tubular section of the sequenced *Usnea baileyi*. A–C, clade *Usnea baileyi*-1; tubular section loosely arachnoid and white or orange-yellow (even in same branch), and the subcortical/medullary pigment is salmon-coloured (A = PU26, B = PU01, C = PU37). D–F, clade *Usnea baileyi*-2; tubular section denser and more spongy, white to pale yellow or cream-coloured, and the subcortical/medullary pigment is pale yellow-orange (D = PU24, E = PU44, F = Ohmura 4488a). Scales: A–F = 0.5 mm. In colour online.

in Japan: stictic acid (98%) with squamic acid as accessory and thamnolic acid (2%).

Phylogenetic notes. The six sequences from the Philippines (PU02, PU12, PU22, PU50, PU67, PU68) cluster into a fully supported clade (BP = 100) with three *U. bismolliuscula* specimens from Taiwan (Li251, Li322, Li261); the identity of one specimen (Li261), stictic acid-deficient, should, however, be checked. Twenty sequences from Japan and Taiwan were added to this study, often with stictic acid as the main medullary compound (except YO4840). One sequenced specimen (PU67) also contains barbatic acid with stictic acid. This sequence, however, is of low quality and appears as a long branch in the phylogeny (Fig. 2D).

Our phylogenetic analysis shows that in the Philippines there are two distinct lineages within the *Usnea bismolliuscula* morphotype (perforations of the cortex); one is described here as a new species, *U. yoshihitoi* (Figs 2 & 9; see under this taxon for differences with *U. bismolliuscula*). This is the first phylogenetic evidence that perforation of the cortex may have evolved several times within the genus.

Distribution. *Usnea bismolliuscula* is known from India (Awasthi 1986), Australia (Stevens 1999), Japan and Taiwan (Ohmura 2001, 2012). It was reported for the first time in the Philippines, in Bukidnon (Mindanao), by Timbreza *et al.* (2017). Our study shows that it is a common species found in

Mindanao (Marilog Forest Reserve) and Negros (Balinsasayao Twin Lakes Natural Park, Cuernos de Negros) where it occurs on tree trunks (e.g. *Pinus* sp., coconut palm) and on thin branches of shrubs (e.g. *Medinilla* sp.). It can also be found in anthropized habitats. It is reported here for the first time from the island of Negros.

Selected specimens examined. Philippines: *Mindanao*: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1227 m, 7.45938°N, 125.25106°E, on *Pinus* sp., 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/897b (BRIT), DNA-code: PU02, AG 2019/950d (dupl. G, PNH, CMHU, BRIT), DNA-code: PU50, AG 2019/951 (G), DNA-code: PU22, AG 2019/957a (G), DNA-code: PU12. *Negros*: Negros Oriental, Dumaguete City, Balinsasayao Twin Lakes Natural Park, 893 m, 9.35281°N, 123.18253°E, on branches on the ground, 2019, A. Gerlach (with A. D. Nietes) AG 2019/627b (BRIT).

Usnea brasiliensis (Zahlbr.) Motyka

Lich. Gen. Usnea, Stud. Monogr. (Leopoli) 2: 486 (1937); type: Brazil, São Paulo, near Lagoas, Exp. Acad. Vindobon., 1901, Schiffner (W—holotype!). %C/M/A = 6.5/38.5/10; A/M = 0.3; M/C = 6.4. Chemistry: usnic, protocetraric and psoromic acids (chemistry by Clerc in 1996).

For a detailed description and figures of *Usnea brasiliensis*, see Gerlach *et al.* (2020).

Thallus erect-shrubby; *trunk* concolorous with the branches; *branches* irregular in longitudinal and transversal sections; *lateral branches* constricted at ramification point, *annular cracks* few to numerous, with medullar regeneration; *fibrils* slender; *papillae* verrucose; *soralia* minute, circular to irregularly shaped, even with cortex to slightly stipitate, slightly convex, cortical medulla thin, sparse, distinct; *isidiomorphs* rare to numerous, lying horizontally on the branches; *cortex* thin to moderately thin, shiny; *medulla* thick, lax to dense; *central axis* thin. %C/M/A: 5.5–7/33–35.5/18–20; A/M = 0.5–0.6; A/C = 2.8–3.2; M/C = 6.4; (n = 2).

Chemistry. Medulla K–, P+ yellow turning red. TLC: protocetraric and ±psoromic acids (n = 2).

Taxonomic notes. *Usnea brasiliensis* can be recognized by the shrubby thallus with constricted lateral branches, by the minute consoralia ±even with cortex, by the shiny, thin to moderately thick cortex, ((5–)5.4–6.8%–8.2(–10.5)), the thick medulla ((26.5–)30.5–33.3%–36.1(–37.5)) with an M/C ratio smaller than 7, highlighting a relatively thick cortex and a not too large medulla (Gerlach *et al.* 2020), and the presence of protocetraric, ±psoromic acids in the medulla. The two specimens collected in the Philippines share the characteristics mentioned above except that their soralia remain well delimited, apparently not forming consoralia.

We found a herbarium specimen collected in Luzon and apparently belonging to *U. brasiliensis* s. lat. (B 56256). It has a CMA of the *tenuicorticata*-type (ratio medulla/cortex higher than 7) and an interesting chemistry with protocetraric acid and lobaric acid; the soralia are punctiform, with a thin cortical margin, with many isidiomorphs, fusing together to form consoralia as in *U. cornuta* Körb. This specimen could be a new chemotype of *U. tenuicorticata* P. Clerc & A. Gerlach. Molecular analysis of

this chemotype is necessary to confirm whether *U. tenuicorticata* is present in the Philippines.

Phylogenetic notes. Sequences were obtained for two specimens belonging to the *U. brasiliensis* aggregate (PU41, PU52) (Fig. 2E). PU41 clustered together with *U. brasiliensis* s. str. but on a long branch (similarity between *Usnea brasiliensis* epitype and PU41 = 0.91 [below 98.5%]), which indicates that they probably do not correspond to the same lineage. Since PU41 is phylogenetically closely related to and shares a similar phenotype with *U. brasiliensis* s. str., only diverging in their geography, we could consider it as a potentially unnamed allo-cryptic species (Lücking *et al.* 2021). Our results indicate that what we consider morphologically and chemically as *U. brasiliensis* s. lat. in the Philippines seems to be a phylogenetically highly heterogeneous complex that needs further study.

Distribution. *Usnea brasiliensis* is known for South and North America, Macaronesia, Japan and Taiwan (see Gerlach *et al.* (2020) for more details). This is the first evidence that the *U. brasiliensis* aggregate occurs in the Philippines (Mindanao and Luzon Islands).

Selected specimens examined. Philippines: *Mindanao*: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1258 m, 7.48853°N, 125.25288°E, Mt Malambo, base, by the road, right in front of Royal Mandala forest farm, anthropized environment, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/995b (BRIT), DNA-code: PU41; *ibid.*, 1188 m, 7.45960°N, 125.24522°E, disturbed forest with *Pinus*, abandoned house, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/950c (G), DNA-code: PU52.

Usnea confusa Asahina

Lich. Jpn. 3, 97 (1956); type: Japan, Honshu, Prov. Suruga, Subashiri-guchi, Mt Fuji, 7 July 1952, Y. Asahina 5277, thallus C (TNS—lectotype!). %C/M/A = 4.6/38.2/14.5. Chemistry: usnic, constictic, salazinic and protocetraric (trace) acids (Ohmura 2001; Ohmura & Clerc 2019).

For figures, see Ohmura & Clerc (2019).

Thallus shrubby, 2.5–7(–9) cm long, with anisotomic-dichotomous ramifications; *basal part* often concolorous with main branches, sometimes paler or blackish near the holdfast, sometimes with annular cracks; *main branches* slightly irregular in longitudinal section, terete in transversal section, ±distinctly segmented; *segments* cylindrical to often ±swollen; *lateral branches* distinctly constricted at attachment points; *foveolae*, *maculae* and *pseudocyphellae* absent; *papillae* often numerous, ±densely covering the branches; *tuberles* absent; *fibrils* slender, never densely arranged but scattered and unevenly distributed in the whole thallus; *fiberles* scattered in whole thallus; *soralia* minute, a) when numerous fusing together to form larger consoralia, sometimes completely covering terminal branches, b) irregular, c) ±even with cortex, d) plane, e) without a well-delimited cortical rim, f) numerous in mature specimens, g) forming consoralia, h) mainly located in terminal branches; *isidiomorphs* few to numerous, sometimes densely covering the branches; *isidiofibrils* often present, few to numerous, sometimes densely covering the branches; *cortex* thin to moderately thick (5–7%–10%),

Species/Abbrv	Δ	
1. <i>Usnea confusa</i> _LC479119_Japan_ID-TNS-YO7376	G	C T T C T A T T
2. <i>Usnea confusa</i> _LC479122_Japan_ID-TNS-YO10392B	G	C T T C T A T T
3. <i>Usnea confusa</i> _LC479120_Japan_ID-TNS-YO8494A	G	C T T C T A T T
4. <i>Usnea confusa</i> _LC479124_Japan_ID-TNS-YO10991	G	C T T C T A T T
5. <i>Usnea aff. cornuta</i> -3_KJ406274_United-Kingdom_ID-AA10	A	A C C C T T T T
6. <i>Usnea aff. cornuta</i> -3_FR799083_Scotland_ID-EDNA10-00740	A	A C C C T T T T
7. <i>Usnea aff. cornuta</i> -3_JN943507_Scotland_ID-EDNA10-00740	A	A C C C T T T T
8. <i>Usnea cornuta</i> FR799085_Ireland_ID-EDNA09-01124	A	C C C G A T A A
9. <i>Usnea cornuta</i> FR799086_England_ID-EDNA09-01127	A	C C C G A T A A
10. <i>Usnea cornuta</i> JN943532_Wales_ID-EDNA09-02134	A	C C C G A T A A
11. <i>Usnea cornuta</i> FR799084_Scotland_ID-EDNA09-02345	A	C C C G A T A A
12. <i>Usnea cornuta</i> JN943526_Scotland_ID-EDNA09-02345	A	C C C G A T A A
13. <i>Usnea cornuta</i> JN943559_England_ID-EDNA09-01127	A	C C C G A T A A
14. <i>Usnea cornuta</i> JN943562_Ireland_ID-EDNA09-01124	A	C C C G A T A A
15. <i>Usnea cornuta</i> JN943561_Ireland_ID-EDNA09-01125	A	C C C G A T A A
16. <i>Usnea cornuta</i> FR799087_Wales_ID-EDNA09-02134	A	C C C G A T A A
17. <i>Usnea cornuta</i> FR799088_Ireland_ID-EDNA09-01125	A	C C C G A T A A
18. <i>Usnea cornuta</i> MF669859_Brazil_ID-17BR	A	C C C G A T A A
19. <i>Usnea cornuta</i> MF669861_Brazil_ID-19BR	A	C C C G A T A A
20. <i>Usnea cornuta</i> MF669828_Brazil_ID-30BR	A	C C C G A T A A
21. <i>Usnea cornuta</i> MF669856_Spain_ID-EAC4491	A	C C C G A T - -
22. <i>Usnea cornuta</i> MF669854_Spain_ID-EAC4489	A	C C C G A T - -
23. <i>Usnea cornuta</i> MW241013_Portugal_ID-EAC4487	A	C C C G A T - -
24. <i>Usnea cornuta</i> MF669856_Spain	-	C C C G A - - -
25. <i>Usnea cornuta</i> MF669854_Spain	-	C C C G A - - -
26. <i>Usnea cornuta</i> MW241013_Portugal	-	C C C G A - - -

Figure 4. Alignment of the three clades of the *Usnea cornuta* aggregate showing the variable columns diagnostic for the clades: *U. confusa* vs *U. cornuta* (small clade: rows 5–7), 5 substitutions, including 2 transversions; *U. confusa* vs *U. cornuta* (large clade: rows 8–26), 8 substitutions, including 5 transversions; *U. cornuta* (small vs large clade): 5 substitutions, all transversions. In colour online.

shiny; *medulla* thick (29–32%–36), dense to lax; *axis* thin to moderately thin (13–22%–32). CMA of the *cornuta*-type; (*n* = 13).

Apothecia absent.

Chemistry. Medulla K+ yellow turning red. TLC: constictic, salazinic and \pm protocetraric acids (*n* = 13).

Taxonomic notes. *Usnea confusa* belongs to the *U. cornuta* aggregate. It was considered as a synonym of *U. cornuta* by Clerc (2004) and recently lectotypified by Ohmura & Clerc (2019). Morphologically it is difficult to find any differences between these two taxa. Both can be recognized by the erect-shrubby thallus, the minute soralia, the numerous papillae covering the branches, the presence of isidiofibrils, and the presence of salazinic and constictic acids in the medulla. *Usnea confusa* and *U. cornuta* can be considered allo-(phylo-) cryptic taxa *sensu* Dal Forno *et al.* (2022), meaning they have the same phenotype and are phylogenetically closely related but differ mainly in their geographical distribution (Asia vs Europe).

