The saxicolous species of the genus Usnea subgenus Usnea (Parmeliaceae) in Argentina and Uruguay

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ABSTRACT. Eight primarily saxicolous Usnea subgenus Usnea species are reported from Argentina and Uruguay: U. amblyoclada (Müll. Arg.) Zahlbr. (syn. nov. U. pinnata Räsänen), U. densirostra Motyka, U. durietzii Motyka (syn. nov. U. caespitia Motyka), U. exigua J.M. Rodr. & P. Clerc sp. nov., U. fastuosa (Müll. Arg.) Zahlbr., U. hieronymii Kremp. (syn. nov. U. hieronymii var. adusta Kremp.), U. lutii J.M. Rodr. & P. Clerc sp. nov. and Usnea saxidilatata J.M. Rodr. & P. Clerc sp. nov. are described with morphological, anatomical and chemical data. Their taxonomy and distribution are discussed. A key to the saxicolous species, including those occurring secondarily on rocks (i.e., U. columbiana Motyka, U. cornuta Körb., U. dasaea Stirt. and U. cf. perhispidella J. Steiner) is provided.

KEYWORDS. South America, taxonomy, lichens, systematics.

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Usnea is a speciose and cosmopolitan genus easily identified by the fruticose thallus with a central axis and the presence of usnic acid in the cortex. At the species level, the taxonomy of the genus remains very complex, due to the high intraspecific morphological variation. In the last decades, numerous taxonomical studies have been published in North America (Clerc 2007; Clerc & Herrera–Campos 1997; Halonen et al. 1998; Herrera–Campos et al. 1998, 2001), Europe (Clerc 1984, 1987a, 1987b, 1992, 1997, 2004; Fos & Clerc 2000; James et al. 1992), Africa (Clerc 2006; Swinscow & Krog 1974, 1975, 1976a, 1976b, 1978, 1979), Australia (Stevens 2004) and Japan (Ohmura 2001; Ohmura & Kanda 2004; Ohmura & Kashiwadani 2000). So far, Argentinean and South American species have not received a taxonomic treatment using a species concept as defined in Clerc (1998).

Most *Usnea* species are primarily corticolous, occurring secondarily on rock when environmental conditions are optimal. In the subgenus *Usnea*, taxa mainly or exclusively saxicolous are rare (Clerc & Herrera Campos 1997). In Argentina, however, numerous communities of saxicolous lichens, including *Usnea* species growing almost exclusively on rocks, occur. Motyka mentioned four of saxicolous *Usnea* from Argentina in his monograph (1936–1938): *U. amblyoclada* (Müll. Arg.) Zahlbr.,

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U. densirostra Motyka, *U. durietzii* Motyka *and U. hieronymii* Kremp. Other floristic studies mentioned saxicolous *Usnea* species occurring in Argentina (Räsänen 1939; Lamb 1958; Osorio 1968, 1987). Climate, geology and vegetation of Uruguay are similar to central East Argentina, and hence similar communities with saxicolous *Usnea* species occur in these regions. Osorio (1967, 1980, 1981, 1982, 1992, 1993, 1995, 1996, 2001, 2005) inventoried these communities in Uruguay.

Walker (1985) in her monograph of subgenus Neuropogon included Usnea durietzii in this group and shortly discussed U. amblyoclada, U. densirostra and U. hieronymii to differentiate them from the Neuropogon species. Wirtz et al. (2006), however, showed that Neuropogon is polyphyletic. But none of the species discussed here display the variegated black pigmentation and the black or reddish rufous brown apothecial disks that are typical for Neuropogon species.

The aim of the present study is to provide detailed and modern descriptions of seven species as well as distribution maps of the primarily saxicolous *Usnea* species occurring in Argentina, taking also into account material from Uruguay. All species occurring primarily and secondarily on rocks are included in the key.

MATERIAL AND METHODS

Specimens were collected mainly by the first author between 2004 and 2008 in the different phytogeographical units of Argentina (Cabrera 1971). In addition saxicolous specimens collected in 1989 by Sibylle Vermont Grundlehner in the Tucuman province and deposited in G were studied. Herbarium specimens from BAB, BAFC, BM, CORD, CTES, G, LIL, M, MERL, MVM, PC, SI, TUR, W and the private collections of Hector Osorio (Uruguay) were studied.

The species concept follows Clerc (1998). Discriminating between characters that are strongly modified by environmental factors and those that are more intrinsic to a species is a key element in the systematics of *Usnea* (Clerc 1998). We selected a variety of characters useful in the discrimination of the saxicolous species. The following features were found to be of high taxonomic value: habit, pigmentation of the trunk, shape of branches and segments, presence of pseudocyphellae, morphology of soralia and isidiomorphs, thickness of cortex, medulla and central axis, presence of pigments in the medulla and chemistry. Characters found to be of little or no value in the delimitation of species were, for example: type of branching, morphology of papillae and colour of the thallus.

Morphological characters were studied according to Clerc & Herrera Campos (1997), Clerc (1998) and Herrera Campos et al. (1998). The thickness of cortex (C), medulla (M) and central axis (A) were measured and the thickness of each structure was calculated in percentages of the whole width of the measured branch (CMA; Clerc 1984, 1987a). In specimens with apothecia, spore width and length of 10 to 20 spores were measured. Significant differences of spore length and width between species were tested with non parametric Kruskal Wallis tests, using Infostat (Infostat, 2009). Lichen substances were studied by thin layer chromatography with A, B, C and G solvents, following Culberson & Ammann (1979) and White & James (1985). The spot test reactions with K, C and Pd are mentioned for each chemotype.

RESULTS AND DISCUSSION

A. Morphology

Thallus. The species growing primarily on rocks are usually shrubby and compact, with short thalli and strongly divergent branches (**Figs. 2A, 3A, 6A & 7A**). Corticolous species growing incidentally on rocks may be sub-pendulous or pendulous, with branches hanging, divergent or running \pm parallel.

Trunk and basal part. The pigmentation of the trunk in the first few mm from the holdfast is diagnostic for many species (**Figs. 5A & 6A**) (Clerc 1998). However, the basal part is frequently covered by dust or sand crystals, obscurring the basal part, and hence the pigmentation.

Some species described here exhibit a special kind of holdfast that seems to proliferate horizontally at the surface of the substrate with numerous branches growing vertically and tightly appressed (**Figs. 4A, 5A, 6A, 7B & 8A**). This kind of holdfast, called a proliferating holdfast, has been described in species of subg. *Neuropogon* (Walker 1985, fig. 20). Ontogenetic studies are needed in order to fully

Species	n	Length	Width			
U. densirostra	64	(6.4–) 7.0– <u>7.8</u> –8.6 (–11.2)	(3.2-) 3.8-4.6-5.4 (-7.5)			
U. exigua	20	(5.6-) 6.3-7.1-7.9 (-8.8)	(3.2-) 3.9-4.7-5.5 (-6.4)			
U. fastuosa	63	(6.4–) 6.8–7.9–9.0 (–10.4)	(3.2-) 4.0-5.0-6.0 (-7.2)			
U. hieronymii	89	(6.4-) 7.6-8.4-9.2 (-10.4)	(4.0-) 4.6- <u>5.4</u> -6.2 (-7.2)			

Table 1. Spores size of the saxicolous fertile species of *Usnea* subgenus *Usnea* in Argentina and Uruguay The average values, standard deviation, and extreme values of length and width are given in μ m; n = number of spores measured.

understand this special kind of holdfast proliferation, occurring only in saxicolous species. Sometimes, as in *Usnea densirostra* for instance, many large branches arise from the basal part giving the false impression of a proliferating holdfast. However, when looking carefully it can be seen that all these branches diverge from one unique trunk.

Branches. In longitudinal section, main branches can be cylindrical, tapered or irregular (Clerc & Herrera Campos 1997). Lateral branches may be distinctly narrowed at their point of attachment. In transversal sections the main branches are terete, ridged, alate or elliptic (Herrera Campos et al. 1998). When the branches are distinctly segmented, segments are cylindrical or inflated in longitudinal sections. Segments can be deformed by the presence of depressions (foveoles) and transversal furrows.

Fibrils, papillae, fibercles. See descriptions and taxonomic importance of these structures in Clerc (1998), Clerc & Herrera Campos (1997), Herrera Campos & Clerc (1998).

Pseudocyphellae and maculae. Pseudocyphellae are common among saxicolous species in Argentina. They appear as breaks in the cortex, exposing the medulla but never producing soredia. Pseudocyphellae are elongated, twisted, circular or irregular (Figs. 6B & 7C). Maculae are whitish areas on the branches with a thinner cortex (Ohmura 2001). They can be punctiform to effigurate (Fig. 4C). Some species described here display maculae with a broken cortex, and hence with the medulla exposed; these are regarded as pseudocyphellae (Fig. 5C).

Soralia are decorticated areas of the thallus where soredia and/or isidiomorphs are produced. The morphology of soralia is one of the most important characters in the taxonomy of *Usnea* (Clerc 1998). Different types of soralia have been described by Clerc (1987). The origin of the soralia is also important, i.e. arising *ad initio* on the cortex, from fibercles, from pseudocyphellae, from eroded tubercles or from cracks.

Isidiomorphs and isidio–fibrils. Isidiomorphs (Clerc 1998) are frequently produced in soralia of saxicolous *Usnea* species in Argentina (Figs. 3C, 7D & 8C). They are often black pigmented at their top, probably as a result of the saxicolous exposition (Øvstedal & Lewis Smith 2001; Wirtz et al. 2006). Walker (1985) suggested that some species of the subgenus *Neuropogon* have pseudoisidia (isidia–like structures lacking a true original cortex) in contrast with other species with true isidia (with true primary cortex and a longer size than pseudoisidia). However, no true isidia have been found in *Usnea* so far. Isidio–fibrils were described by Truong et al. (2011).

Apothecia. The location and morphology of apothecia are uniform in saxicolous species of the genus *Usnea* in Argentina. Nevertheless, the distribution of fibrils on the apothecia margin might have some taxonomic importance. A common modification linked to the saxicolous habitat is that apothecia tend to become flat and the disc to break (**Figs. 2A, 4B, 5B & 6A**).

B. Anatomy

Spores. According to Clerc (1984) spore size has often a taxonomic value in the delimitation of fertile species. Spore width and length were significantly higher (Kruskal Wallis test p<0.05) in *U. hieronymii* than the other species (**Table 1**). Spore length of *Usnea exigua* was significantly shorter than the rest of the species. Spore width did not differ significantly among species with the exception of *U. hieronymii*. Spore size of *U. densirostra* and *U. fastuosa* was not significantly different. However, since the values of spore length and width overlap between the species, they remain difficult to use as taxonomic characters.

Species	n	Cortex %	Medulla %	Axis %		
U. amblyoclada	28	(3.0)-4.8-6.9-9.0-(11.0)	(8.0)-12.5-16.6-20.7-(24.0)	(32.5)-42.6-52.8-63.0-(75.0)		
U. densirostra	25	(3.6)-4.7-6.5-8.3-(10.7)	(8.6)-10.9-15.5-20.1-(28.0)	(27.0)-45.1-55.9-66.8-(69.0)		
U. durietzii	44	(4.2)-5.5-7.2-8.9-(10.8)	(18.2)-22.2-25.9-29.6-(33.9)	(19.0)-27.3-33.6-37.3-(44.0)		
U. exigua	15	(4.0)-4.8-6.1-7.4-(8.5)	(12.5)-17.1-21.4-25.7-(28.5)	(34.0)-36.6-44.9-53.2-(61.3)		
U. fastuosa	18	(6.0)-6.7-8.0-9.3-(11.0)	(4.9)-6.5-9.1-11.7-(14.7)	(56.0)-60.1-65.7-71.3-(74.1)		
U. hieronymii	14	(4.3)-5.1-7.3-9.4-(11.0)	(7.2)-8.5-11.1-13.7-(15.7)	(48.9)-55.1-63.0-70.9-(73.8)		
U. lutii	22	(3.5)-4.6-6.1-7.6-(8.5)	(6.0)-9.2-12.8-16.4-(22.8)	(37.4)-54.5-62.3-70.1-(74.0)		
U. saxidilatata	19	(2.5)-4.2-5.5-6.8-(7.3)	(8.6)-14.8-20.7-26.6-(33.5)	(22.0)-36.3-47.5-58.7-(68.9)		

Table 2. Cortex, medulla and axis (CMA) percentages of the saxicolous species of *Usnea* subgenus *Usnea* in Argentina and Uruguay. The average value, standard deviation and extreme values are given; n = total of individuals measured.

Cortex. In some species treated here the cortex displays a dense pattern of cracks, especially close to the basal part. Cracks can be annular, longitudinal or irregular with the medulla sometimes bursting outside them. In longitudinal section of branches the cortex can be mat, glossy or vitreous.

Medulla. Three types of medulla can be found (Clerc & Herrera-Campos 1997): a lax medulla, with few conspicuous hyphae visible; a dense medulla with agglutinated hyphae but still visible individually and a compact medulla with agglutinated hyphae that are not visible individually. In some species, the medulla is slightly orange pigmented, which could be due to the decomposition of lichen acids.

Central axis. Thick main branches of saxicolous species (over 10 mm) have commonly a central axis that is hollow in the basal part. But unlike the species of the *Usnea baileyi* group, the central axis of these species is not hollow throughout the branches. Sometimes the axis of main branches can be irregular and not cylindrical in transversal sections.

The CMA values of the species treated in this work are summarized in **Table 2**.

C. Chemistry

The main compounds and the accesory substances detected by TLC in exclusively saxicolous species occurring in Argentina are listed in **Table 3**. Except for diffractaic acid (depside) all compounds

Table 3. Main medullar secondary metabolites in Argentinean and Uruguaian saxicolous *Usnea* species. n = number of specimens analyzed. Ch. = chemotype. + = main substance, present in all the specimens examined. \pm = accessory substance, not constant. - = not present. Dif, diffractaic acid. Fum, fumarprotocetraric. Gal, galbinic. Nor, norstictic. Pro, protocetraric. Sal, salazinic. Usn, usnic. Un I, unknown I. Un II, unknown II. Un III, unknown III. All specimens have usnic acid in the cortex.

Species	n		Nor	Sal	Gal	Pro	Fum	Un I	UnII	UnIII	Dif
U. amblyoclada	23	Ch. 1	+	+	_	±	<u>+</u>	_	_	_	_
	5	Ch. 2	+	+	+	_	_	_	_	_	_
U. densirostra	11	Ch. 1	+	+	_	<u>+</u>	\pm	_	_	_	_
	3	Ch. 2	_	+	_	_	_	_	_	_	_
U. durietzii	16	Ch. 1	+	_	_	_	_	_	_	_	_
	6	Ch. 2	+	+	_	_	_	_	_	_	_
	3	Ch. 3	_	_	_	_	_	_	_	_	_
U. exigua	5	Ch. 1	_	_	_	+	_	+	_	_	_
U. fastuosa	16	Ch. 1	+	+	_	_	_	_	+	+	_
	11	Ch. 2	_	_	_	+	+	_	+	+	_
U. hieronymii	17	Ch. 1	+	_	_	\pm	_	_	_	_	\pm
	2	Ch. 2	_	_	_	+	_	_	_	_	_
	1	Ch. 3	_	_	_	_	_	_	_	_	+
U. lutii	13	Ch. 1	+	_	_	<u>+</u>	_	_	_	_	_
U. saxidilatata	15	Ch. 1	+	_	_	_	_	_	_	_	_

are depsidones of the ß–orcinol group. Three unknown substances are detected: unknown I (Rf: 6/ 2/5 solvents A/B/C yellow after UV) found in *Usnea exigua*; unknown II (Rf: 5/1/3 solvents A/B/C yellow after UV) and unknown III (Rf: 6/2/4 solvents A/B/C yellow after UV), both found in *U. fastuosa*. The accessory substances not defined chemotypes.

D. Ecology and distribution

In Argentina, saxicolous species of the genus *Usnea* occur in mountains areas, mainly on rock outcrops. Among the primarily saxicolous species *U. amblyoclada* and *U. durietzii* are the only species that have been found to occur rarely also on shrubs. Additionally some primarily corticolous species, such as *U. columbiana*, *U. cornuta* and *U. dasaea*, occur occasionally on rocks. The saxicolous species frequently colonize large surfaces of exposed boulders and can sometimes be locally very abundant (**Supplementary Fig. 1**).

The orographic system of Southern South America from west to east corresponds to the Andes (including pre-Andes) and the Sierra Chaco Mountains (Sierras Pampeanas) (Fig. 1). Between them and towards the Atlantic Ocean stretch large portions of lowlands and valleys with woodlands, shrublands and grasslands. In Buenos Aires province the Ventania and Tandilia chains form very old mountains at low altitude in the middle of the Pampean steppe region. These systems are considered as true "continental islands" or "traps" in the Pampas (De la Sota et al. 2004). There is a continuity between these mountains and those from Uruguay and Brazil. The gradient of climate and vegetation from north to south and from west to east hence influences the presence of Usnea species.

Primarily saxicolous species of *Usnea* in Argentina show different distribution patterns (**Supplementary Fig. 2**). *Usnea amblyoclada* and *U. durietzii* are the commonest saxicolous species in Argentina, the later occurring only in the Andes. *Usnea saxidilatata* is common in the higher mountains of the Central Andes and the Sierra Chaco (above 2000 m), where the climate is temperate to cold. *Usnea hieronymii* also occurs in the higher mountains, but is, however, lacking from the Central Andes.

The fertile species *Usnea densirostra* is the commonest saxicolous species in the eastern

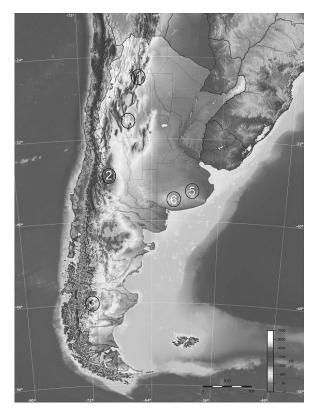


Figure 1. Map of Argentina showing the main mountains chains. 1–3. Andes (1. Northern Andes 2. Central Andes.
3. Patagonia). 4. Sierra Chaco mountains (Sierras Pampeanas).
5. Tandilia. 6. Ventania.

mountains and in Uruguay where the climate is warmer. It is rare in the Sierra Chaco and there is only one specimen known from Patagonia. *Usnea fastuosa* and *U. exigua* have been found only in the Province of Buenos Aires and in Uruguay.