Phylogenetic notes. We sequenced four specimens (PU03, PU10, PU18, PU38) that clustered together with the Japanese specimens identified as *Usnea confusa*-1 by Ohmura & Clerc (2019) in a supported clade (Fig. 2C). *Usnea confusa* is phylogenetically close to *Usnea cornuta* s. str. and whether both species are separate or not is controversial.

The *U. cornuta* aggregate was studied by Gerlach *et al.* (2019), who reconstructed a phylogenetic tree based on a coalescence approach with three molecular markers. They found 14 lineages

and suggested that lineage 5 (more specifically the subclade 5A) corresponds to *U. cornuta* s. str. In this multilocus study, sequences from *U. confusa* were not included. Later, the phylogenetic position of *U. confusa* was investigated and two clades were found, both in the vicinity of *U. cornuta* s. str. (Ohmura & Clerc 2019). According to these authors, their results based on ITS sequences do not allow the confirmation or rejection of the conspecificity of both taxa.

Lücking *et al.* (2020), with an expanded ITS dataset, agreed that lineage 5 (Gerlach *et al.* 2019) corresponds to *Usnea cornuta* s. str. but also identified many other, possibly unnamed lineages (*U. aff. cornuta* 1–10). Gerlach *et al.* (2019) pointed out that even lineage 5 includes smaller subgroups whose relationships are poorly understood. Whether these putative unnamed subgroups can be considered as separate species or not should be carefully analyzed case by case, especially when only ITS data are available. Here we propose to accept *U. confusa* as a separate species based on genetic distance (between *U. confusa* and *U. cornuta* = 98.7–99%; see Fig. 4), and because all specimens of *U. confusa* form a coherent unit within a well-supported clade with only Asian specimens. Although the genetic distance is minor, barcode evidence from other taxa shows that closely related species in *Usnea* display a genetic distance of 99–99.5% (Lücking *et al.* 2020). It is important to note, however, that a definitive decision regarding the conspecificity of *Usnea cornuta* s. str. and *Usnea confusa* will only be possible if based on multilocus analyses and the study of type material.

Distribution. *Usnea confusa* was previously known only from Japan (Ohmura & Clerc 2019). This is the first record for the Philippines (Mindanao and Negros).

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganahan, Marilog Forest Reserve, 1227 m, 7.45938°N, 125.25106°E, on the new Baganinhan road, 2019, A. Gerlach (with *M. Dal Forno* & *J. Nobleza*) AG 2019/893b (BRIT, PNH), DNA-code: PU38; *ibid.*, on *Pinus* sp., 2019, A. Gerlach (with *M. Dal Forno* & *J. Nobleza*) AG 2019/897c (G), DNA-code: PU03, AG 2019/995c (G), DNA-code: PU10, AG 2019/996b (BRIT), DNA-code: PU18. Negros: Negros Oriental, Dumaguete City, Taclobo, Larena Drive, Balinsasayao Twin Lakes Natural Park, highest point reached, 1040 m, 9.35947°N, 123.17361°E, on tree trunk, 2019, *M. Dal Forno* (with *J. Shevock* & *D. Salas*) 3471a (BRIT).

Usnea croceorubescens Vain.

Bot. Mag., Tokyo 35, 46 (1921); type: Japan, Prov. Kushiro, in arbore, 21.8.1918, A. Yasuda 234 (TUR-V—holotype!; TNS—isotype!). %C/M/A = 10/19.5/42; A/M = 2.1; A/C = 4.3; M/C = 2.0. Chemistry: usnic, barbatic, 4-O-demethylbarbatic, salazinic acids and protocetraric acid (trace) (= *Usnea pangiana* *sensu* Ohmura (2001) non Stirt.).

For a detailed description of this taxon, see Ohmura (2001; under *U. pangiana*); for figures see Clerc (2016).

Thallus erect-shrubby to sometimes subpendulous (B 73551); *trunk* concolorous with main branches, rarely black-reddish only on the first mm above the first ramification, with numerous annular cracks; *lateral branches* not constricted at attachment point; *annular cracks* numerous on the whole thallus; *branches* cylindrical to tapered in longitudinal section, terete in transversal section; *fibrils* slender,

irregular distributed, few to numerous; *soralia* minute, circular, slightly stipitate, plane to capitate, cortical margin indistinct, few to numerous; *isidiomorphs* few; *cortex* moderately thick to thick, matt; *medulla* thin to moderately thick, dense to compact; *central axis* thin to thick. %C/M/A = 9.5–11–14.5/7–16.5–27.5/25–44.5–63; A/M = 2–2.5–3.5; M/C = 0.7–1.5–2; A/C = 2.5–4–4.5; (n = 12).

Chemistry. Medulla K+ yellow turning red. TLC: barbatic and salazinic and \pm norstictic acids (n = 12).

Nomenclatural note. This taxon was named *U. pangiana* Stir. by Ohmura (2001). However, as Clerc (2016) pointed out, the holotype of *U. pangiana* has much larger and stipitate soralia, not *cornuta*-like in morphology, that are probably growing out of fiberles or tubercles. Although Clerc (2016) treated this taxon as *U. hondoensis* Asahina, the name *U. croceorubescens* Vain. should be applied since it was published earlier (in 1956 and 1921 respectively). The morphology and chemistry of the type specimens of *U. croceorubescens*, including the ratios of cortex, medulla and axis, coincide well with the range of description provided by Ohmura (2001). However, as described in the protologue of *U. croceorubescens* ('Stratum myelohypicum crebre contextum, partim croceo-rubescens'), the medulla is partly yellow-red in colour while it is white in most parts. This colour finds its origin in the deposition of salazinic acid crystals, which might be caused by withering of the thallus in old parts. Such rusty coloration by withering is also common in many lichens that contain salazinic acid. Although the epithet '*croceorubescens*' is not representative of the features of this taxon, the earliest legitimate name should be applied according to ICN 11.3 (Shenzhen Code).

Taxonomic notes. *Usnea croceorubescens* is characterized by the erect-shrubby to subpendulous sorediate thallus, with non-constricted lateral branches, by the presence of numerous thin annular cracks (sometimes best seen in transversal section) especially near the base, by the punctiform soralia that are even to slightly stipitate and often regularly distributed in the whole thallus, rarely with isidiomorphs, by the matt, moderately thick to thick cortex and by the presence of barbatic and salazinic acids as main secondary metabolites.

Usnea aciculifera Vain. has a different %C/M/A, soralia that are more or less aggregated in small groups and stictic acid in the medulla. *Usnea setulosa* Motyka, a South American species, is morphologically similar (soralia and %C/M/A). However, this species has a black base and salazinic acid in the medulla. Several other species are known to produce barbatic acid in the medulla: *Usnea dendritica* Stir. seems to be the most similar species due to the presence of annular cracks and the similar chemistry; however, it is richly apotheciate and differs mainly by the shape of the rare soralia developed from the top of eroded papillae, which are distinctly stipitate in thicker branches (Ohmura 2001).

Phylogenetic notes. Four sequenced specimens (PU23, PU31, PU34, PU46) form a well-supported subclade (BP = 98) within the *Usnea croceorubescens* clade from Japan (Fig. 2C).

Distribution. *Usnea croceorubescens* is known from Japan and Taiwan (Ohmura 2001, 2012; as *U. pangiana*). This is the first record for the Philippines where it is relatively common (Luzon, Mindanao and Negros).

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1279 m, 7.48936°N, 125.25365°E, 2019, Mt Malambo, open area with *Pinus* sp., A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/992b (BRIT), DNA-code: PU23. Negros: Negros Oriental, Dumaguete City, Tacloba, Larena Drive, Balinsasayao Twin Lakes Natural Park, highest point reached, 1040 m, 9.35947°N, 123.17361°E, on tree trunk, 2019, M. Dal Forno (with J. Shevock & D. Salas) 3471b (BRIT), DNA-code: PU31; Dumaguete City, Santa Catalina, San Pedro, Cuernos de Negros, 1324 m, 9.24092°N, 123.11626°E, mid elevation, forest edge (*Cyphellostereum*, *Crocynia*, *Cryptothecia*), 2019, A. Gerlach (with M. Dal Forno, A. D. Nietes) AG 2019/852a-b (BRIT, dupl. PNH), DNA-code: PU34, AG 2019/850a (G), DNA-code: PU46.

Usnea dasaea Stir.

Scott. Natural. 6, 104 (1881); type: Madeira, Funchal, Payne (BM —holotype!). %C/M/A = 9.5/26.5/28. Chemistry: usnic, norstictic, galbinic and salazinic acids.

For a detailed description of this taxon, see Clerc & Herrera-Campos (1997), Ohmura (2001) and Clerc (2007); for figures see Clerc & Herrera-Campos (1997) and Ohmura (2012).

Thallus erect-shrubby to subpendulous; *trunk* often concolorous, sometimes reddish; *lateral branches* \pm constricted at ramification point; *branches* irregular in longitudinal section, terete in transversal section; *foveolae* rarely present; *fibrils* spinulose, usually densely covering some parts of the branches; *papillae* inconspicuous; *soralia* minute, irregular, even with cortex, plane, cortical margin indistinct, few to numerous, distinct to confluent; *isidiophibrils* few to numerous; *cortex* thin, shiny; *medulla* thin to moderately thick, often dense (rarely lax); *central axis* thin to moderately thin. %C/M/A = 4–6.5–8/26.5–30–36.5/19–28–32; A/M = 0.7–0.8–0.9; M/C = 4.5–4.6–6.5; A/C = 4–4.5–4.7; (n = 9).

Chemistry. Medulla K+ yellow turning red. TLC: salazinic, norstictic and galbinic acids (n = 9).

Taxonomic notes. *Usnea dasaea* is characterized by the irregular branches in longitudinal section, terete in transversal section, often partly densely covered by spinulose fibrils, the C/M/A of *cornuta*-type, the minute, plane and often irregular soralia and the presence of galbinic acid in the medulla. For differences with *U. paleograndisora* and *U. spinulifera*, see under these taxa.

Phylogenetic notes. Two specimens from the Philippines (PU09, PU21) clustered with one specimen from Japan (AB051056). The specimen from Portugal (DN121) is in their vicinity but their relationship is not supported (Fig. 2A). According to Gerlach *et al.* (2019), *Usnea dasaea* (from Brazil) appears to form two separate lineages (lineage 1: 35BR; lineage 2: 34BR, 37BR, 128BR), although they were poorly supported. These lineages are not closely related to the lineage from Asia which suggests that *Usnea dasaea* is polyphyletic (Fig. 2A).

Distribution. *Usnea dasaea* is known from Europe, North America, South America, Africa, Asia (Clerc & Herrera-Campos 1997) and Australasia (Stevens 1999 (as *U. undulata*); Bannister *et al.* 2020). However, since it is a polyphyletic complex

(Gerlach *et al.* 2019), it is difficult to have an exact idea of its distribution. For the Philippines, it has been reported for Luzon (Galinato *et al.* 2017, 2018). It is recorded here for the first time from the southern Philippines, specifically Mindanao.

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 7.45672°N, 125.23962°E, 1095 m, open road, disturbed, close to the main road near Lawi Lawi Resort, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/969c (BRIT), DNA-code: PU09; Mt Malambo, open area with *Pinus* sp., 1279 m, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/980b (BRIT), DNA-code: PU21.

Usnea himalayana C. Bab.

Hook. J. Bot. **4**, 243 (1852); lectotype (*fide* Awasthi 1986): Himalaya (India, Uttar Pradesh), Kumaon, Binsar, c. 2300 m, R. Strachey & J E. Winterbottom s. n. (H-NYL 36377—lectotype; BM—isolectotype). Chemistry: usnic and salazinic acids.

For a detailed description and figures of this taxon, see Ohmura (2001, 2012).

Thallus pendulous, often entangled with many attachment points; *trunk* concolorous; *lateral branches* distinctly constricted at ramification point; *branches* irregular in longitudinal section, terete in transversal section; *segments* ±sausage-like; *foveolae* and *transversal furrow* often present, sometimes numerous; *pseudocyphellae* often present, linear; *soralia* minute, circular, distinct, few, present mainly on fibrils; *cortex* thin, shiny; *medulla* wide, lax; *central axis* thin. %C/M/A ($n = 8$) = (1.5–)2.4–3.6–4.8(–5.5)/(35–)36.5–39.6–42.7/(7–)8.9–13.5–18.1(–20); A/M = (0.2–)0.3–0.4–0.5(–0.6); M/C = (6.5–)6.1–12.3–18.5(–26.8); A/C = (2.4–)2.5–3.8–6.2(–6.6); ($n = 4$).

Chemistry. 1) Medulla K+ yellow turning red; TLC: salazinic, ±norstictic and ±protocetraric (trace) acids ($n = 3$). 2) Medulla K+ yellow ($n = 1$); TLC: constictic acid ($n = 1$).