Key to Primarily and Secondarily Saxicolous Species

- 1. Without soralia and isidiomorphs 2
- 1. With soralia and isidiomorphs 5
 - Elongated pseudocyphellae and/or maculae absent on main branches (they might be present on fibrils however). Thallus arising from an individual trunk, holdfast not proliferating. U. densirostra
- Medulla K ± yellowish brown and Pd + red orange (protocetraric acid); thallus always small (to 2–3 cm) U. exigua

- 4 Maculae absent, pseudocyphellae present, branches irregular, not cylindrical, not distinctly annulated; segments ± ridged, medulla white U. hieronymii
- Maculae present, pseudocyphellae absent (in terminal branches the maculae may look like pseudocyphellae), branches distinctly cylindrical and annulated; segments terete, medulla orange U. fastuosa
- 5. Thallus without red dots 6
 - 6. Thallus arising from a proliferating holdfast; elongate pseudocyphellae present or not7
- Foveoles usually present on primary branches close to the basal part; medulla moderately thin (14.8–20.7%–26.6), axis moderately thick (36.3–47.5%–58.7) U. saxidilatata
- 7. Foveoles absent; medulla thin (9.2–12.8%–16.4), axis very thick (54.5–62.3%–70.1) U. lutii
 - Cortex thick (7.1–9.7%–12.3) and mat, medulla thin (10.0–13.8%– 17.6), lateral branches never constricted; base distinctly jet black pigmented; foveoles and transversal furrow never present; soralia minute arising at the top of papillae U. columbiana
- True fibrils absent or few, with instead numerous small isidiomorphs often developing into longer isidiofibrils, growing from punctiform soralia on main and secondary branches; stictic acid as main substance always present U. cf. perhispidella
- - Isidiomorphs thick, usually not clustered but often sitting alone on a punctiform soralia; black-tipped, always present; soralia punctiform, never enlarging and never confluent, ± stipitate, numerous, densely disposed, occurring on fibercles; medulla compact to dense U. amblyoclada
- Fibrils short and spinulose, densely but ±irregularly covering restricted parts (rarely the entire length) of branches; soralia punctiform, enlarging towards terminal branches, not confluent; galbinic acid always present U. dasaea

THE SPECIES

- Usnea amblyoclada (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 6: 534. 1930.
- Usnea barbata var. amblyoclada Müll. Arg., Flora 72: 509. 1889. TYPE: ARGENTINA. Felsen am Fuss der Sierra Ventana, 1881, *Lorentz* (G!, holotype).
 CMA: 8.5/25.5/32 (thallus a), 7/16.5/53 (thallus b). Chemistry: usnic, salazinic and norstictic acids (both specimens; Clerc & Herrera–Campos 1997).

= Usnea pinnata Räsänen, TYPE: ARGENTINA. Circa Córdoba, 1280 m., 1935, Hosseus (H!, holotype), *syn. nov.*. CMA: 5.2/23.9/42 (thallus a), 7.3/ 17.8/49.8 (thallus b). Chemistry: usnic, salazinic, norstictic and protocetraric (faint) acids (thalli a & b).

Illustrations. Clerc and Herrera-Campos (1997), pp. 287 & 288; Brodo et al. (2001), p. 273.

For a detailed description of the species, see Clerc & Herrera–Campos (1997) and Clerc (2007) and for the distribution in Argentina see Rodriguez & Estrabou (2008).

Diagnosis. This species is characterized by the spinulous fibrils, the numerous fibercles, the punctiform and never coalescing soralia and the thin and glossy cortex.

Chemistry. 1. Usnic, norstictic, salazinic, \pm protocetraric and \pm fumarprotocetraric acids (n = 23), K+ yellow turning red, medulla C–, Pd+ red or Pd–. 2. Usnic, norstictic, galbinic and salazinic acids (n = 5), medulla K+ yellow turning red, C–, Pd+ pale orange-yellow.

Variation. The specimens collected in Argentina present the same morphological variation as described by Clerc & Herrera–Campos (1997) for North American specimens.

Taxonomical notes. In Argentina, the main chemotype contains salazinic and norstictic acids (galbinic acid was found in only 15% of the specimens studied; **Table 3**), whereas galbinic acid is found in 96% of the specimens studied in North America (Clerc & Herrera–Campos 1997). Walker (1985) reported similar results in her study of South American specimens. Except for the presence of soralia and isidiomorphs and the absence of apothecia, *Usnea amblyoclada* is similar in morphology, anatomy and chemistry with *U. densirostra*. However, the later never produces galbinic acid. *Usnea densirostra* is probably the fertile counterpart of *U. amblyoclada*. *Usnea pinnata* is morphologically, anatomically and chemically identical with *U. amblyoclada*.

Ecology and distribution. Usnea amblyoclada is the most common primarily saxicolous species in Argentina. It is confined to mountain chains in central and Northern Argentina exhibiting a wide ecological and altitudinal range (100–3000 m). This species is very common in the central mountains (Sierra Chaco and Pre–Andes) where Usnea densirostra is very rare. In the eastern mountains and in Uruguay, U. densirostra is more frequent than U. amblyoclada. Walker (1985) suggested that U. amblyoclada is confined to the northern part of South America. Our results show that this species is present in every mountain chain of Argentina and Uruguay, except in Patagonia.

Representative specimens examined. Argentina. BUENOS AIRES: Dpto. Tandil, Tandil, 37°20'26.7"S, 59°11'22.7"W, 337 m, Rodriguez & Fantini 0167 (LIL); Dpto. Tornquist, Sierra de la Ventana, S38°04'37.5", W62°00'06.5", 521 m, Rodriguez & Fantini 161 (LIL). CATAMARCA: Dpto. Ambato, Vuelta de Ambato, 28°03'59.6"S, 65°54'22.0"W, 1646 m, Rodriguez & Fantini 224 (LIL). CORDOBA: Dpto. Calamuchita, Camino de los Linderos, S32°04'06.2"S, 64°52'29.9"W, 1748 m, Rodríguez 1802 (LIL). Dpto. Punilla, Capilla del Monte, Nicora 2738 (SI). LA RIOJA: Dpto. Capital, Pellici 22327 (CORD); Dpto. Famatina, Sierra de Famatina, Mina San Juan, Kurtz 14087 (CORD); Ruta Nacional 78, Cuesta La Agüadita, 28°44'30.1"S, 67°35'40.6"W, 2059 m, Rodríguez & Fantini 221 (LIL); Dpto. Castro Barros, Anillaco, 28°47'56.7"S, 66°59'49.6"W, 1735 m, Rodríguez & Fantini 232 (LIL). MISIONES: Dpto. San Ignacio, Campos del Teyú Cuaré, Ferraro et al. 79573 (CTES). SALTA: Dpto. Santa Victoria, Parque Nacional Baritú, margen del río Lipeo, Ferraro 8744 (CTES). SAN JUAN: Dpto. Valle Fértil, Ischigualasto, C° el Morado, Américo Cortez 244785 (CTES). SAN LUIS: Dpto. Junín, Merlo, 32°19'32,1"S, 64°58'52.5"W, 1110 m,

Rodríguez 062 (LIL); Dpto. General Pedernera, San José del Morro, 33°08'69.1"S, 65°23'33.5"W, 1365 m, *Rodríguez 1002* (LIL). TUCUMAN: Dpto. Tafí del Valle, El Infiernillo, 1900 m, *Grundlehner 51.28.3* (G). URUGUAY. MALDONADO: Cerro del Toro, Cumbre, 34°51'45.1"S, 55°15'26.8"W, 246 m, *Rodriguez 971*. LAVALLEJA: Camino a Salto del Penitente, 6 km de RN 8, 34°22'52.1"S, 55°04'34.9", 345 m, *Rodriguez 969* (MVM).

Usnea densirostra Taylor, Hook. London J. Bot., 6: 192. 1847. Fig. 2 Usnea barbata (L.) var. densirostra (Taylor) Müll.

Arg., Flora 64: 83. 1981. TYPE. URUGUAY. Montevideo, *Darwin* (ASU!, isotype), (G!, isotype) CMA: 7/18/48; Chemistry: usnic, norstictic and salazinic acids.

Description. Thallus shrubby, compact, very rigid, up to 6 cm long (Fig. 2A), with both isotomicdichotomous and anisotomic-dichotomous ramifications; trunk inconspicuous to 9 mm long (see remark in the "Morphology/basal part" chapter), reddish brown or concolorous with main branches, with annular cracks (Fig. 2C); branches irregular to tapering, sometimes slightly attenuated toward their basal part, with lateral branches not narrowed at point of attachment; terminal branches thick, usually with black tips; segments cylindrical and terete to ridged, with cortex irregularly cracked and displaying a rough surface; fibrils spinulous (Fig. 2B), short and thick (1.5-2.5 mm) always present and regularly distributed on whole thallus, usually with black tips; fibercles few; tubercles and papillae absent; pseudocyphellae and maculae absent on main branches (but sometimes present on fibrils); soralia and isidiomorphs absent; cortex mat to slightly glossy and cracked; thin (3.6-) 4.7-6.5%-8.3 (-10.7) (Fig. 2D); medulla compact, white, \pm thin (8.6-) 10.9-15.5%-20.1 (-28.0) (Fig. 2D); axis thick (27.0-) 45.1–55.9%–66.8 (–69.0) (n = 25) (**Fig. 2D**), usually fistulose in main branches close to the base and irregular in longitudinal section, often brownish pigmented.