Taxonomic notes. Morphologically, what is called here *U. himalayana* is similar to *U. articulata* (L.) Hoffm. Both taxa have sausage-like inflated branches with or without pseudocyphellae, a thin (1.5–5.5%) and glossy cortex, a lax and wide (35–45%) medulla, a thin (7–20%) central axis, a low A/M ratio (0.2–0.6), a fairly large M/C ratio (6.5–26.8) and thus a *tenuicorticata*-type of C/M/A (Ohmura 2001, 2012; Nadel & Clerc 2022). The type of *Usnea himalayana* (collected in India, Himalaya) produces salazinic acid in the medulla whereas the type of *U. articulata* (collected in the UK) has protocetraric acid. The diffractaic acid chemotype of *U. articulata* was found in Taiwan (Ohmura 2012); the salazinic, diffractaic and protocetraric acid chemotypes were found in Africa (Swinscow & Krog 1976; Nadel & Clerc 2022). Despite this similar morphology and anatomy, our ITS phylogeny (Fig. 2E) shows that both species are not closely related. See below for differences with *Usnea nidifica*, another pendulous species occurring in the Philippines.

Phylogenetic notes. Unfortunately, no ITS data from specimens of *U. himalayana* collected in the Philippines are available. We used ITS data from three specimens collected in Malaysia and

Taiwan. These specimens are closely related to *U. nidifica* (Fig. 2E).

Distribution. Known from the Himalayan region (India, Nepal, Sikkim) (Motyka 1936–38 (as *U. dichotoma*); Awasthi 1986; Ohmura 2001), from Malaysia, the Philippines and Taiwan (Ohmura 2012). Recently reported for the Philippines from Mindanao (Bukidnon Province) by Timbreza *et al.* (2017). In our study, only herbarium specimens were analyzed (Mindanao and Luzon). The species is recorded here for the first time from Luzon. Also new to Papua New Guinea.

Selected specimens examined. **Philippines:** Luzon: Benguet Province, Mt Santo Tomas, S of Baguio, along road from telecommunication station to Baguio, 2100 m, 16°18'N, 120°35'E, 1987, H. Sipman 21744 (B 73258).—**Papua New Guinea:** Simbu: Bismarck Range, Mt Wilhelm, Pindaunde Valley, SE of Lake Aunde, 1966, D. J. Hill 12578 (G 262519).

Usnea krogiana P. Clerc

Lichenologist **38**, 199 (2006); type: Spain, Canary Islands, La Gomera, Alajero, Lomo de la Mulata, 1320–1340 m, on *Erica arborea*, 23-Sept-1986, P. Clerc (G—holotype!; BM, UPS—isotypes). %C/M/A = 11/9/60 (holotype). Chemistry: stictic, constictic (trace), cryptostictic, menegazziaic (trace), and norstictic (trace) acids (holotype).

For a detailed description and figures of this taxon, see Clerc (2006).

Thallus erect-shrubby; *trunk* with a sharply delimited jet black pigmentation, with thin annular cracks; *lateral branches* not constricted at ramification point; annular cracks sometimes present in the whole thallus; *branches* tapering to cylindrical in longitudinal section, terete in transversal section; *soralia* minute, circular, even to slightly stipitate; *cortex* thick, matt; *medulla* thin, dense to compact; *central axis* moderately thick to thick. %C/M/A = 10–15–20/10.5–11.7–13/39–46.5–54; A/M = 3.7–3.9–4.1; M/C = 0.5–0.9–1.3; A/C = 2–3.5–5.5; ($n = 3$).

Chemistry. Medulla K+ yellow. TLC: stictic, constictic, cryptostictic, menegazziaic and norstictic acids.

Taxonomic notes. *Usnea krogiana* is characterized by the shrubby-sorediate thallus with lateral branches not constricted at attachment points, the black base with a sharply delimited pigmentation, the thick axis that gives the distinct rigidity to the thallus, the matt cortex, the numerous minute soralia with conspicuous isidiomorphs and by the presence of the stictic acid group in the medulla (Clerc 2006). The only sequenced specimen (PU35) corresponds well with *U. krogiana* with the exception of the axis that is moderately thick (43%) (axis thickness in Clerc (2016): (44–)53.6–62.5%–71.4(–79)) and by the chemistry (salazinic acid instead of stictic acid). The presence of salazinic acid in *U. krogiana* was reported for the first time as a new chemotype from the islands of São Tomé and Príncipe by Nadel & Clerc (2022), based on a sequenced specimen.

Phylogenetic notes. The only sequenced specimen (PU35) clustered with strong support with a specimen recently identified as

U. krogiana from São Tome and Principe (Nadel & Clerc 2022) (Fig. 2C).

Distribution. *Usnea krogiana* occurs in Macaronesia and the West Indies (Clerc 2006), and in Africa (Nadel & Clerc 2022). It is reported here for the first time for Asia in the Philippines (Negros and Mindanao).

Selected specimens examined. **Philippines:** Negros Oriental, Dumaguete City, Santa Catalina, San Pedro, Cuernos de Negros, forest going up the ridge to peak Hapon Hapon, 1368 m, 9.24245°N, 123.11779°E, 2019, M. Dal Forno, A. Gerlach & A. D. Nieten 3635a (G), DNA-code: PU35.

Usnea longissima Ach.

Lichenogr. Universalis, 626 (1810); type: [actually Poland], Lausitz Region (Lusatia), Mosig (H-ACH 1893—holotype). Chemistry: usnic and diffractaic acids (P. M. Jørgensen, 1975).

For a detailed description of this taxon, see Halonen *et al.* (1998), Ohmura (2001) and Clerc (2011).

Thallus pendulous, entangled, sparsely branching with ramifications of the filamentous type; *main branches* cylindrical in longitudinal section and terete in transversal section, with cortex scaling off, leaving a dull, rough, whitish, ecorcicate surface, with many perpendicular secondary branches resembling long fibrils that are not constricted at ramification points; *maculae* numerous, spirally arranged close to the basal part of the lateral branches; *soralia* occasional, minute, $\leq 1/2$ branch diameter; *isidiomorphs* few to absent; *cortex* thin when present (2–3.5%); *medulla* thin (6–12%), compact, non-pigmented; *axis* thick (69–86%), non-pigmented; ($n = 1$).

Chemistry. Medulla K–. TLC ($n = 1$): diffractaic acid.

Taxonomic notes. *Usnea longissima* can be easily confused with specimens belonging to the *U. pectinata* aggr., especially when the latter have an eroded cortex and a non-pigmented central axis. Moreover, both taxa might produce diffractaic acid in the medulla. In that case, the presence of the spirally arranged maculae in the lateral branches is a diagnostic character of *U. longissima*. *Usnea pectinata* might also have maculae but these are ±elongated, of irregular shape, and never spirally arranged. The specimen found in the TUR herbarium has the characteristic pseudocyphellae and diffractaic acid in the medulla.

Phylogenetic notes. DNA from the TUR herbarium specimen was not extracted. *Usnea longissima* belongs to the subgenus *Dolichousnea* Y. Ohmura (Ohmura 2001, 2002).

Distribution. *Usnea longissima* is a circumpolar, Northern Hemisphere species, found in Europe, North America and Asia. In the Philippines, Vainio (1909), Herre (1963) and Galinato *et al.* (2017, 2018) have reported it for Luzon at higher elevations.

Specimen examined. **Philippines:** Luzon: Benguet Province, Pauai, 2134 m, Vainio (TUR-V 591).

Usnea nidifica Taylor

London J. Bot. 6, 191 (1847); holotype: Norfolk Island, C. Babington & Thomas s. n. (FH). Chemistry: usnic, norstictic, protocetraric and salazinic acids (Ohmura 2001).

For a detailed description and figures of this taxon, see Ohmura (2001, 2012).

Thallus pendulous, entangled with several attachment points; *trunk* concolorous with main branches; *lateral branches* not constricted but most likely slightly to distinctly enlarged at ramification point; *branches* irregular in longitudinal section, terete on transversal section with annular to irregular longitudinal cracks; *segments* cylindrical to slightly swollen, not sausage-like; *pseudocyphellae* absent; *fibrils* slender, irregularly distributed; *soralia* minute to enlarged, circular to irregular, even on the crack edges when well developed (MDF 3554, B 83619); *isidiomorphs* present, sometimes numerous; *cortex* thin to moderately thin, matt; *medulla* dense, moderately thick to thick; *central axis* thin to moderately thin. %C/M/A ($n = 10$) = (4–)4.3–5.7–7.1(–8)/(21.5–)23.2–28.3–33.4(–42)/(20–)23.3–30.3–37.3(–42); A/M = (0.6–)0.7–1.1–1.5(–1.9); M/C = (3.2–)3.4–5.6–7.8(–8.8); A/C = (3.7–)4.5–5.5–6.5; ($n = 6$).

Chemistry. Medulla K+ yellow turning red. TLC: 1) salazinic, norstictic and protocetraric (trace) acids ($n = 5$); 2) salazinic and constictic acids ($n = 1$).

Taxonomic notes. The analyzed specimens have pendulous thalli with irregular branches and ±inflated segments, irregularly shaped soralia developing from cracks or directly from the cortex, partially aggregating to form irregular masses of soralia, a thin to moderately thin cortex (4–6–8%) and salazinic and norstictic acids as main medullary substances.

The herbarium specimen B 60 0073552 collected in Luzon by H. Sipman with short pendulous thalli (6 cm long) has rounded and slightly stipitate soralia which are somewhat atypical for this species. However, the irregular branches which are more or less inflated in some parts, the glossy surface of the cortex, the chemistry, and the %C/M/A (6/34/20) correspond well with *U. nidifica*. Another specimen (B 60 0073550 collected in 1987 in Luzon by Sipman) has the same rounded soralia and a different chemistry (constictic acid instead of salazinic).

As commented by Stevens (1991, 1999) and Ohmura (2001), *U. nidifica* seems to be a highly variable species. Indeed, Stevens (1999) mentioned seven taxa as possible synonyms and Ohmura (2001) synonymized eight taxa under this species. A taxonomic revision based on molecular data analyzed from specimens collected in the whole Indo-Pacific area will be necessary to better understand this taxon.

In our phylogeny, *U. himalayana* is a sister clade to *U. nidifica*. However, the former species does not produce soralia and has an *U. articulata*-type of morphology, with swollen and distinctly articulate branches, a thinner cortex (1.5–5.5%), a much larger and lax medulla (35–43%), a much thinner axis (7–20%) and consequently a lower A/M (0.2–0.6). *Usnea bismoliuscula* is another similar species. It differs, however, in the presence of perforations in the cortex, in the conglutinated medullary hyphae and in the chemistry (stictic acid group).

Phylogenetic notes. Four sequenced specimens from the Philippines (PU28, PU30, PU33, PU54) cluster into a supported clade (PP = 69) sister to *U. himalayana* (see above) (Fig. 2E).

Distribution. *Usnea nidifica* is known from Asia (Japan, Java, India, Malaysia, Sulawesi and Taiwan), Africa (Comoro Islands, Mauritius, the Seychelles, Socotra), Australasia (Australia, New Caledonia, New Zealand, Papua New Guinea, Philippines) and the Pacific Islands (Fiji, Mariana Islands, Norfolk Island, Tahiti) (Motyka 1936–38; Stevens 1991, 1999; Ohmura 2001, 2012; Galloway 2007). *Usnea nidifica* was recently reported for the Philippines from Mindanao (Bukidnon Province) by Timbreza *et al.* (2017). One specimen is recorded for Palawan (GBIF), but its identification needs to be confirmed. It is reported here for the first time from Negros (Balinsasayao Twin Lakes Natural Park).

Selected specimens examined. Philippines: Negros: Negros Oriental, Dumaguete City, Tacloban, Larena Drive, Balinsasayao Twin Lakes Natural Park, fernery behind restaurant, 909 m, 9.36083°N, 123.17846°E, planted edible ferns and coconut palms, on coconut tree, 2019, M. Dal Forno (with A. Gerlach & A. D. Nieten) 3483 (BRIT), DNA-code: PU33; *ibid.*, on coconut palm, 2019, A. Gerlach (with A. D. Nieten) AG 2019/636c (G), DNA-code: PU54; *ibid.*, 2019, M. Dal Forno 3496 (G), DNA-code: PU28; *ibid.*, road before the park entrance, trees by the road, 782 m, 9.36707°N, 123.18211°E, anthropized area, on fallen branch, 2019, M. Dal Forno 3554 (G), DNA-code: PU30. Palawan Island: Distr. Brooke's Point, along trail from Macagua, at E-foot, to summit of Mt Mantalingahan, 900 m, 26 iv 1991, H. Sipman & B. Tan (B 60 0083619).

Usnea norsticornuta A. Gerlach & P. Clerc sp. nov.

Mycobank No.: MB 848355

Differs from *U. cornuta* by the thicker cortex (6.5–8.2%–10) on average and a larger ratio axis/medulla (0.6–1.2–1.8(–2)), the presence of norstictic acid as the main medullary substance and by its phylogenetic position.

Type: Philippines, Mindanao, Davao del Sur, Marilog District, Davao City: Baganihan, Marilog Forest Reserve, 7.48936°N, 125.25365°E, 1279 m, 29 December 2019, Mt Malambo, open area with *Pinus* sp., A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/1005 (G—holotype). %C/M/A = 10/28.5/24; A/M = 0.8; M/C = 2.9; A/C = 2.4. Chemistry: usnic, salazinic, norstictic and protocetraric (trace) acids. GenBank Accession no.: OQ591858, DNA-code: PU11.

(Fig. 5)

Thallus erect-shrubby, up to 8 cm long; ramifications anisotomic-dichotomous; *trunk* concolorous with the branches; *branches* 0.9–1.5 mm diam., irregular; *segments* terete, sometimes slightly inflated; *lateral branches* slightly but distinctly constricted at the attachment point; *foveoles*, *maculae* and *pseudocypellae* absent; *papillae* rare, inconspicuous (early stages of fibrils?); *fibrils* slender, irregularly distributed; *fiberles* numerous especially on main branches; *soralia* small, punctiform, sometimes enlarging but remaining < 1/2 branch diameter, originating from small and young fiberles, irregularly shaped to ±circular when mature (top view), even with cortex to slightly stipitate (side view), surface

±plane to ±convex, without a cortical margin, usually numerous (9–16/0.25 mm²) but sometimes fewer to almost absent, sometimes aggregating but without losing their individuality; *isidiomorphs* few to numerous; *cortex* shiny, moderately thin to moderately thick (6.5–8.2%–10); *medulla* dense, moderately thin to thick, (21–)21.9–27.1%–32.3(–33.5); *central axis* thin to moderately thin (20–)21–29.8%–38.6(–42); A/M = 0.6–1.2–1.8(–2); M/C = 2.3–3.5–4.7(–5); A/C = (2.3–)2.4–3.5–4.6(–5); (n = 6).

Apothecia and *pycnidia* not seen.

Chemistry. Medulla K+ yellow turning red. TLC: salazinic, norstictic and ±protocetraric (trace) acids (n = 6).

Etymology. This name refers to the similarity with *Usnea cornuta* and the presence of norstictic acid in the medulla.

Taxonomic notes. *Usnea norsticornuta* belongs to the *Usnea cornuta* aggregate; it has an erect-shrubby sorediate thallus with slightly constricted lateral branches, minute soralia that are even with the cortex surface (Fig. 5) and a soft cortex when cut with a razor blade. It differs from *U. cornuta* s. str. by the thicker cortex ((3.0–)5.0–6.4%–7.8(–11.5), n = 93 in *U. cornuta* s. str.), a larger ratio A/M ((0.3–)0.5–0.8–1.1(–2.1) in *U. cornuta*) and a smaller ratio M/C ((2.2–)3.7–5.3–6.9(–10.5) in *U. cornuta* s. str.). It differs from all other species of the *U. cornuta* aggr. by the presence of norstictic acid as the main medullary substance (Gerlach *et al.* 2020).

Usnea pygmoidea (Asahina) Ohmura, another species belonging to the *U. cornuta* aggr. found in the Philippines, differs from *U. norsticornuta* mainly by the absence of norstictic acid and by the thinner, on average, cortex (3–8%). In eastern Asia, several species have norstictic acid (±salazinic acid, ±protocetraric acid) as the sole main medullary substance (Ohmura 2001): *U. dendritica*, *U. masudana* Asahina, *U. pseudogatae* Asahina and *U. sinensis* Motyka have numerous apothecia and no soralia; *U. rubicunda* Stirt. and *U. rubrotincta* Stirt. have a red-pigmented cortex; *Usnea baileyi* has a tubular cortex; *U. angulata* is a pendulous species with trapezoidal segments; *U. dasaea* has parts of branches with numerous and densely distributed spinulose fibrils; *U. glabrescens* s. lat. has larger soralia and a jet black-pigmented basal part; *U. praetervisa* (Asahina) P. Clerc has a jet black-pigmented basal part and a different type of C/M/A; *U. nidifica* has irregular soralia originating in ±longitudinal, irregular cracks in the cortex (see under that species).

Phylogenetic notes. The specimen PU11 is a singleton phylogenetically close to *U. himalayana* and *U. nidifica*. It is not related to any other species of the *Usnea cornuta* aggregate distinguished by Gerlach *et al.* (2020) (Fig. 2E).

Distribution. Known so far only in the Philippines archipelago: Mindanao (Marilog Forest Reserve), Negros (Cuernos de Negros) and Luzon.

Selected paratypes. Philippines: Negros: Negros Oriental, Dumaguete City, Santa Catalina, San Pedro, Cuernos de Negros, 1523 m, 9.24918°N, 123.12500°E, forest going down past peak Hapon Hapon to Kanaway, fallen *Usnea*, close to mossy fern forest, 2019, A. Gerlach (with M. Dal Forno & A. D. Nieten) AG 2019/817 (BRIT). Luzon: Pampanga Province, Camp Stotsenburg (Mt Pinatubo) 1927, A. D. E. Elmer 22062 (B 56256, B 37149).

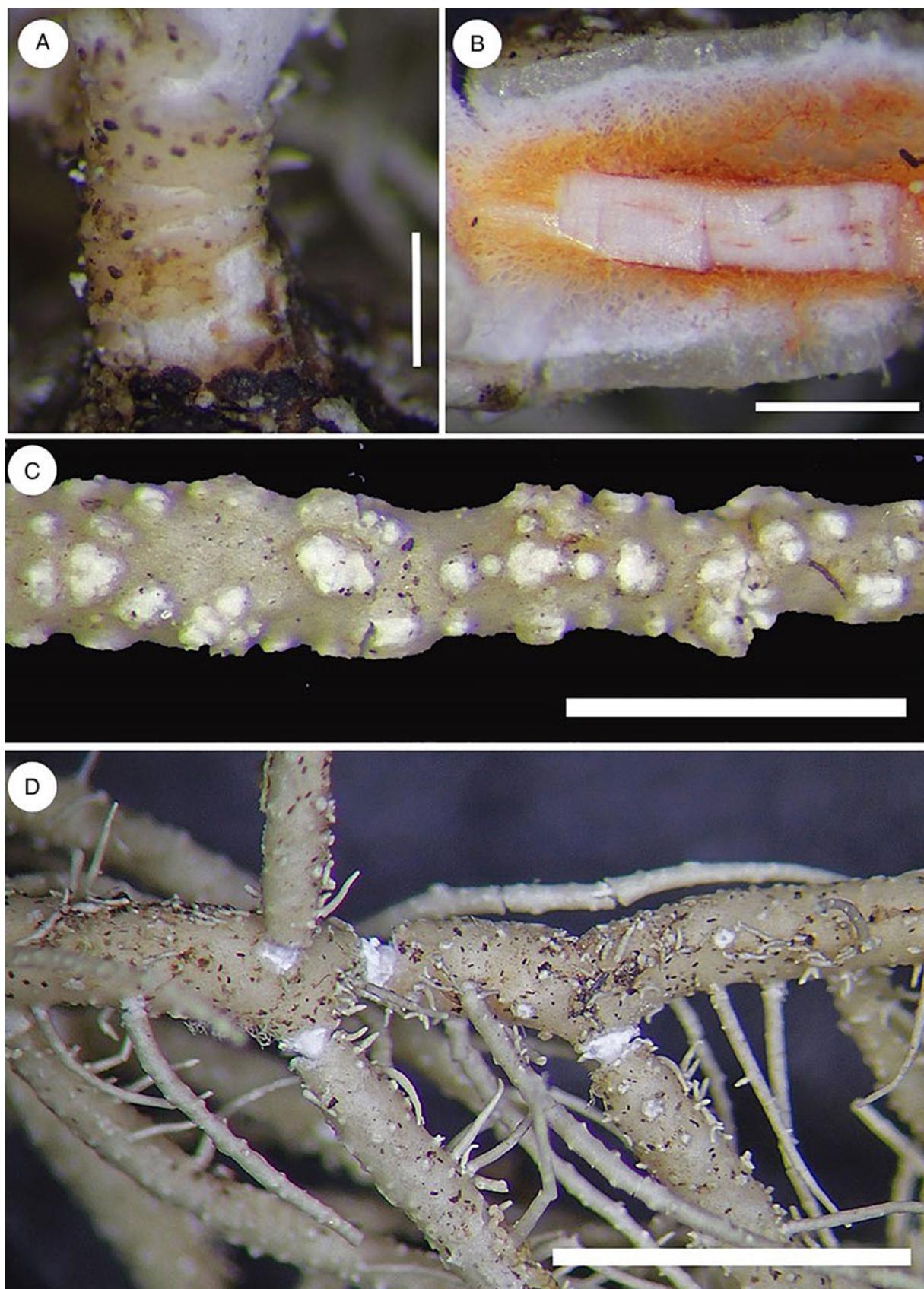


Figure 5. *Usnea norsticornuta* (PU11). A, trunk concolorous with the branches. B, section of branch. C, soralia punctiform, even with cortex to slightly stipitate, sometimes aggregating. D, branch segments slightly inflated and lateral branches slightly constricted. Scales: A = 0.5 mm; B-D = 1 mm. In colour online.

Usnea paleograndisora A. Gerlach & P. Clerc sp. nov.

Mycobank No.: MB 848357

Usnea paleograndisora is characterized by an orange subcortical pigmentation not continuous in the whole thallus, in combination with enlarging and excavate soralia and the presence of galbinic acid. It has a moderately thick (on average) and shiny cortex.

Type: Philippines, Mindanao, Davao del Sur, Marilog District, Davao City, Baganahan, Marilog Forest Reserve, 1215 m, 7.46423°N, 125.25430°E, 30 December 2019, trail with native plants close to a new road, on branches, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/1008b (G—holotype). Chemistry: usnic, salazinic, galbinic and norstictic acids. %C/M/A = 8/26.5/31; A/M = 1.1; A/C = 3.8; M/C = 3.3. GenBank Accession no.: OQ591859, DNA-code: PU42.

(Fig. 6)

Thallus shrubby entangled, up to 8 cm long; *ramifications* anisotomic-dichotomous; *trunk* concolorous with the branches; *branches* 0.5–1.4 mm diam., tapering to slightly irregular; *segments* terete, not inflated; *lateral branches* not to slightly constricted at the attachment point; *foveoles* and *maculae* absent; *papillae* rare, inconspicuous (early stages of fibrils?); *fibrils* usually spinulose (to 3 mm), often densely covering the branches, often present on the whole thallus or more rarely covering only some branches; *soralia* large ($\geq 1/2$ branch diameter) on terminal branches; circular to sometimes encircling the branches exposing the central axis; even with cortex to \pm excavate; concave to plane,

when circular and \pm plane then with a thin but distinct cortical margin, dense on the terminal branches and on the apices of fibrils; aggregating to form large consoralia at terminal branches and fibrils; *isidiomorphs* few to abundant, remaining short within the soralia; *isidiofibrils* present (?), inconspicuous; *cortex* moderately thin to moderately thick (7.5–8%–8.5), shiny, sometimes with faint orange patches due to the subcortical pigmentation; *medulla* moderately thick (25.5–26.6%–28), dense, with a weak to strong orange, thin subcortical pigmentation continuously or irregularly distributed along the branches; *axis* moderately thin, (30–31%–32); ($n = 8$).

Apothecia and *pycnidia* not seen.

Chemistry. Medulla K+ yellow turning red. TLC: usnic, salazinic, norstictic and galbinic acids ($n = 7$).

Etymology. The name refers to the morphological similarity with *Usnea grandisora* Truong & P. Clerc and their geographical distribution in the Palaeotropics.

Taxonomic notes. *Usnea paleograndisora* is characterized by the shrubby entangled thallus with more than one attachment point to the substratum, by the presence of a thin orange subcortical pigmentation (sometimes not continuous), by the lateral branches not- to slightly constricted (Fig. 6), and by the presence of galbinic acid as main medullary chemistry. The soralia are large, circular to irregular, covering the terminal branches and fibrils, concave to plane and \pm excavate, never stipitate. In addition, the cortex is moderately thick (on average) to thick, shiny in

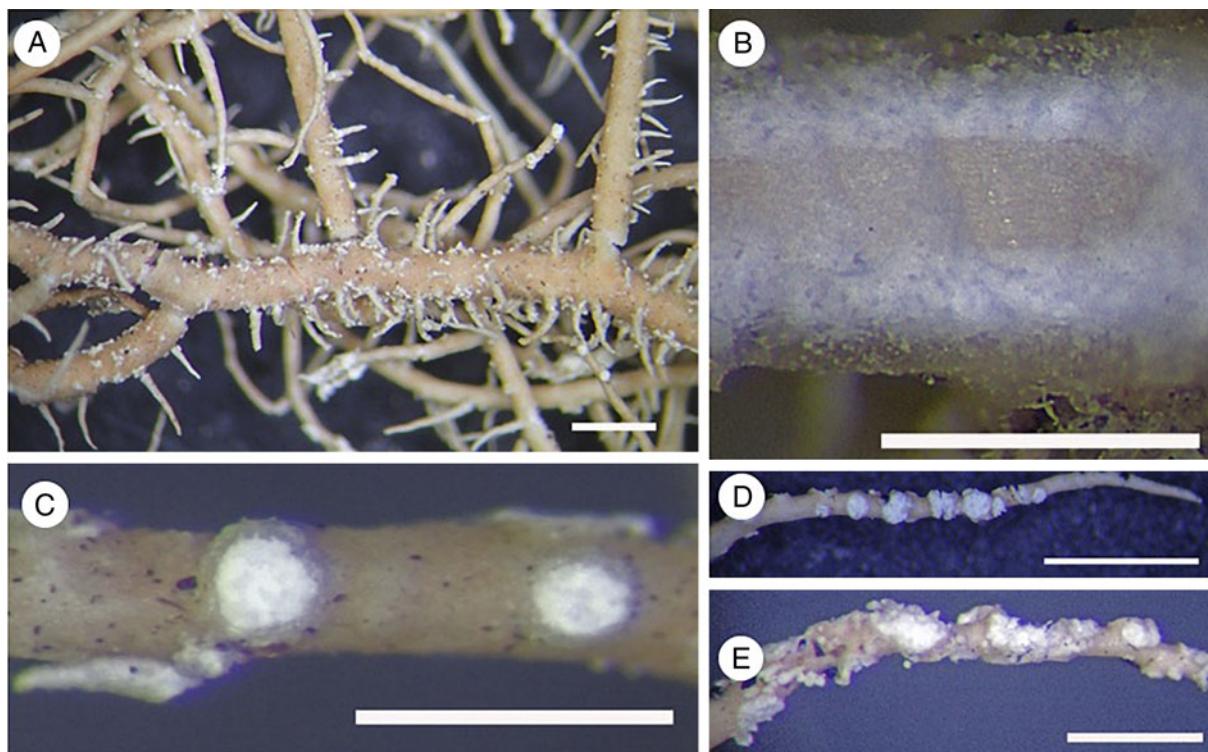


Figure 6. *Usnea paleograndisora* (PU42). A, branch covered by spinulose fibrils, with a faint red pigmentation and slightly constricted lateral branches. B, section of branch. C, soralia with a distinct cortical margin. D, large consoralia at terminal branches. E, excavate soralia at terminal fibrils with isidiomorphs. Scales: A & D = 1 mm; B, C & E = 0.5 mm. In colour online.

longitudinal section. The density of spinulose fibrils can vary greatly among specimens from few to numerous, as can the disposition from regular to irregular.