Apothecia always present (Fig. 2A), terminal or subterminal to lateral, up to 15 mm in diameter, becoming flat when mature; disc yellowish, with or without pruina, with fibrils both on the margin and

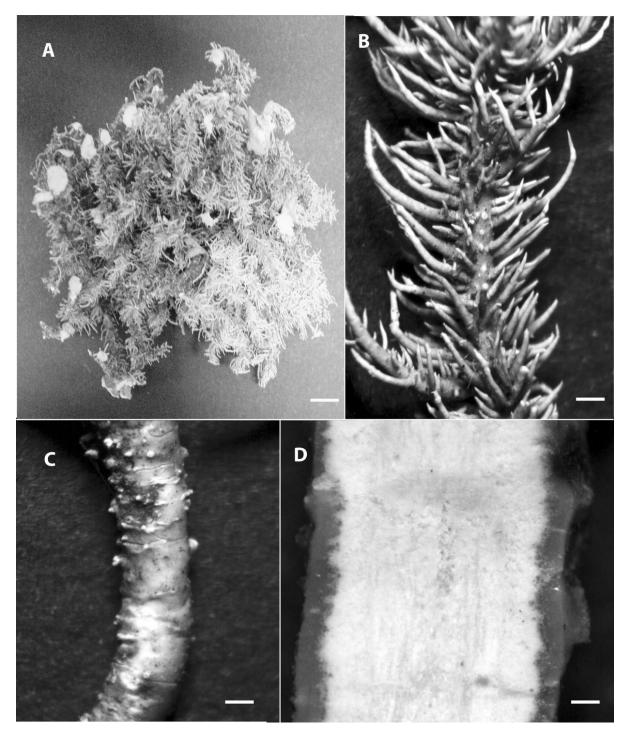


Figure 2. Usnea densirostra. **A.** Thallus (Rodriguez & Fantini 168). **B.** Terminal branch with spinulous fibrils (Rodriguez & Fantini 168). **C.** Trunk (Rodriguez & Fantini 168). **D.** Cortex, medulla, and axis (Rodriguez & Fantini 168). Scale. A = 10 mm. B = 1 mm. C = 0.67 mm & D = 0.25 mm.

on the underside; spores simple and hyaline, (6.4–) 7.0–7.8–8.6 (–11.2) \times (3.2–) 3.8–4.6–5.4 (–7.5) µm (n = 64) (**Table 1**); pycnidia present on fibrils and terminal branches; conidia sublageliform, 7.3 µm long in average (n = 23).

Chemistry. 1. Usnic, norstictic, salazinic, \pm protocetraric and \pm fumarprotocetraric acids (n = 11), medulla K+ yellow turning red, C-, Pd+ red or Pd-. 2. Usnic and salazinic acids (n = 3), medulla K+ yellow to orange, C-, Pd-.

Variation. The characters that show the largest variability are the frequency of apothecia, the density of fibrils and fibercles and the morphology of the axis.

Diagnosis. The diagnostic characters are: the simple, not proliferating base, the spinulous and dense fibrils, the absence of maculae or pseupdocyphellae, the well delimited trunk and the presence of salazinic acid as main substance in the medulla.

Taxonomical notes. Walker (1985) suggested that Usnea hieronymi Kremp. could be the fertile counterpart of U. amblyoclada and be conspecific with U. densirostra. However, U. hieronymii has tubercles, pseudocyphellae and a black base with a proliferating holdfast. Moreover the medulla of U. hieronymii is slightly thinner and without salazinic acid.

Ecology and distribution. Usnea densirostra grows exclusively on rocks. It is the commonest saxicolous species in the Ventania and Tandilia hills as well as in the mountains of Uruguay where the climate is warm and sub-tropical. This species colonizes rock outcrops apparently without any specific preference. It is commonly found together with Usnea fastuosa in humid sites. On the other hand, it occupies exposed and dry rocks together with U. amblyoclada. Usnea densirostra is very rare in other regions, for example in the Córdoba and Neuquén provinces where it was cited by Motyka (1936-1938) and Lamb (1958). So far, this species has been recorded in South America from Argentina, Brazil, México, Paraguay, Peru and Uruguay (Motyka 1936-1938; Osorio 1987, 1997).

Representative specimens examined. ARGENTINA. BUENOS AIRES: Dpto. Tandil, Tandil, $37^{\circ}20'26.7''$ S, $59^{\circ}11'22.7''$ W, 337 m, *Rodriguez. & Fantini 168* (LIL). Dpto. Tornquist, Sierra de la Ventana, $38^{\circ}04'37.5''$ S, $62^{\circ}00'06.5''$ W, 521 m, *Rodriguez. & Fantini* 163 (LIL). CORDOBA: Dpto. Calamuchita, Athos Pampa, *Estrabou 1830* (herb. Estrabou). NEUQUEN: Nahuel Huapi, *Edith Hein 00058* (LIL). URUGUAY. LAVALLEJA: 6 km Ruta Nacional 8 hacia el Salto del Penitente $34^{\circ} 22' 52.1''$ S, $55^{\circ} 04' 34.9''$ W, *Rodriguez 968* (G).

Usnea durietzii Motyka, Lich. Gen. Usnea Stud. Monogr. Pars Syst. 2: 503. 1936–1938. Neuropogon durietzii (Motyka) D. J. Galloway & Quilhot, Gayana 55 (2): 142. 1998. TYPE: CHILE. Insula Elisabetha, ad saxa erratica, 1882, Lechler (UPS!, holotype; G!, Isotype). CMA: 6/31/26. Chemistry: usnic, norstictic and salazinic acids. = Usnea caespitia Motyka in Lich. Gen. Usnea
Stud. Monogr. Pars Syst. 2: 500. 1936–1938. TYPE: BOLIVIA. Pelca–La Paz, Haumapampa, ad rupem graniticam, 3700 m., 1910, Planz 118 (LBL! holotype), syn. nov.. CMA: 4.5/33.5/19. Chemistry:

usnic and norstictic acids.

Description. Thallus erect, rigid, up to 4 cm (Fig. 3A), yellow to greyish green, usually with red dots especially visible in the basal part and sometimes in the whole thallus, mainly with anisotomic-dichotomous ramifications; trunk inconspicuous to up to 6 mm, often darker than main branches to black pigmented (Fig. 3B); branches \pm irregular to fusiform; lateral branches distinctly to \pm narrowed at point of attachment; terminal branches sometimes with black tips; segments cylindrical and terete to strongly inflated; foveoles and transversal furrows absent; fibrils scarce to numerous, short (2-3 mm), spinulous, irregularly distributed; fibercles absent; tubercles absent; papillae hemispherical to verrucose, often inconspicuous but always present; pseudocyphellae and maculae absent; soralia arising from the cortex ad initio, on lateral branches, initially punctiform, often enlarging or fusing together in irregular patches, always remaining plane, slightly capitate or excavated only when fully developed (Fig. 3C), isidiomorphs always present, often abundant and very crowded, usually with black tips (Fig. 3C); cortex glossy and \pm thin (4.2–) 5.5–7.2%–8.9 (-10.8); medulla lax to dense, moderately thick, (18.2–) 22.2–25.9%–29.6 (–33.9); axis \pm thin (19.0-) 27.3-33.6%-37.3 (-44.0) (n = 44)(Fig. 3D).

Apothecia very rare, lateral, up to 7 mm of diameter, with marginal fibrils, disk yellow slightly pruinose; pycnidia not seen.

Chemistry. 1. Usnic and norstictic acids (n = 16), K+ red, C-, Pd+ yellow. 2. Usnic, norstictic and salazinic acids (n = 6), medulla K+ yellow turning red, C-, Pd+ yellow orange. 3. Usnic acid (n = 3); spot tests: K-, C-, Pd-.

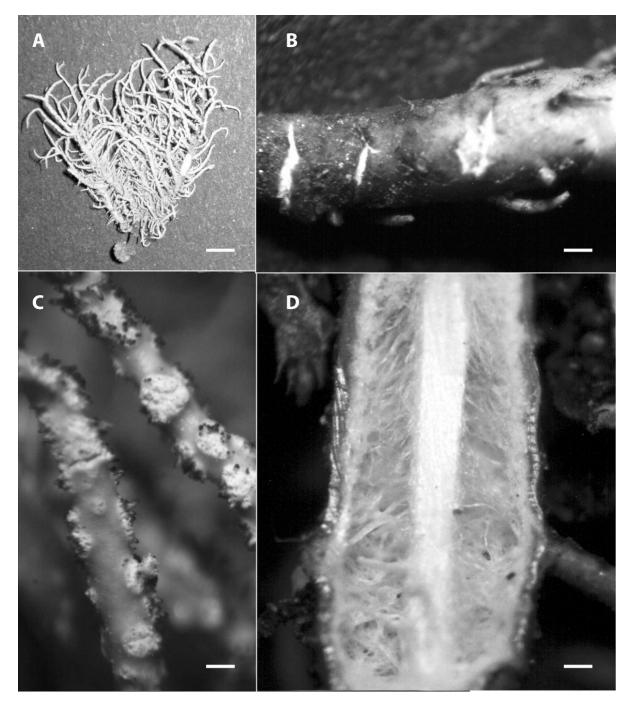


Figure 3. Usnea durietzii. **A.** Thallus (*Rodriguez 789*). **B.** Trunk (*Rodriguez 789*). **C.** Plane to slightly capitate soralia (*Rodriguez 858*). **D.** Cortex, medulla, and axis (*Rodriguez 0055*). Scale. A = 5 mm. B = 0.33 mm. C = 0.25 mm. D = 0.33 mm.