Usnea grandisora has the same type of soralia, but without a distinct cortical rim when circular and plane. The subcortical pigment is much stronger in this species and thus visible through the cortex, giving a distinct reddish colour to the thallus. Furthermore, and this is the most important and significant difference, *U. grandisora* has a much thinner medulla ((9.5–)13.7–18.1%–22.5(–26), $n = 15$), a thicker cortex ((8.5–)9.2–11.2%–13.2 (16)) and central axis ((29–) 31.9–41.3%–50.7(–58)), with a higher A/M ((1.1–)1.2–2.5–3.8(–6)) and lower M/C ((0.9–)1.2–1.7–2.3(–2.7)). The presence of *U. grandisora* in the Philippines (Paguirigan *et al.* 2020) needs to be checked.

Usnea subdasaea Truong & P. Clerc, another neotropical species (widely distributed in South America), shares with *U. paleograndisora* the subcortical pigmentation and the same chemistry, but differs by having a thinner cortex ((3–)4.6–6.4%–8.2(–9.5), $n = 14$), by the more constricted lateral branches and by the minute, plane to stipitate soralia, rarely enlarging or fusing in irregular patches (Truong *et al.* 2011). The presence of *U. subdasaea* in the Philippines (Paguirigan *et al.* 2020) is dubious and needs to be checked.

Usnea sorediosula Motyka, an African species, also with a shrubby-sorediate thallus, with a red-orange subcortical pigment, differs from *U. paleograndisora* mainly by the absence of galbinic acid (protocetraric acid instead). Moreover, the lateral branches are not constricted, the soralia are punctiform (not large as in *U. paleograndisora*) and the cortex and central axis are thicker (8–10% and 40–50% respectively) (Nadel & Clerc 2022). According to these authors, the occurrence of this species in the Philippines (Galinato *et al.* 2018) is dubious and should be checked. Furthermore, *U. sorediosula* is phylogenetically unrelated to *U. paleograndisora* (Fig. 2B & C).

Usnea bicolorata Motyka, another African species with a subcortical orange pigment, differs from *U. paleograndisora* mainly by the jet black-pigment and by the *cornuta-tenuicorticata* type of C/M/A (M/C = 4.4–6–7.8(–8)) (Nadel & Clerc 2022).

Usnea dorogawensis Asahina differs from *U. paleograndisora* by the inflated branches, the concave soralia with granular soredia and few isidiomorphs, and by the presence of stictic and lobaric acids (Ohmura 2001). For differences with *U. spinulifera*, see under that taxon.

Phylogenetic notes. There are three sequenced specimens from the Philippines (PU42, PU47, PU48) in a highly supported clade (BP = 100) (Fig. 2B). At first glance, *U. paleograndisora* is closely related to *U. subdasaea*, *U. spinulifera* and *U. dasaea*. However, their relationship is not supported by ITS phylogeny. The relationship with *Usnea grandisora* remains unknown until the type of this species is sequenced using NGS sequencing methodology.

Distribution. *Usnea paleograndisora* is known only from the Philippines, specifically from Mindanao (Marilog Forest Reserve). The species occurs on branches of trees (e.g. *Medinilla* sp., *Pinus* sp.).

Selected paratypes. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1200 m, 7.46245°N, 125.25488°E, on upwards trail, on thin branches, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/1018b (G), DNA-code: PU48; *ibid.*, 1186 m,

close to Mt Malambo, CMU nursery, anthropized environment, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/998b (BRIT), DNA-code: PU47.

Usnea pectinata Taylor

London J. Bot. **6**, 191 (1847); type: Bangladesh, Sylhet, *Wallich* s. n. (FH—holotype; M—isotype!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids (isotype).

U. schadenbergiana Göpp. & Stein. *Jahresber. Schles. Gesellsch. f. Vaterl. Kultur* **60**, 228 (1882); type: Philippines, Siriban in Mindanao, an Laurineen-Aesten im Aufstieg zum Vulkan Apo bei etwa 1600 m, *Schadenberg* s. n. (G, S—isotypes!). %C/M/A = 7/6/74; A/M = 12.5; A/C = 10.5; M/C = 0.8 (isotype—G). Chemistry: usnic, norstictic, menegazziaic, cryptostictic, stictic and constictic acids.

Usnea squarrosa Vain. *Philipp. J. Sci.*, C, *Bot.* **4**(5), 654 (1909); type: Philippines, Mindanao, Castra Keithley prope lacum Lanao, Mary Strong Clemens 1308: Prov. Zamboanga, Port. Banga, For. Bur. 9396 *Whitford* & *Hutchinson* (TUR-V—syntypes!). %C/M/A (573) = 8/11/63; A/M = 5.8; A/C = 8; M/C = 1.4. %C/M/A (574) = 3/9.5/74; A/M = 7.7; M/C = 3; A/C = 24.6. %C/M/A (572) = 4/15.5/62; A/M = 4; M/C = 4; A/C = 15.8. Chemistry: diffractaic, salazinic and protocetraric (trace) acids.

U. misamensis (Vain.) Motyka, *Lich. Gen. Usnea Stud. Monogr. Pars Syst.* **2**, 418 (1938). —*Usnea longissima* Ach. var. *misamensis* Vain. *Philipp. J. Sci.* **4**, 655 (1909); type: Philippines, Mindanao, Prov. Misamis, Mt Malindang, 5.1906, E. A. Mearns & W T Hutchinson 4807 (TUR-V 599—holotype!). %C/M/A = 9.5/20/42; A/M = 2.1; A/C = 4.5; M/C = 2.1 (holotype). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

Usnea hossei Vain. *Ann. Soc. Zool. Bot. Fenn. Vanamo* **I**, 34 (1921); type: Thailand, Siam, Dio Sutep, 1675 m, 1904, C. C. Hosseus s. n. (TUR-V 475—holotype!). %C/M/A = 6.5/12.5/62; A/M = 5; A/C = 9.5; M/C = 2 (TUR-V 477); %C/M/A = 6.5/13.5/60; A/M = 4.5; A/C = 9; M/C = 2 (TUR-V 475). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids.

For a complete description and figures, see Ohmura (2001, 2012) and Nadel & Clerc (2022).

Thallus pendulous, often entangled with the substratum; *trunk* concolorous with the main branches, sometimes with a reddish tinge in the first mm below the first ramifications, with several attachment points to the substratum; *lateral branches* often slightly broadened at ramification point; *cracks* often inconspicuous, usually present and annular, few to numerous, sometimes with cortex regeneration areas between the segments, sometimes irregular giving a decorticate appearance in some branches (B 600146192); *branches* irregular (longitudinal section) and often terete (transversal section), rarely with papillae giving an angular aspect to some main branches (B 600143608); *maculae* often faint, punctiform to irregular, to distinct (salazinic strain); *pseudocyphellae* often absent, linear when present; *fibrils* long and slender, few to numerous, irregularly distributed; *soralia* minute, circular to irregular at edges of cracks, stipitate, capitate, cortical rim indistinct, few to numerous, distinct; *cortex* thin to thick (4–9%–16), shiny to matt; *medulla* thin to moderately thin (8–12%–19), dense to compact; *central axis* moderately thick to thick on average (38.5–57.5%–71), often fistulous at least in part of the axis, often with a brown-yellowish pigmentation (B 600146192, AG 1004). %C/M/A = 7–10.5–16/8–14–19/38.5–54–71; ($n = 19$).

Chemistry. 1) Medulla K+ yellow; TLC: stictic, cryptostictic, menegazziaic, constictic and norstictic acids, \pm fatty acid ($n = 10$). 2) Medulla K-, P+ red; TLC: protocetraric acid, \pm fatty acid ($n = 3$). 3) Medulla K+ yellow turning red; TLC: salazinic, norstictic and \pm protocetraric (trace) acids ($n = 2$). 4) Medulla K+ yellow turning red; TLC: salazinic and constictic acids ($n = 1$). 5) Medulla K+ yellow turning red; TLC: barbatic, salazinic and 4-O-demethylbarbatic acids ($n = 1$).

Taxonomic notes. *Usnea pectinata* is treated in the broad sense; all specimens studied here shared a pendulous thallus with an almost solid, brown- to yellow-pigmented axis that only partially becomes fistulate. The lateral branches are often slightly broadened at the base, the cortex is moderately thick to thick on average (>9%), the medulla is thin to moderately thin (8–12%–19), and the axis is \pm thick to thick (38.5–57.5%–71). The base is sometimes reddish tinged. The main branches can be decorticated like those in the type of *U. pectinata* (B 45057, B 56989 thallus number one) or more or less smooth, when irregular cracks are few or absent (B 56989 thallus number two). The presence of maculae on the cortex surface is often faint, being strong and punctiform in only one specimen (AG 627a). One herbarium specimen identified as *Usnea angulata* (B 600143608) corresponds to the extreme variability found in the *Usnea pectinata* aggr. in the Philippines: it is a coarse morphotype with numerous papillae occurring in ridges that develop longitudinally or at angles along the main branches, forming more or less angulate plates, and stictic acid as main medullary chemistry.

The *Usnea pectinata* aggr. is extremely variable in morphology (even if we looked at different branches in the same thallus) and also in chemistry; for this reason, this group should be reviewed using molecular techniques to verify the taxonomic value of the chemotypes and better understand the variation found in this species. Many names may be resurrected in the future and some cryptic species may be revealed.

Phylogenetic notes. Five sequenced specimens from the Philippines (PU15, PU17, PU29, PU32, PU49) clustered into a well-supported clade named *Usnea pectinata* aggregate (or *Eumitria pectinata* aggregate) (Fig. 2A). The sequenced specimens (YO 2989, YO 4373) correspond well to the type and Ohmura (2012) also mentioned decorticate main branches for Taiwan specimens. The five sequenced specimens from the Philippines do not have really decorticated main branches as shown by Ohmura (2012, fig. 24C) but annular cracks in the main branches which can present medullary tissue in between when well developed (very visible in PU49). These specimens clustered within a small ‘Asian subclade’. Moreover, the sequenced specimens do not contain stictic acid as is present in *U. pectinata*. Instead, the chemistry of this ‘small Asian clade’ is also surprising: protocetraric (with or without diffractaic) and salazinic plus diffractaic acids.

From all specimens with stictic acid analyzed from the Philippines, we obtained only one sequence (PU17). Its position is not phylogenetically close to the Asian specimens of *U. pectinata* (YO 2989, YO 4373 and Li308). The long branches and a lack of support indicate that it is not conspecific with these Asian specimens or those from Africa (Fig. 2A). It could represent *Usnea schadenbergiana*, the older name for the stictic acid chemotype. However, we refrain from using this name here due to the fact that morphologically we cannot separate the samples of the stictic acid chemotype found in the Philippines from those found in Japan and Taiwan. The phylogeny of the *U. pectinata*

clade is quite complicated, with several lineages in Africa and Asia (Temu *et al.* 2019; Lücking *et al.* 2020; Nadel & Clerc 2022; Temu *et al.* 2022), and we may be facing a complex of cryptic species here but more studies are required before making a decision. A deeper study with molecular tools and taking into account all the species and geographical range is necessary to understand the taxonomic boundaries in this complex aggregate.

Distribution. *Usnea pectinata* is widely found in the Philippines. It has been reported from the islands of Luzon and Mindanao (Bukidnon Province) by Herre (1963), Gruezo (1979), Sipman *et al.* (2013) and Timbreza *et al.* (2017). It is recorded here for the first time from Negros and Palawan. The specimens analyzed here occur mainly in secondary forest, planted edible ferns and coconut palms, over coconut palm bark.