Variation. Usnea durietzii is a very polymorphic species, especially in the shape of branches and segments. Red dots are sometimes present on the whole thallus, being inconspicuous and only visible close to the base in other thalli. Lateral branches are usually constricted at the base, at least on the basal ramifications, but this character tends to be less distinctive in large (and older) thalli with very stiff

branches. Soralia are also variable (in relation to the age and developmental stage of thalli), being punctiform to enlarging to the diameter of the branch or fusing in irregular patches. They however always remain even with the cortex, being only slightly excavating or globose when fully developed.

Diagnosis. Usnea durietzii is characterized by the irregular and inflated branches, usually constricted at

the base and the conspicuous red dots visible at least close to the base; the typical soralia remaining plane even when enlarging and by its anatomy characterized by a thin and glossy cortex, a lax medulla and a thin axis.

Taxonomic notes. Walker (1985) considered this taxon to belong to the subgenus Neuropogon based on the black pigmentation present on the isidiomorphs and sometimes at the tips of lateral branches. Nevertheless this character is quite variable and seems to be correlated with the saxicolous habitat. Phylogenetic studies showed that Usnea durietzii has unresolved relationships with the Neuropogon group (Wirtz et al. 2006). The black pigmentation is never present as distinct bands on the cortex of branches as in the other Neuropogon species. Specimens with apothecia have a yellow disk whereas the Neuropogon species have a black or reddish brown disk (Walker 1985). For these reasons we consider U. durietzii to belong to sub. Usnea and not to Neuropogon gr. Usnea caespitia Motyka was separated from U. durietzii based on the density of branches (Motyka 1936-1938) and on the K reaction (reddish in U. caespitia). However, the soralia morphology, the red pigmentation, the branches morphology and the chemistry fit perfectly in the variation of U. durietzii. The distribution range is also similar. We selected the name U. durietzii instead of U. caespitia because it is best known and has been more cited in the literature.

In Argentina, above 2500 m, *Usnea durietzii* exhibits compact forms, with more irregular branches and extensive black pigmentation that could lead to a misidentification with *U. saxidilatata.* However, the base without proliferating holdfast, the presence of red dots, the lax medulla and the absence of pseudocyphellae distinguish the former species from the latter. In addition, in *U. saxidilatata*, the soralia never enlarge like those in *U. durietzii*.

Ecology and distribution. Usnea durietzii is primarily saxicolous and grows very rarely on shrubs. It is very frequent in high mountains where the rocks outcrops are common and the climate is temperate to cold. In the Sierra Chaco above 2000 m, this species is found together with U. saxidilatata, where it replaces U. amblyoclada in abundance. *Usnea durietzii* has been recorded from the whole Andean Cordillera: Argentina, Bolivia, Chile, Colombia, Ecuador, Panamá and Venezuela (Walker 1985). In Argentina it is distributed in the Central and North Andes and in the highest part of the Sierra Chaco (above 1700 m). Motyka (1936–1938) recorded it in Patagonia. Räsänen (1941) mentioned *U. durietzii* from the Mendoza province; this material was, however, a mixture of *U. durietzii* and *U. saxidilatata*.

Representative specimens examined. ARGENTINA. CORDOBA: Dpto. Calamuchita, Camino de los Linderos, 32°04'06.2"S, 64°52'29.9"W, 1748 m, *Rodríguez 411* (LIL). Dpto. Punilla, Camino de las Altas Cumbres, *Rodriguez 426* (LIL). Dpto. Cruz del Eje, Río Yuspe, *Rodriguez 1780* (LIL). MENDOZA: Dpto. Lujan de Cuyo, Cordón del Plata, Camino a Vallecitos, 32° 59' 45,6"S, 69° 20' 22.2"W, 2399 m, *Rodríguez 0057* (G). Dpto. Las Heras, Quebrada del Cajón de Minas, 1800–2000 m, *Ruiz Leal 5858* (MERL). SAN LUIS: Dpto. Junín, Merlo, 32° 19' 32.1"S, 64° 38' 52.5"W, 1100 m, *Rodríguez 0063* (LIL). TUCUMAN: Dpto. Tafí del Valle, El Infiernillo, 2870 m, *Grundlehner 10.28.3* (G).

Usnea exigua J.M. Rodr. & P. Clerc sp. nov. Mycobank number: MB 519178 Fig. 4
Fungi saxicola. Thallus 3 cm altus, erectus. Basis dilata. Rami principales porcati at irregularis. Soralia absens. Cortex tenuis (6.1%). Medulla moderate tenuis (21.4%). Axis moderate crassus (44.9%). Apothecia communis, sporae 7.1 × 4.7 μm. Acidum usnicum, acidum protocetraricum et substantia ignota (TLC A:6/B:2/C:5) continens.

TYPE: ARGENTINA. BUENOS AIRES: Sierra de la Ventana, Cerro Bahía Blanca, *Adler 35612* (CTES, holotype, G, H, isotypes).CMA: 7/25/36. Chemistry: usnic, protocetraric and unknown I acids.

Description. Thallus short, up to 3 cm, erect, rigid, poorly ramified (**Fig. 4A**), mainly with anisotomic dichotomous ramifications; trunk with proliferating holdfast (**Fig. 4A**), concolorous to slightly brownish, attenuated towards the base; branches \pm fusiform to irregular; lateral branches few, often very short, fibril–like, not narrowed at point of attachment; segments inconspicuous, cylindrical and terete to ridged; fibrils absent or few (probably lateral branches in a initial stage of development); fibercles absent; tubercles short,

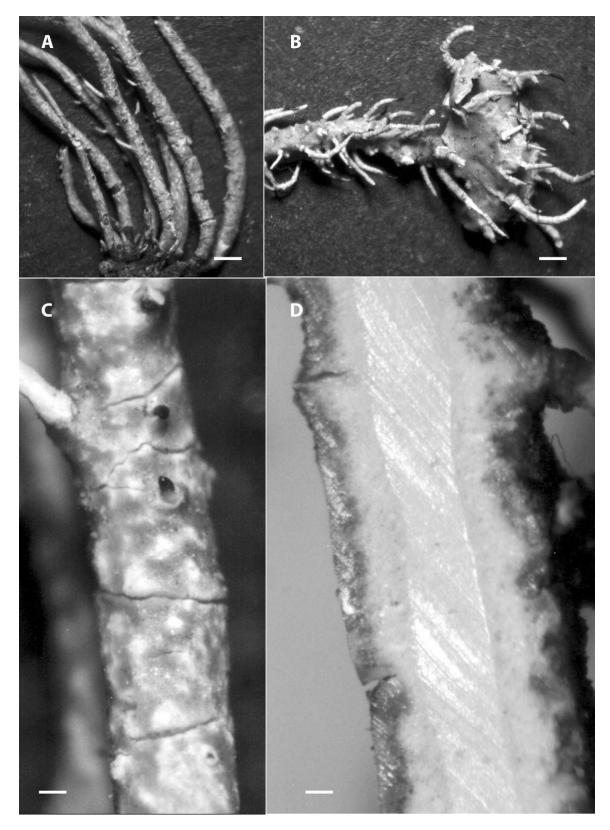


Figure 4. Usnea exigua. **A.** Thallus with proliferating holdfast (holotype). **B.** Terminal branches with terminal apothecia (holotype). **C.** Terminal branch with irregular maculae (holotype). **D.** Cortex, medulla, and axis (*Ruiz* BAFC). Scale. A & B = 1 mm. C & D = 0.33 mm.

eroded at their summit, irregularly distributed but sometimes very frequent on some branches, when absent then maculae numerous; papillae absent; pseudocyphellae absent; maculae irregular to elongated, irregularly distributed, when absent then tubercles numerous (**Fig. 4C**); transversal furrows small and rare; soralia and isidiomorphs absent; cortex mat, with conspicuous reticulations on main branches, thin (4.0–) 4.8–6.1%–7.4 (–8.5); medulla compact to dense, \pm thin (12.5–) 17.1–21.4%–25.7 (–28.5); axis solid, moderately thick (34.0–) 36.6– 44.9%–53.2 (–61.3) (n = 15) (**Fig. 4D**).

Apothecia usually present, few to numerous, mainly serial, sometimes subterminal or terminal (**Fig. 4B**), with few marginal fibrils, disk slightly pruinose; spores simple and hyaline, (5.6–) 6.3–7.1–7.9 (–8.8) × (3.2–) 3.9–4.7–5.5 (–6.4) μ m (n = 39) (**Table 1**); pycnidia and conidia not seen.

Chemistry. Usnic, protocetraric acids and unknown I (n = 5), medulla K+ yellowish brown to K-, C-, Pd+ red.

Variation. The morphology of the branches varies from being fusiform to irregular. The study of more specimens is however needed to have a better idea of the variation of this taxon.