Selected specimens examined. **Philippines:** *Mindanao*: Davao del Sur, Marilog District, Davao City, Baganahan, Marilog Forest Reserve, 1227 m, 7.45938°N, 125.25106°E, anthropized environment, on *Pinus*, 2019, A. Gerlach (with *M. Dal Forno* & *J. Nobleza*) AG 2019/996c (G), DNA-code: PU17; *ibid.*, 1095 m, open road, disturbed, close to the main road near Lawi Lawi Resort, 2019, A. Gerlach (with *Dal Forno* & *J. Nobleza*) AG 2019/979 (BRIT), DNA-code: PU15. *Negros*: Negros Oriental, Dumaguete City, Balinsasayao Twin Lakes Natural Park, 893 m, 9.35281°N, 123.18253°E, on fallen branches, 2019, A. Gerlach (with *A. D. Nietes*) AG 2019/627 (BRIT); Negros Oriental, Dumaguete City, Taclobo, Larena Drive, Balinsasayao Twin Lakes Natural Park, fernery behind restaurant, 909 m, 9.36083°N, 123.17846°E, on coconut tree, 2019, *M. Dal Forno* (with *A. Gerlach* & *A. D. Nietes*) 3482 (BRIT), DNA-code: PU32, 3497 (G), DNA-code: PU29; *ibid.*, on coconut palm, 2019, A. Gerlach (with *A. D. Nietes*) AG 2019/636a (G), DNA-code: PU49. *Palawan*: Distr. Brooke’s Point, along trail from Macagua, at E-foot, to summit of Mt Mantalingahan, 1100 m, in mossy primary forest on ridge, 1991, *H. Sipman* & *B. Tan* 29976 (B 83618).

Usnea cf. pygmoidea (Asahina) Y. Ohmura

J. Jpn. Bot. **43**, 130 (1968).—*Usnea confusa* Asahina subsp. *pygmoidea* Asahina; type: Japan, Honshu, Prov. Kai, Yoshida-guchi 1-gome, Mt Fuji, 10.8.1952, *M. Togashi* s. n. (TNS—holotype!). Chemistry: usnic, norstictic, menegazziaic, stictic and constictic acids (Ohmura 2001).

Taxonomic notes. *Usnea pygmoidea* belongs to the *U. cornuta* aggregate; for a full description of *U. pygmoidea*, see Ohmura (2001, 2012). It is recognized by the inflated branches which are glossy on the surface, the stipitate and irregularly elongated soralia, the presence of granular soredia together with isidiomorphs (Fig. 7B–D), and the presence of salazinic or stictic acids as major substances (Ohmura 2001). The cortex is thin to moderately thin (3–8%), the medulla lax, moderately thick to thick (26–40%), and the central axis thin (13–33%) (Ohmura 2001). The specimen analyzed here has a similar morphology, anatomy (%C/M/A: 4.5/34.5/22) and chemistry (stictic acid as main medullary compound), differing from *U. pygmoidea* by its black base (Fig. 7A) and by its ITS sequence. *Usnea pygmoidea* (sorediate) is considered as the secondary species of *U. orientalis* Motyka (apothecia) in the species pair concept (Shen *et al.* 2012). In our phylogenetic analysis, their relationship is unresolved (Fig. 2C).

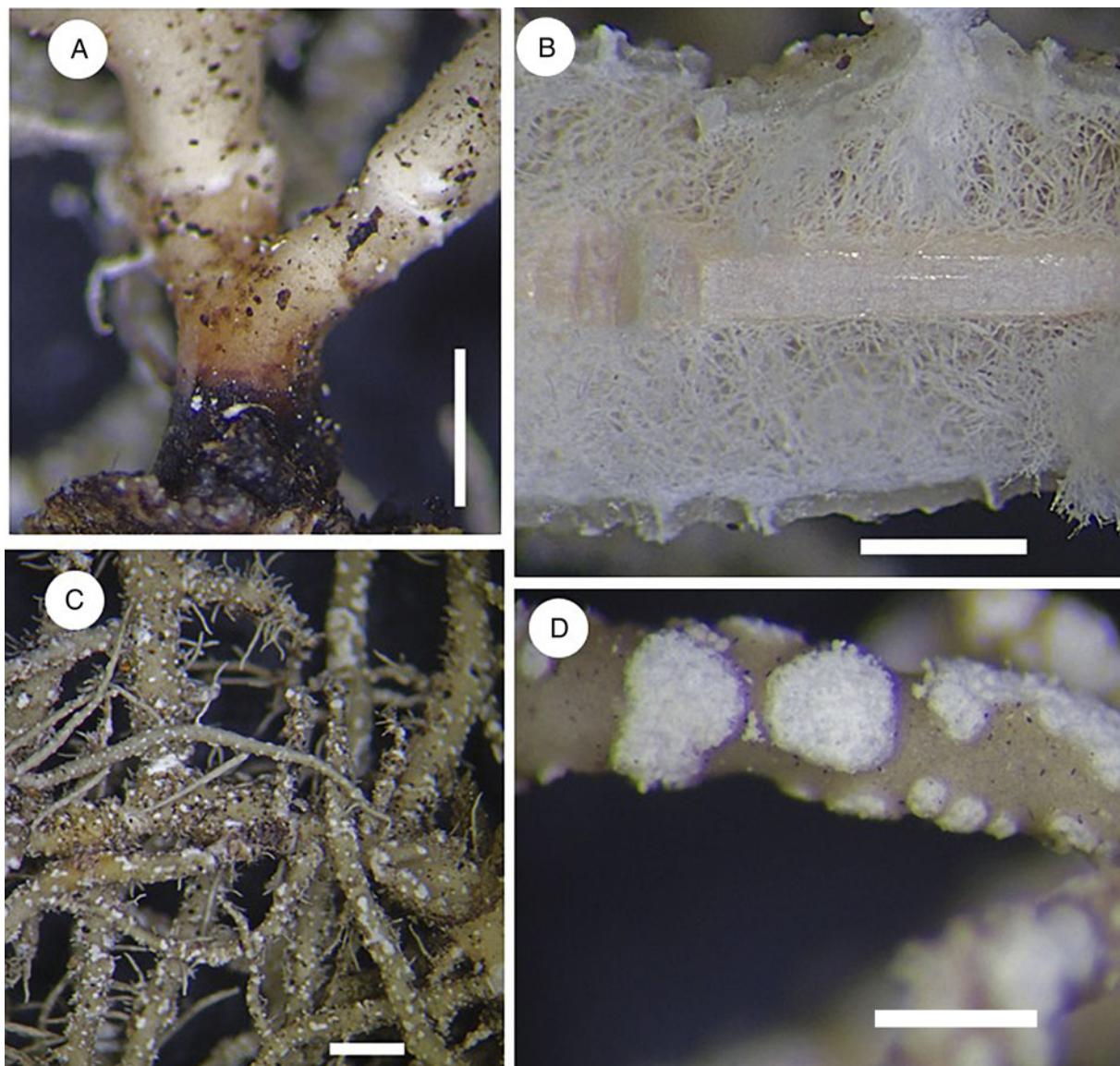


Figure 7. *Usnea* cf. *pygmoidea* (PU40). A, black base. B, section of branch. C, general aspect of the thallus showing many soralia, isidiomorphs and isidiofibrils. D, stipitate and irregular elongated soralia. Scales: A & D = 0.5 mm; B & C = 1 mm. In colour online.

Phylogenetic notes. The specimen PU40 is a singleton close to *Usnea articulata* (BP = 89; Fig. 2E), and not related to *U. pygmoidea* from Japan (YO 3144c, YO 2736) (Fig. 2C). The specimen studied here probably belongs to a new taxon, despite its aforementioned phenotypic similarities.

Distribution. *Usnea pygmoidea* occurs in Japan and Taiwan (Ohmura 2001). It was reported for the Philippines in Mindanao by Timbreza *et al.* (2017) and Galinato *et al.* (2018).

Specimen examined. Philippines: Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1202 m, 7.45392°N, 125.24509°E, close to the main road to the Lawi Lawi Resort, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/909 (G), DNA-code: PU40.

Usnea rubicunda Stirz.

Scott. Natural. 6, 102 (1881); type: England, 1879, Holmes (BM—holotype). Chemistry: usnic, stictic, constictic, menegazziaic and norstictic acids (Ohmura 2001).

For a complete description and figures, see Ohmura (2001, 2008).

Thallus erect-shrubby to subpendulous; **trunk** concolorous with the thallus, often single, sometimes with several attachment points to the substratum; **lateral branches** cylindrical at ramification point; **branches** cylindrical and terete; **soralia** minute, circular, stipitate, without distinct cortical margin, few to numerous, with few to numerous isidiomorphs, present on main branches and sometimes also on the fibrils; **cortex** with a red pigmentation on the cortex surface, often homogeneous and diffuse in the whole thallus, or rarely with spots of red pigmentation,

moderately thick to thick (8–12%–15), shiny, sometimes vitreous; *medulla* thin to moderately thick (13–20%–29), dense to compact; *central axis* moderately thin on average (26–35.5%–54). %C/M/A = 8–12–15/13–20–29/26–35.5–54 with an A/M = (0.8–2–4); A/C = 1–1.7–3.6; M/C = 2.2–3–5.4; (n = 5).

Chemistry. Medulla K+ yellow. TLC: stictic, cryptostictic, menegazziaic, constictic and norstictic acids (n = 5).

Taxonomic notes. *Usnea rubicunda* can be easily recognized by the erect-shrubby to subpendulous thallus, with lateral branches cylindrical at ramification point, by the thick and shiny cortex, with a red pigment which is often diffuse (homogeneous) in the whole thallus, the stipitate and rounded soralia with many isidiomorphs, and by the presence of stictic acid. *Usnea rubrotincta* is a similar species, also red-pigmented in the cortex. It differs mainly by the morphology of the soralia and the subterminal and terminal branches (Ohmura 2008) and by the chemistry (salazinic acid instead of stictic), although this last character might not have the same value in different parts of the world. In Japan, for instance, it clearly separates both species but not in Taiwan (Y. Ohmura, personal communication). The pattern of pigmentation in this species is also quite different from the one in *U. rubrotincta* (see under *U. rubrotincta* for more details).

Phylogenetic notes. Three ITS sequences from the Philippines (PU27, PU51, PU53) clustered into two phylogenetically close clades: *rubicunda*-1, with one specimen from Taiwan and *rubicunda*-2 with one specimen from Japan (Fig. 2E). *Usnea rubicunda* is a polyphyletic taxon (Truong et al. 2013a; Lücking et al. 2020). Given that the type of *U. rubicunda* is from Great Britain (Stirton 1881), we follow Lücking et al. (2020) and consider the cluster including all specimens from Great Britain and several from South America as *U. rubicunda* s. str. (Fig. 2E).

Distribution. *Usnea rubicunda* was reported from the Philippines for Luzon (Benguet, Ifugao, Kalinga, Nueva Vizcaya) and Mindanao (Bukidnon) Islands by Herre (1963), Gruezo (1979), Bawingan et al. (2000), Santiago et al. (2013) and Galinato et al. (2017). It is the first record for Negros.

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganahan, Marilog Forest Reserve, 1188 m, 7.45960°N, 125.24522°E, disturbed forest, abandoned house, on *Pinus* sp., 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/950b (G), DNA-code: PU53. Negros: Negros Oriental, Dumaguete City, Santa Catalina, San Pedro, Cuernos de Negros, 1337 m, 9.24099°N, 123.11667°E, open area close to camping site, from the canopy of trees, 2019, A. Gerlach (with M. Dal Forno & A. D. Nietes) AG 2019/847 (BRIT, PNH), DNA-code: PU51; Dumaguete City, Tacloba, Larena Drive, Balinsasayao Twin Lakes Natural Park, fernery behind restaurant, 909 m, 9.36083°N, 123.17846°E, planted edible ferns and coconut palms, on coconut tree, 2019, M. Dal Forno (with A. Gerlach & A. D. Nietes) 3494 (BRIT), DNA-code: PU27.

Usnea rubrotincta Stirt.

Scott. Natural. 6, 103 (1881).—*Usnea rubescens* var. *rubrotincta* (Stirt.) Motyka, *Lich. Gen. Usnea Stud. Monogr. Pars Syst.* 2, 348 (1937); type: Madeira, Funchal, J. Payne s. n. (BM—

holotype!). Chemistry: usnic, norstictic, protocetraric and salazinic acids (Ohmura 2001).

For a complete description and figures, see Ohmura (2001).

Thallus erect-shrubby to subpendulous; *trunk* concolorous with the thallus, single; *lateral branches* cylindrical at ramification point; *branches* cylindrical and terete; *soralia* minute, circular, stipitate, without distinct cortical margin, few to numerous, with few to numerous isidiomorphs, present mainly in fibrils; *cortex* with a red pigmentation on the cortex surface, often in spotted pattern, thick (10–11%–12), shiny; *medulla* thin (15–20%–30), compact; *central axis* moderately thick (20–37.5%–47); (n = 3).

Chemistry. Medulla K+ yellow turning red. TLC: salazinic, norstictic and protocetraric (trace) acids (n = 3).

Taxonomic notes. *Usnea rubrotincta* can be recognized by the shiny and thick cortex (10–12%), the moderately thick central axis (20–47%), the spotted red pigmentation pattern at the cortex surface, and by the soralia that occur mainly in the fibrils.

Phylogenetic notes. We have only one sequenced specimen (PU06) that clustered within an *Usnea rubrotincta* clade from Japan and Taiwan with good support (BP = 96) (Fig. 2E). Lücking et al. (2020), with an expanded ITS global tree, suggested that *Usnea rubrotincta* (type from Madeira) could represent two different species. Again, to clarify the position of *Usnea rubrotincta* the type should be sequenced and further analyses using multilocus data should be performed.

Distribution. The species was reported for the Philippines from the islands of Luzon and Mindanao (Bukidnon) by Herre (1963), Gruezo (1979) and Timbreza et al. (2017).

Specimen examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganahan, Marilog Forest Reserve, after the first cave, edge of a forest close to the river, 1169 m, 7.46024°N, 125.25790°E, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/891b (BRIT), DNA-code: PU06.

Usnea spinulifera (Vain.) Motyka

MycoBank No.: 10013630

Lichenum Generis Usnea, Pars systematica 518 (1936–38).—*Usnea florida* var. *perplexans* f. *spinulifera* Vain.; type: Brasilia, Minas, Lafayette, 1000 m, ad ramulos arborum, 1885, E. Vainio (TUR-V 828—lectotype designated here, MBT10013630). Chemistry: usnic, salazinic, norstictic and galbinic acids. %C/M/A = 6/30.5/27; A/M = 0.9; A/C = 4.4; M/C = 5.1.

(Fig. 8)

(Typus). *Thallus* shrubby and ±soft, up to 6 cm long, with mainly anisotomous-dichotomous ramifications; *basal part* short, branching off just above the holdfast, concolorous with main branches; *main branches* 0.6–1.2 mm thick, irregular in longitudinal section, terete in transversal section, not distinctly segmented; *segments* cylindrical to slightly swollen, terete in cross-section; *lateral branches* slightly constricted at attachment point; *terminal branches* moderately thin with few ramifications; *foveolae* and

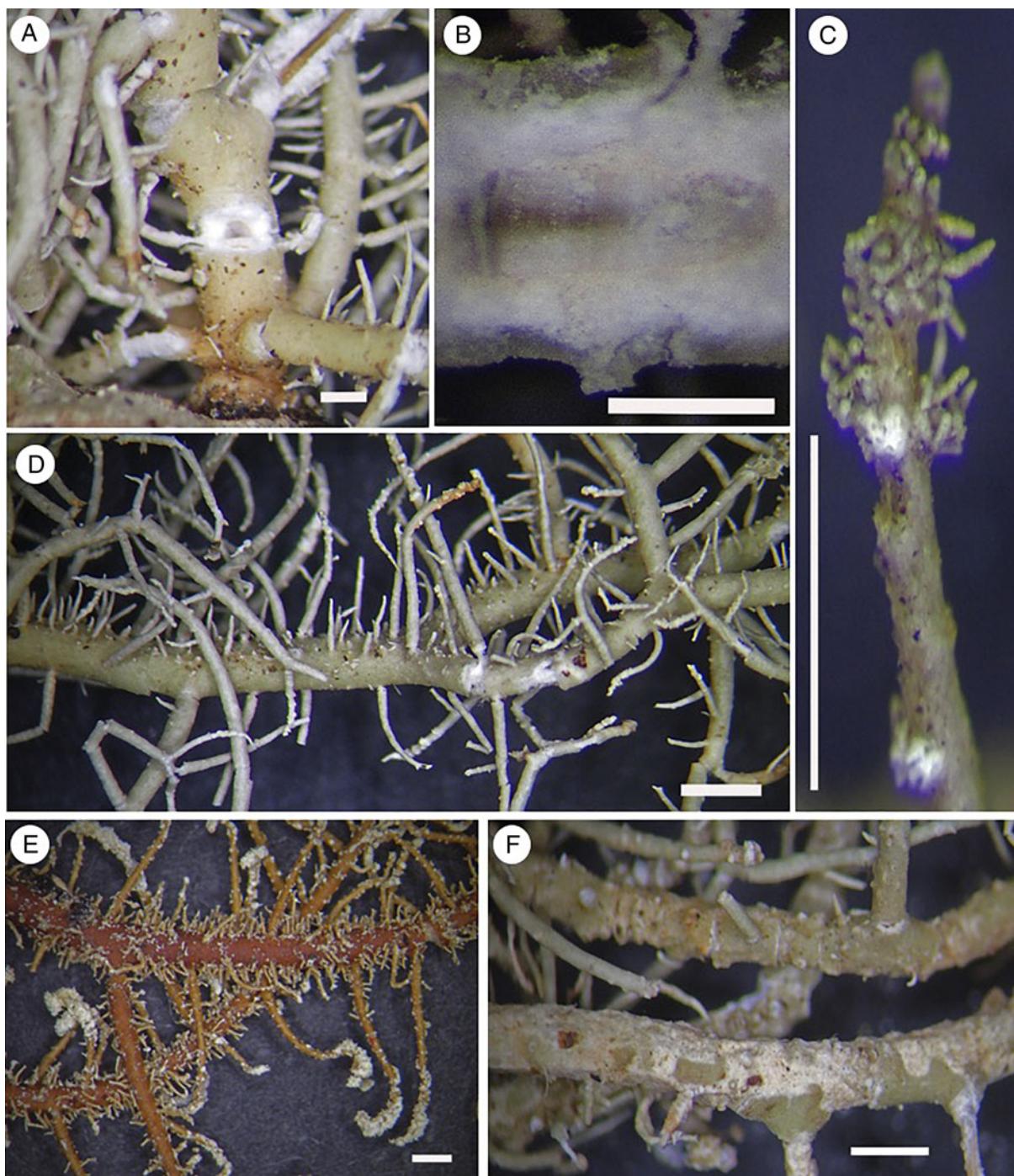


Figure 8. *Usnea spinulifera* (A–D, PU20; E, TUR-V—lectotype). A, basal part short, branching off just above the holdfast, concolorous with main branches. B, section of branch. C, soralia fuse together with many isidiomorphs at end of fibril; D, branch covered with spinulose fibrils and slightly constricted lateral branches; E, general aspect of thallus showing whitish club-like bulk of soralia at curved apices of fibrils. *Usnea angulata* (PU04). F, branch covered with schizidia. Scales: A, D & E = 1 mm; B, C & F = 0.5 mm. In colour online.

transverse furrows rare; *maculae* and *pseudocypellae* absent; *papillae* absent; *tubercles* absent; *fibrils* spinulose, up to 1 mm long (most of them) to longer (up to 2 mm) and \pm slender, densely arranged on main and secondary branches; *fibercles* few on main and secondary branches, numerous in terminal parts, turning into soralia; *soralia* large when mature, 120–200 μm , larger than half the diameter of the branch, \pm circular in top view, even with the cortex in side view, surface plane to

slightly convex, cortical rim indistinct, spaced, 5–8 soralia/0.25 mm^2 , except at the extremities of branches where they typically fuse together building a thick and \pm curved, whitish club-like bulk of soredia and isidiomorphs (consoralia) with the axis left naked at the extremity of the terminal branch when all the soredia are shed, localized mostly at the apices of the thallus; *isidiomorphs* short and frequent, in young and mature soralia; *isidiomorfils* not rare. *Cortex* shiny, thin, of the *merrillii*-type

plectenchyma ((6–)6.6–8.5%–10.4(–12)) ($n = 18$); *medulla* thick, dense, often orange-pigmented close to the central axis ((15.5–)22.4–26.6%–30.8(33.5)); *axis* thin ((20–)24–29.7%–35.4(–44)); A/M = (0.6–)0.7–1.2–1.7(–2.8); A/C = (2.2–)2.8–3.6–4.4(–5.5); M/C = (1.3–)2.2–3.4–4.6(–5.8). C/M/A of the *cornuta*-type.

Apothecia and *pycnidia* not seen.

Chemistry. Medulla K+ yellow turning dark red, P+ orange-red. TLC ($n = 1$): salazinic, norstictic and galbinic acids.

Taxonomic notes. Based mainly on the galbinic acid chemistry and the presence of densely distributed spinulose fibrils, *Usnea spinulifera* was synonymized with *U. dasaea* Stirt. by Clerc & Herrera-Campos (1997). However, phylogenetic evidence (Fig. 2B) coupled with detailed morphological and anatomical investigations make the clear separation of both taxa possible. *Usnea spinulifera* differs from *U. dasaea* mainly by the soralia that become enlarged, especially at the apices of branches where they fuse and build whitish club-like thick and sometimes spinulose (isidiomorphs) consoralia ending abruptly at the branches. Specimens from the Philippines have an inconspicuous, irregularly distributed light orangish subcortical pigmentation. However, the type specimen from Brazil and all specimens collected in Brazil and identified as *U. spinulifera* lack an orange subcortical pigmentation. This variability supports the observation that in the *U. dasaea* aggr. the subcortical pigment might not be a constant character (Gerlach et al. 2019).

Phylogenetic notes. Four specimens from the Philippines (PU20, PU05, PU08, PU39) clustered in a well-supported clade (BP = 100) with two specimens from Brazil (39BR, 33BR). *Usnea dasaea* (type from Portugal) presents a wide list of synonyms, including *U. spinulifera* (Clerc & Herrera-Campos 1997). Gerlach et al. (2019) suggested for the first time that *U. dasaea* is polyphyletic and only two ITS sequences (JN086283 and JN086284) would indicate the phylogenetic position of *U. dasaea*; however, the low quality of these sequences make the topology unreliable (Lücking et al. 2020). Recently a new ITS sequence from Portugal was generated, indicating the probable identity of *Usnea dasaea* s. str. Based on the chemistry, the morphology of soralia and the presence of Brazilian specimens (Fig. 2B), we decided to name this clade, containing the four specimens from the Philippines, *U. spinulifera* (Fig. 8).

Distribution. So far, *Usnea spinulifera* is found to occur only in Brazil, Costa Rica and the Philippines.

Selected specimens examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1169 m, 7.46024°N, 125.25790°E, after the first cave, edge of a forest close to the river, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/891a (G), DNA-code: PU05; *ibid.*, 1227 m, on the new Baganihan road, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/893c (BRIT), DNA-code: PU39; *ibid.*, 1095 m, 7.45788°N, 125.23925°E, open road, disturbed, close to the main road near Lawi Lawi Resort, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/969a, b (BRIT, G), DNA-code: PU08; Lawi Lawi Resort, Arakan, Datu Ladayon, Mt Malambo surroundings, close to CMU nursery and private property near Bussay Waterfall, 1185 m, 7.4815°N, 125.26204°E, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG19/1003 (G), DNA-code: PU20.

Usnea cf. subflammea P. Clerc

Lichenologist 38, 206 (2006); type: Portugal, Azores, Pico, 700 m, 1993, Purvis & James 5166 (BM!—holotype; G!—isotype). %C/M/A = 13.5/13.5/47. Chemistry: usnic, stictic, constictic and menegazziaic acids, with traces of norstictic acid (Clerc 2006).

Taxonomic notes. The specimen identified is similar to *Usnea subflammea*, meaning it has an erect-shrubby sorediate thallus with a thick (12.5%), matt cortex and pruinose appearance, a thin and compact medulla (17%) and ±thin axis (40%), with tubercles; lateral branches not constricted, main branches cylindrical and terete. The base is brownish and annulated. Soralia are mainly minute, sometimes large. We found only one juvenile thallus with these morphological characters, which is not enough to describe it as new to science.

Phylogenetic notes. We obtained one sequence (PU43) which clustered with *Usnea subflammea* from Brazil (65BR, 66BR) but without support (Fig. 2B). One ITS sequence of *Usnea subflammea* from the Canary Islands (type locality; Clerc 2006) clustered outside this group which suggests that the lineage found in the Philippines and Brazil could be a different, unnamed species (Gerlach et al. 2019, fig. 1: black stars).

Specimen examined. **Philippines:** Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1215 m, 7.46423°N, 125.25430°E, trail with native plants close to a new road, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/1008c (BRIT), DNA-code: PU43.

Usnea subscabrosa Motyka

Lich. Gen. Usnea Stud. Monogr. Pars Syst. 2, 313 (1937); type: Portugal, 1877, Newton (H—holotype!). %C/M/A = 14/13.5/45; A/M = 3.3; A/C = 3.2; M/C = 1. Chemistry: usnic and protocetraric acids (Clerc 1992).

For a detailed description of this taxon, see Clerc (1992), Herrera-Campos et al. (1998), Clerc (2007) and Truong et al. (2013b).

Thallus erect-shrubby, 5 cm long; **trunk** concolorous with main branches; **main branches** tapering to cylindrical in longitudinal section and terete in transversal section; **lateral branches** not constricted at ramification points; **fibrils** few, irregularly distributed; **fiberles** numerous; **soralia** minute, < 1/2 branch diameter, irregular (top view), even with cortex (side view), plane without cortical rim, dense (6–12/0.25 mm²), well distinct, remaining isolated, in subterminal and terminal branches; **isidiomorphs** few and short; **cortex** thick, vitreous; **medulla** thick; **axis** thin. %C/M/A = 11.5/29/19; A/M = 0.7; A/C = 1.7; M/C = 2.5; ($n = 1$).