Diagnosis. This species can be recognized by its poorly ramified and short thallus with a proliferating holdfast, its branches that are \pm fusiform and protocetraric acid as main substance.

Taxonomic notes. Young thalli of *Usnea hieronymii* that are not well developed can resemble *U. exigua*, however, the former species has a black base, cylindrical to irregular branches, and a thin medulla (8.5–11.1%–13.7). The spores of *U. exigua* are smaller. *Usnea exigua* differs from *U. fastuosa* in branches morphology, trunk pigmentation and in the thickness and colour of the medulla.

Ecology and distribution. Usnea exigua grows on exposed and dry rocks outcrops. It shares its habitat with *U. amblyoclada* and *U. densirostra.* This species has been collected in the eastern mountains of Argentina and Uruguay.

Additional specimens examined. ARGENTINA. BUENOS AIRES: Dpto. Tandil, Sierra del Tigre, XI–1989, *Ruiz* (BAFC). URUGUAY. LAVALLEJA: 6 km Ruta Nacional 8 hacia el Salto del Penitente, 34° 22' 52.1"S, 55° 04' 34.9"W, 345 m, *Rodríguez 967* (G). Maldonado: Cerro del Toro. Cumbre, 34° 51′ 45.1″S, 55° 15′ 26.8″O, 246 m, *Rodríguez 965* (G). Sierra de las Animas, *Osorio 6927* (MVM).

Usnea fastuosa (Müll. Arg.) Zahlbr., Cat. Lich. Univ. 6: 564. 1930 Fig. 5 Usnea barbata var. fastuosa Müll. Arg., Flora 72: 509.

1889. TYPE: ARGENTINA. BUENOS AIRES: Punta de Pigue [Pigüe], 1881, *Lorentz* (G! holotype). CMA: 12/12/52 (thallus a), 10.5/14.5/50 (thallus b). Chemistry: usnic, norstictic, connorstictic, salazinic (faint) acids (thalli a & b).

Description. Thallus shrubby to subpendulous, up to 7 cm, very rigid, green greyish in the field, moderately ramified, mainly with anisotomicdichotomous ramifications; trunk with proliferating holdfast (Fig. 5A), brownish to black, black pigmentation sometimes extending to main branches with conspicuous annular or reticular cracks; branches irregular to cylindrical; lateral branches not narrowed at point of attachment; segments cylindrical, terete to slightly ridged; fibrils absent or present (young branches?), up to 5 mm; tubercles present, sometimes scarce, irregularly distributed, frequent on terminal branches under the apothecia (Fig. 5B); papillae absent; pseudochyphellae absent; maculae always present, mainly on secondary and terminal branches, punctiform, elongated and/or irregular, sometimes fusing together (Fig. 5C), often developing into pseudocyphellae on terminal branches; foveoles absent; soralia and isidiomorphs absent; cortex conspicuously cracked, mat to slightly glossy, \pm thick (6.0–) 6.7–8.0%–9.3 (– 11.0); medulla compact, often orange pigmented and extremely thin (4.9-) 6.5-9.1%-11.7 (-14.7); axis sometimes fistulous on main branches, very thick (56.0-) 60.1-65.7%-71.3 (-74.1) (n = 18) (Fig. 5D).

Apothecia always present, mainly lateral, with few marginal fibrils (**Fig. 5B**), disc not pruinose, spores simple and hyaline, (6.4–) 6.8–7.9–9.0 (–10.4) \times (3.2–) 4.0–5.0–6.0 (–7.2) µm (n = 63) (**Table 1**), pycnidia and conidia not seen.

Chemistry. 1. Salazinic, norstictic acids, unknown II and III (n = 16), medulla K+ yellow turning red, C-, Pd+ yellow orange. 2. Protocetraric, fumarprotocetraric acids, unknown II and III (n =11), medulla K+ yellow brownish to K-, C-, Pd+ red.

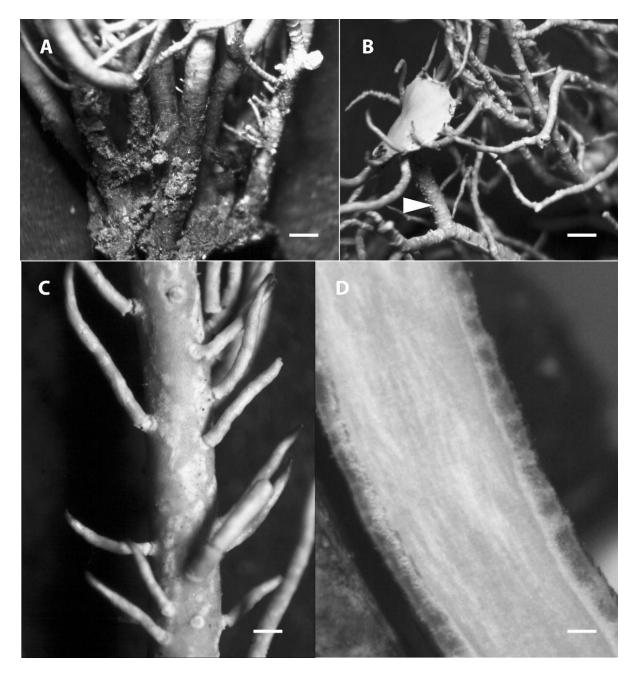


Figure 5. Usnea fastuosa. **A.** Trunk with proliferating holdfast (*Rodriguez 166*). **B.** Terminal branches with tubercles (arrow) and apothecia (*Rodriguez 166*). **C.** Irregular maculae (*Rodriguez 166*). **D.** Cortex, medulla, and axis (*Osorio 7332*). Scale. A & B = 1 mm. C = 0.25 mm. D = 0.33 mm.

Variation. The density of ramifications and tubercles are the most variable characters in this species. Morphology and distribution of the maculae are also variable. Chemotype 1 is more frequent in Eastern Argentina whereas chemotype 2 is more frequent in Uruguay. Specimens with chemotype II tend to have fewer tubercles in the terminal branches under the apothecia, fewer fibrils and branches that are more cylindrical. However, these characters are

very variable in *Usnea* and also among specimens of the same species.

Diagnosis. The diagnostic features of this species are the extremely thin and orange pigmented medulla, the large axis, the cylindrical branches, the presence of maculae and the unknown substances II and III in the medulla.

Taxonomic notes. Usnea fastuosa resembles *U. amaliae.* However, the latter lacks the black base, the

tubercles, the fibrils and the orange medulla. The ramification in *U. amaliae* is isotomic–dichotomous, the medullar substances are psoromic and conpsoromic acids, the cortex is thicker and the distribution range corresponds to the tropical Andes in Bolivia. For differences with *U. densirostra* and *U. hieronymi* see under these species.

Ecology and distribution. Usnea fastuosa grows strictly on rocks in humid areas and is locally abundant in its distribution range. It is commonly found sharing the rocks surface with others saxicolous species like *U. densirostra* or *U. exigua*. In Argentina, the distribution corresponds with the Ventania and Tandilia mountains from the East of the Buenos Aires province. This species is also present in Uruguay.

Representative specimens examined. ARGENTINA. BUENOS AIRES: Dpto. Tandil, Tandil, 37°20'26.7"S, 59°11'22.7"O, 337 m, *Rodriguez & Fantini 168* (LIL). Dpto. Tornquist, Sierra de la Ventana, 38°04'37.5"S, 62°00'06.5", 521 m, *Rodriguez & Fantini 166* (LIL). URUGUAY. MALDONADO: Pan de Azúcar, 300 m, *Verter 122005* (G). Sierra de las Animas, *Osorio* 122004 (G).

Usnea hieronymii Kremp. Flora 61: 436. 1878.

Fig. 6

TYPE: ARGENTINA. prope. Oran, Sierra Tucreman (Tucumán), ad saxa, *Lorentz & Hieronymus* (M! lectotype designated here; G! isotype).
CMA: 4.5/33.5/19. Chemistry: usnic and norstictic acids.

= Usnea hieronymii var. adusta Kremp. Flora 61: 436. 1878. TYPE: ARGENTINA, prope. Oran, Sierra Tucreman (Tucumán), ad saxa, 7–8000, Lorentz & Hieronymus (M! lectotype designated here). syn. nov.

Description. Thallus shrubby, erect, up to 7 cm long, very rigid (**Fig. 6A**), with anisotomic–dichotomous ramifications; trunk with a proliferating holdfast and with black pigmentation sometimes extending above the first ramification, with cracks in a reticular pattern; branches cylindrical to \pm irregular, lateral branches not narrowed at point of attachment; segments cylindrical and terete to ridged; fibrils scarce to abundant, 2–4 mm long; fibercles common mainly in the basal part of the thallus; tubercles numerous, sometimes eroded at the top (**Fig. 6C**); papillae absent; pseudocyphellae

absent or present, if present very conspicuous, elongated, twisted and sometimes slightly stipitate on the top of ridges (**Fig. 6B**), distributed on the whole thallus; maculae absent, terminal branches thick with few ramifications and tips black pigmented; foveoles sometimes present; soralia and isidiomorphs absent; cortex glossy, \pm thin (4.3–) 5.1–7.3%–9.4 (–11.0); medulla compact and thin (7.2–) 8.5–11.1%–13.7 (–15.7); axis very thick (48.9–) 55.1–63.0%–70.9 (–73.8) (n = 14) (**Fig. 6D**).