Chemistry. Medulla K–, Pd+ red. TLC ($n = 1$): protocetraric acid.

Taxonomic notes. The specimen collected in the Philippines is damaged and necrotic (collected on a fallen tree). However, the presence of protocetraric acid in the medulla, the vitreous and thick cortex, the unpigmented basal part and the morphology of soralia leave no doubt about its identity.

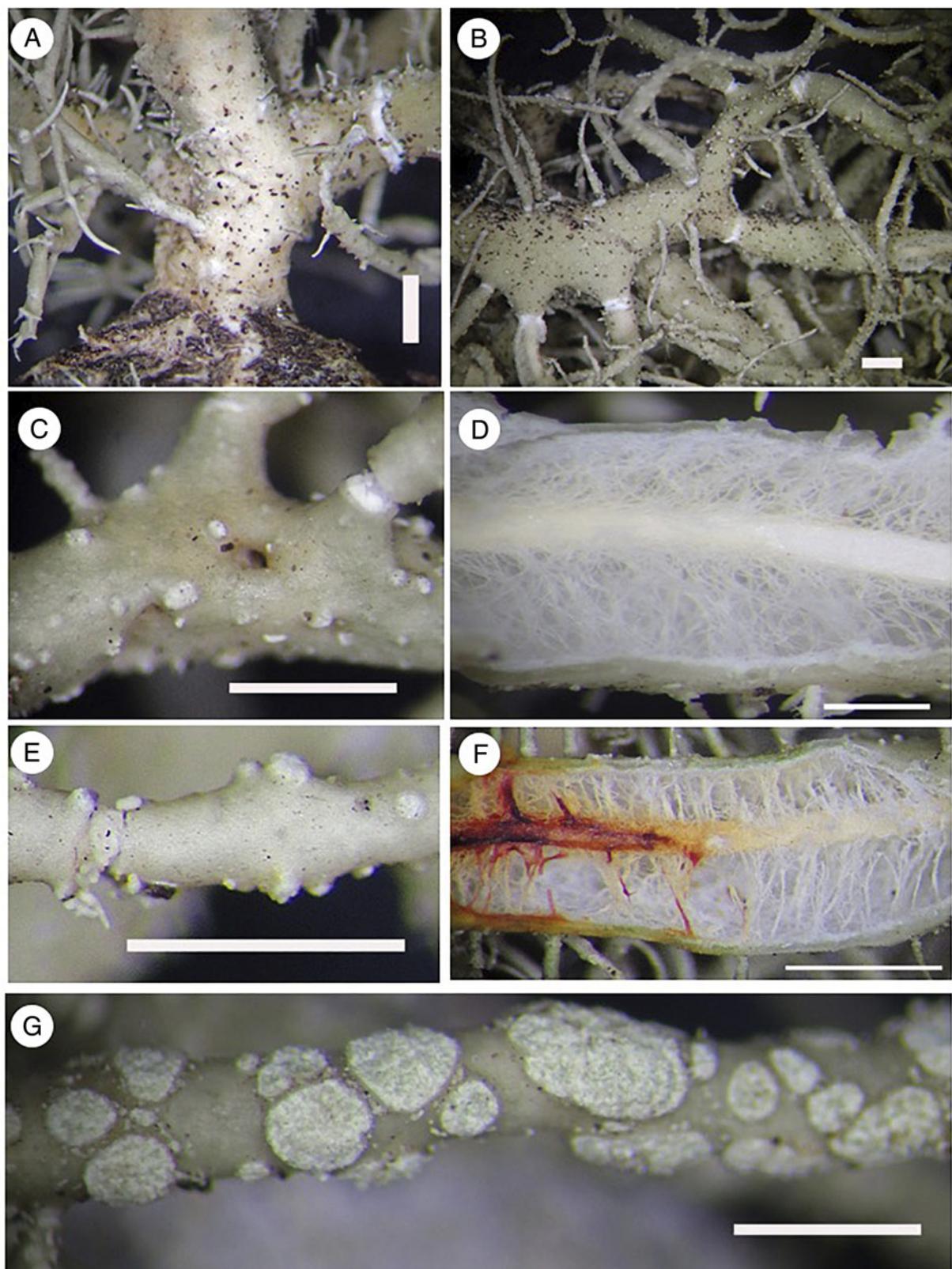


Figure 9. *Usnea yoshihitoi* (PU25). A, short, whitish basal part. B, branches strongly irregular in longitudinal section. C, characteristic perforated foveolae on the cortex surface. D, section of branch showing medulla with hyphae evenly arranged, not conglutinated. E, punctiform and stipitate soralia. *Usnea bismolliuscula* (PU02). F, section of branch showing medulla with conglutinated hyphae. G, large soralia at terminal branch. Scales: A-G = 1 mm. In colour online.

Phylogenetic notes. DNA from the small collected specimen was not extracted. In Gerlach *et al.* (2019), *U. subscabrosa* was part of clade *Usnea*-1, as sister species to an unknown Brazilian species (*Usnea* sp. 4, with galbinic acid).

Distribution. Until now, *Usnea subscabrosa* was found to occur in south-western Europe, Macaronesia, and Northeastern America (Clerc 1992, fig. 5), Mexico (Herrera-Campos *et al.* 1998; Clerc 2007) and South America (Truong *et al.* 2013b). In Asia, it was reported for the north Philippines (Luzon) for the first time by Bawingan *et al.* (2000). This is the first record for the southern Philippines.

Specimen examined. Philippines: Negros: Negros Oriental, Dumaguete City, Tacloban, Larena Drive, Balinsasayao Twin Lakes Natural Park, fallen *Agathis* tree, 1058 m, 9.36111°N, 123.175°E, on fallen tree trunk, 2019, *M. Dal Forno* (with *J. Shevock & D. Salas*) 3438b (BRIT).

Usnea yoshihitoi P. Clerc & A. Gerlach sp. nov.

Mycobank No.: MB 848356

Differs from *Usnea bismolliuscula* by the dense medulla with non-conglutinated hyphae, minute soralia remaining distinct, not forming consoralia, and by its phylogenetic position.

Type: Philippines, Mindanao, Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1227 m, 7.45392°N, 125.24509°E, tropical lowland rainforest, disturbed habitat, on *Pinus* sp., 27 December 2019, A. Gerlach (with *M. Dal Forno & J. Nobleza*) AG 2019/908a (G—holotype). Chemistry: usnic, stictic, constictic, cryptostictic, menegazziaic and norstictic acids. %C/M/A = 4.5/35/20; A/M = 0.6; A/C = 4.3; M/C = 7.5. GenBank Accession no.: OQ591873, DNA-code: PU25.

(Fig. 9)

Thallus shrubby and ±soft, up to 12 cm long, with mainly anisotomic-dichotomous ramifications; *basal part* short, up to 2 mm, usually whitish, more rarely pale brownish or barely blackened close to the holdfast; *main branches* 1.0–1.6 mm thick, strongly irregular in longitudinal section, terete in transversal section, distinctly segmented; *segments* cylindrical to irregularly swollen, terete to strongly flattened in cross-section; *lateral branches* distinctly constricted at attachment point; *terminal branches* moderately thin with few ramifications; *foveolae* and *transverse furrows* frequent, foveolae sometimes perforated and source of the appearance and development of small characteristic holes in the cortex; *maculae* and *pseudocystellae* absent; *papillae* absent; *tuberles* absent; *fibrils* a) thin and slender, often frequent and unevenly distributed, b) tiny young fibrils looking like isidiofibrils but densely present in some parts of branches; *fiberles* frequent in most of the branches, looking like small pseudocystellae; *soralia* punctiform, 50–200 µm, smaller than half the diameter of the branch, shape irregular to ±circular in top view, slightly but distinctly stipitate in side view, surface plane to slightly convex, cortical rim indistinct, spaced, 4–8 soralia/0.25 mm², well distinct, not aggregating or fusing together, localized mostly in the upper third part of the thallus, but sometimes lower down on the secondary branches; *isidiomorphs* short and frequent, mostly in young soralia; *isidiofibrils* not seen; *cortex* shiny, thin, of the *merrillii*-type plectenchyma ((4–)4.3–5.6%–7%)

($n = 8$); *medulla* thick, lax-dense with hyphae evenly arranged, not conglutinated (without irregular spaces of various sizes between them), unpigmented (25–)29.2–33.3%–37.4(–38); C/M/A of the *tenuicorticata-cornuta* type; *axis* thin (16–)16.3–22.4%–28.5(–36); A/M = 0.4–0.7–1(–1.5); A/C = (3–)3.3–4–4.7(–5.3); M/C = (3.6–)4.2–6.3–8.4(–9.3); ($n = 7$).

Apothecia rare (only one apothecium seen), subterminal, up to 4 mm diam.; *ascospores* and *pycnidia* not seen.

Chemistry. 1) Medulla K+ yellow, turning slowly orangish, P+ orange; TLC ($n = 6$): stictic, constictic, cryptostictic, menegazziaic, ±norstictic (weak when present) acids. 2) Medulla K+ yellow turning red, P+ orange-red; TLC ($n = 1$): salazinic and norstictic acids.

Etymology. This taxon is named in honour of our esteemed colleague and friend Yoshihito Ohmura for his major contribution to the study of the genus *Usnea* in Asia.

Taxonomic notes. *Usnea yoshihitoi* is characterized by the shrubby to subpendent thallus with strongly irregular branches in transversal section, with inflated, often flattened segments, the punctiform soralia that are not aggregating, the thin, glossy, often perforated cortex, the thick medulla with densely and evenly arranged, not conglutinated, hyphae (Fig. 9A–E), and the presence mainly of the stictic acid group, more rarely salazinic and norstictic acids as main medullary compounds. Perforations of the cortex are sometimes rare and difficult to find, but were always found in the seven specimens collected. The soralia are sometimes not well developed or not developed at all. In this case, the fiberles remain as minute, whitish pseudocystellae. The presence of tiny fibrils looking like isidiofibrils but developing in the cortex is variable. Isidiomorphs can be absent to numerous. *Usnea yoshihitoi* is the sister clade of *U. bismolliuscula* (Fig. 2D). Both species share a unique character in the genus *Usnea*, the presence of a perforated cortex. *Usnea yoshihitoi* differs from *U. bismolliuscula* by the denser medulla with hyphae that are not conglutinated. Furthermore, the soralia of *U. yoshihitoi* remain minute and distinct whereas in mature thalli of *U. bismolliuscula* the soralia enlarge (>1/2 branch diameter) and aggregate with other soralia and might finally fuse together to form larger irregular or longitudinally stretched consoralia. Young thalli of *U. yoshihitoi* without perforated thalli might be difficult to separate from other species with irregular branches and constricted lateral branches, and DNA-barcoding might be necessary here.

Phylogenetic notes. Five specimens (PU07, PU14, PU16, PU25, PU45) clustered inside a well-supported clade close to *Usnea beckeri* P. Clerc & Nadel, a pendulous-fertile species recently described from Africa (Nadel & Clerc 2022) (Fig. 2D).

Distribution. Corticolous, found so far only in the Philippines, mainly in Mindanao in tropical lowland rainforest in disturbed or undisturbed habitats.

Selected paratypes. Philippines: Mindanao: Davao del Sur, Marilog District, Davao City, Baganihan, Marilog Forest Reserve, 1162 m, 7.45392°N, 125.24509°E, disturbed forest, 2019, A. Gerlach (with *M. Dal Forno & J. Nobleza*) AG 2019/931 (TNS), DNA-code: PU16; *ibid.*, after the first cave, edge of a forest close to the river, 1169 m, 2019, A. Gerlach (with *M. Dal Forno & J. Nobleza*) AG 2019/891c (G), DNA-code: PU07;

ibid., 1131 m, beginning of trail to Epol Waterfall, part way down, on *Pinus* sp., 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/957c (G), DNA-code: PU14; Mt Malambo, open area with *Pinus* sp., 1279 m, 2019, A. Gerlach (with M. Dal Forno & J. Nobleza) AG 2019/992a (BRIT), DNA-code: PU45. Negros: Negros Oriental, Dumaguete City, Santa Catalina, San Pedro, Cuernos de Negros, 1324 m, 9.24092°N, 123.11626°E, tropical lowland rainforest, 2019, A. Gerlach (with M. Dal Forno & A. D. Nietes) AG 2019/852c (G).

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Author Contribution. AG and MDF conceived the study and obtained the funding; AG, MDF and JN performed the fieldwork; AG and PC are responsible for the taxonomy; AG performed the TLC analyses; MDF obtained 54 DNA sequences, YO obtained 21 DNA sequences and BM obtained four DNA sequences; AG and RL performed phylogenetic analyses; PC captured the images showing morphology; AG designed the figures; AG and PC wrote the first draft of the manuscript and all authors reviewed and further contributed.

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Supplementary Material. The Supplementary Material for this article can be found at <https://doi.org/10.1017/S0024282923000579>.

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