Apothecia scarce, mostly terminal and subterminal, sometimes serial with long marginal fibrils, 4–5 mm in diameter, disk \pm pruinose; spores simple and hyaline, (6.4–) 7.6–8.4–9.2 (–10.4) × (4.0–) 4.6–5.4–6.2 (–7.2) µm (n = 89) (**Table 1**); pycnidia not seen.

Chemistry. 1. Usnic, norstictic, \pm protocetraric, \pm diffractaic acids (n = 17); medulla K+ yellow turning red, C- or C+ yellow, KC- or KC+ yellow, Pd+ yellow to reddish. 2. Usnic and protocetraric acids (n = 2); medulla K+ yellow or K-, C-, Pd+ red. 3. Usnic and diffractaic acids (n = 1); medulla K-, C+ yellow, KC+ yellow, Pd-.

Variation. In the type collection, all "individuals" have been meticulously separated from each other so that the colonial growth with proliferating holdfast cannot be recognized anymore. However, in the field, the growth from a proliferating holdfast is a typical character of this species. The presence of pseudocyphellae and the density of tubercles are variable, the tubercles being eroded or not. The frequency and position of apothecia are variable as well as the black pigmentation of the base. The three chemotypes lack any diagnostic morphological or anatomical differentiation.

Diagnosis. Usnea hieronymii is characterized by proliferating holdfast, the black base, the thin, compact and white medulla and the presence of numerous tubercles.

Taxonomic notes. Usnea hieronymii resembles U. fastuosa based on the basal part morphology, the thin cortex and the length of spores. The latter species has an orange and extremely thin medulla (6.5–9.1% –11.7), maculae instead of pseudocyphellae (in terminal branches maculae may develop into pseudocyphellae) and unknown substances II and III in the medulla. For differences

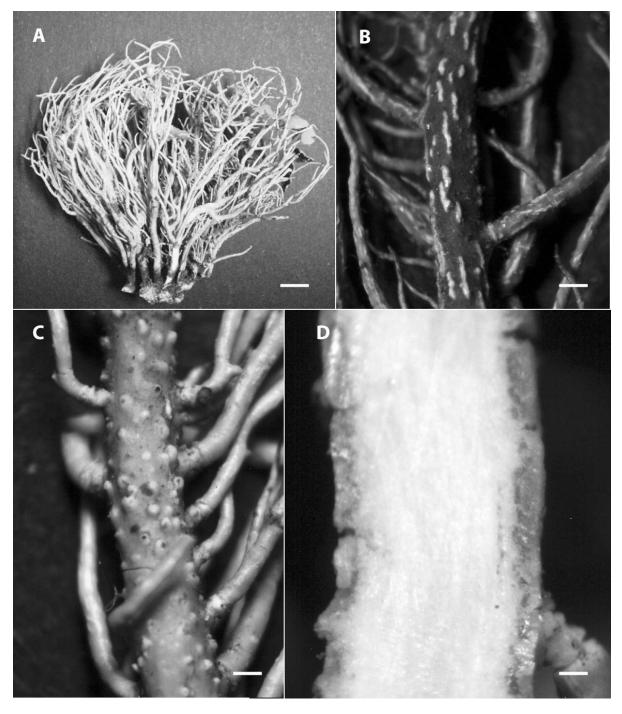


Figure 6. Usnea hieronymii. **A.** Thallus with proliferating holdfast (*Rodriguez 887*). **B.** Terminal branch with elongated pseudocyphellae (*holotype*). **C.** Terminal branch with tubercles (*Rodriguez 887*). **D.** Cortex, medulla, and axis (*Rodriguez 918*). Scale. A = 5 mm. B = 0.5 mm. C = 0.33 mm. D = 0.66 mm.

with *U. densirostra* and *U. exigua*, see under these species. The type material of *U. hieronymii* var. *adusta* is a group of specimens without any difference with *U. hieronymii* beyond the size of the thalli.

Ecology and distribution. This species is strictly saxicoulous, present in the central

mountains of Argentina (Córdoba and Tucumán provinces), growing between 2000 and 3000 m. It has been reported from Argentina, Bolivia and Uruguay (Motyka, 1936–1938). However, the record from Uruguay corresponds to *Usnea fastuosa*.

Representative specimens examined. ARGENTINA. CORDOBA: Dpto. Calamuchita, Camino de los Linderos, 2700 m, *Rodríguez 843* (LIL). Dpto. Punilla, Los Gigantes, *Rodríguez 887* (LIL). TUCUMAN: Dpto. Chicligasta, La Cascada de las Cuevas, 2800 m, *Meyer 13754* (LIL).

Usnea lutii J.M. Rodr. & P Clerc sp. nov. Mycobank number: MB 519179 Fig. 7

- Fungi saxicola. Thallus 9 cm altus, erectus. Basis dilata, brunneolus niger ad distinctum nigrum. Rami principales teretes ad irregulares. Tubercula numerosae. Soralia isidiosa punctiformia. Cortex tenuis (6.1%). Medulla tenuis (12.8%). Axis crassus (62.3%). Apothecia rara. Acidum usnicum, acidum norsticticum et \pm acidum protocetraricum continens.
- TYPE: ARGENTINA. CORDOBA: Dpto. Calamuchita, Cerro Champaqui, 32° 01′ 03.3″S, 64° 56′
 18.8″W, 2640 m, 16 May 2009, *Rodríguez 980* (CTES, holotype, G, H, isotypes). CMA: 5.5/9.1/
 70.8. Chemistry: usnic and norstictic acids.

Description. Thallus erect, rigid, up to 9 cm long (Fig. 7A), branching mainly anisotomicdichotomous; trunk black to brownish, with proliferating holdfast (Fig. 7B), annular and reticulated cracks; branches cylindrical to irregular, lateral branches not narrowed at point of attachment; segments cylindrical and terete to ridged with \pm conspicuous annular and reticulated cracks; fibrils scarce, up to 4 mm long, blackened at the tips; fibercles few to numerous; tubercles numerous; papillae absent; pseudocyphellae irregular to elongated and \pm twisted on lateral branches (Fig. 7C); maculae absent; transversal furrows and foveoles absent; soralia arising from the top of tubercles or on fibercles, punctiform, even with cortex to slightly convex, smaller than half the diameter of the branch, partly or not confluent (Fig. 7D); isidiomorphs blackened at the tips (Fig. 7D); cortex glossy to mat, thin (3.5–) 4.6–6.1%– 7.6 (-8.5), medulla compact, thin (6.0-) 9.2-12.8%-16.4 (-22.8); axis sometimes fistulose in main branches, very thick (37.4-) 54.5-62.3%-70.1 (-74.0) (n = 22) (Fig. 7E).

Apothecia very rare, lateral, up to 5 mm in diameter; disk yellow and slightly pruinose, with marginal fibrils.

Chemistry. Usnic, norstictic and \pm protocetraric acids (n = 13); medulla K+ red, C-, Pd+ yellow to reddish.

Etymology. The specific epithet was chosen in honour of Professor Ricardo Luti from the University of Córdoba. He was one of the first researchers to study the vegetation and ecology of the mountain systems where *Usnea lutii* grows.

Variation. The morphology of the branches and segments is variable in this species. Also the pigmentation of the basal part can vary from black to brown.

Diagnosis. Among the characters that distinguish *Usnea lutii* from the other sorediate saxicolous species are the presence of tubercles and pseudocyphellae, the punctiform never enlarging soralia and the thin medulla.

Taxonomic notes. Usnea lutii is separated from U. saxidilatata based on the thickness of the medulla and axis, the conspicuous presence of tubercles and the absence of foveoles. Also the latter has soralia that are mainly confluent. The presence of pseudocyphellae, tubercles, proliferating holdfast and the blackish pigmentation of the basal part distinguish U. lutii from U. amblyoclada. Usnea lutii has morphological, anatomical and chemical similarities with U. hieronymii. These two species can be considered as forming a species-pair.

Ecology and distribution. This species is exclusively saxicolous. So far, it is known only from the Sierra Chaco mountains in central Argentina above 1700 m.

Additional specimens examined. ARGENTINA. CORDOBA: Dpto. Calamuchita, Cerro Champaqui, 31° 59' 15.1"S, 64° 56' 12.2"W, 2795 m, *Rodríguez 983* (G). Cerro Champaqui, 31° 59' 24.7"S, 64° 56' 11.2"W, 2745 m, *Rodríguez 991* (G) Camino de los Linderos, 2700 m, *Rodríguez 890* (G), 914,1782, 904, 937 (CORD) Dpto. Punilla, Los Gigantes 31° 25' 09.2"S, 64° 48' 34.2" W, 2290 m, *Rodríguez* 785 (G), 909 (CORD). Camino Altas Cumbres, 1700 m, *Rodríguez 906* (CORD). Camino Altas Cumbres 2100 m, *Rodríguez 939* (CORD).

Usnea saxidilatata J.M. Rodr. & P. Clerc sp. nov. Fig. 8

Mycobank number: MB 519180

Fungi saxicola. Thallus 6 cm altus, erectus. Basis dilata. Rami principales porcati at irregularis. Papillae et

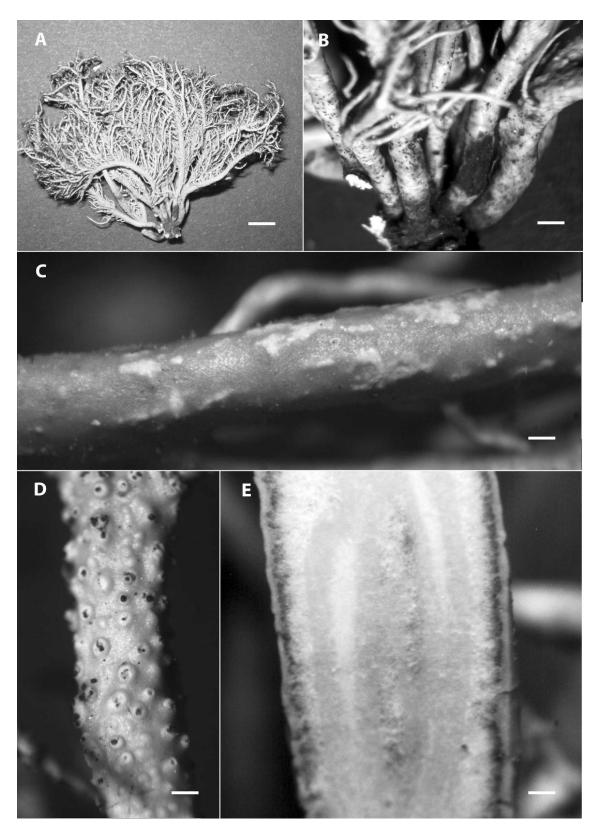


Figure 7. Usnea lutii. **A.** Thallus (holotype). **B.** Trunk with proliferating holdfast (holotype). **C.** Irregular pseudocyphellae (Rodriguez 904). **D.** Tubercles, soralia and isidiomorphs (Rodriguez 904). **E.** cortex, medulla, and axis (Rodriguez 909). Scale. A = 10 mm. B = 1 mm. C, D & E = 0.33 mm.

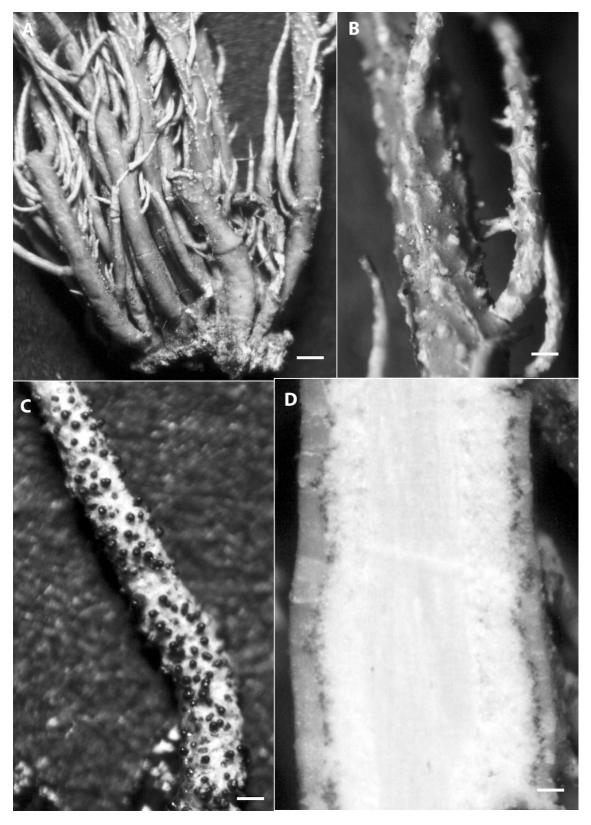


Figure 8. Usnea saxidilatata. **A.** thallus with proliferating holdfast and fibrils (*Grundlehner 13.28.3*). **B.** Punctiform and isolated soralia in early stage (*Grundlehner 13.28.3*). **C.** Soralia totally confluent with black isidiomophs (*Grundlehner 13.28.3*). **D.** Cortex, medulla, and axis (*holotype*). Scale. A = 1 mm. B = 0.28 mm. C & D = 0.25 mm.

tubercula absens. Soralia isidiosa punctiformia. Cortex tenuis (5.5%). Medulla moderate tenuis (22.0%). Axis moderate crassus (47.5%). Apothecia ignota. Acidum usnicum et acidum norsticticum continens.

TYPE: ARGENTINA. MENDOZA: Dpto. Lujan de Cuyo, Cordón del Plata, Camino a Vallecitos, 32° 59' 45,6"S, 69° 20' 22.2"W, 2399 m, *Rodríguez 0056* (CTES, holotype, G, H, isotypes). CMA: 5.8/ 14.1/60. *Chemistry*: usnic and norstictic acids.

Description. Thallus short, up to 6 cm, erect, rigid (Fig. 8A), branching mainly anisotomicdichotomous; trunk concolorous with main branches, slightly attenuated, with proliferating holdfast (Fig. 8A); branches \pm fusiform to irregular, lateral branches narrowed or not at point of attachment; sometimes numerous and crowded; segments conspicuous or not, cylindrical, terete to \pm ridged with \pm conspicuous annular and reticulated cracks; fibrils numerous and short, up to 2 mm long, \pm irregularly crowded; fibercles scarce to numerous; tubercles absent; papillae absent; pseudocyphellae irregular to elongated and \pm twisted on lateral branches (Fig. 8B), sometimes absent; maculae absent; transversal furrows and foveoles always present mainly in basal part; soralia mainly on terminal branches, arising from the cortex ad initio or on fibercles, punctiform (Fig. 8B), even with cortex to slightly convex, smaller than half of the branch, partially to totally confluent on terminal branches (Fig. 8C); isidiomorphs short and thick, blackened at the tips, giving a blackish colour to the branches when numerous (Fig. 8C); cortex mat, thin (2.5-) 4.2-5.5%-6.8 (-7.3); medulla compact to dense, \pm thin (8.6–) 14.8–20.7%–26.6 (–33.5); axis thick, (22.0-) 36.3-47.5%-58.7 (-68.9) (n = 19)(Fig. 8D).

Apothecia not seen.

Chemistry. Usnic and norstictic acids (n = 15), medulla K+ red, C-, Pd+ yellow.

Etymology. The specific epithet represents the saxicolous substrate and the characteristics of the basal part (trunk with proliferating holdfast that means "dilatata" in Latin).

Variation. Specimens from high elevations show more compact forms with more irregular branches and ridged segments. In these conditions, thalli are

more blackish and densely branched, especially in the terminal parts.

Diagnosis. Among the characters that distinguish Usnea saxidilatata from the other sorediate saxicolous species are the punctiform never enlarging and confluent soralia, the \pm thick and compact to dense medulla, the proliferating holdfast and norstictic acid as main medullar substance.

Taxonomic notes. Superficially Usnea saxidilatata resembles the compact forms of U. amblyoclada but the confluent soralia, the presence of pseudocyphellae and the morphology of the basal part readily separate the two species. For differences with U. durietzii, see under this species.

Ecology and distribution. This species is always saxicolous and share its habitat with *Usnea durietzii*. It has been collected in the Andes, Pre–Andes and Sierra Chaco mountains above 2000 m. More collections are needed to understand the whole distribution pattern of this species in South America. The ecological amplitude of this species is similar to the one of *U. durietzii*.

Additional specimens examined. ARGENTINA. CORDOBA: Dpto. Calamuchita, Cerro Champaqui, 31° 59' 15.1"S, 64° 56' 12.2"W, 2795 m, *Rodríguez* 982 (G). Camino de los Linderos, Bifurcación, 32° 01' 05.8"S, 64° 55' 45.1"O, 2665 m, *Rodríguez* 984, 893 (G). Dpto. Punilla, Los Gigantes, 2000 m, Rodriguez 1003 (CTES). MENDOZA: Dpto. Lujan de Cuyo, Cordón del Plata, Vallecitos, 32° 58' 23.6"S, 69° 21' 30.5", 3006 m., *Rodríguez 0059* (LIL). Dpto. Las Heras, Quebrada del Cajón de Minas, 1800–2000 m, *Ruiz Leal 5858* (MERL). TUCUMAN: Dpto. Tafí del Valle, El Infiernillo km 479, 3050 m, *Grundlehner 13.28.3* (G). El Infiernillo km 487, 2800 m, *Grundlehner 24.28.3b* (G).

Secondarily saxicolous species.

Some species like *Usnea columbiana, U. cornuta, U. dasaea,* and *U. cf. perhispidella* can be found occasionally on rocks. They are primarily corticolous and common in Argentina. They will be treated in more details in further contributions.

Excluded taxa

Usnea amaliae Motyka, Lich. Gen. Usnea Stud. Monogr. Pars Syst. 2: 634. 1936–1938. TYPE: BOLIVIA. In Monte Grande Chiquitos, 200 m, 1907 Herzog (M!, holotype). CMA: 12/16/44. *Chemistry*: psoromic and conpsoromic acids.

Usnea amalie was mentioned wrongly for Argentina and Uruguay, due to misidentifications with U. fastuosa, from which it differs by the few ramifications, a reticulate and concolorous trunk and the lack of papillae, tubercles and fibrils. Usnea amaliae has subterminal or lateral apothecia, without or with scarce marginal fibrils. The cortex is mat, reticulate and cracked, thick (10–13%); the medulla is white, thin and compact (14–20%); the axis is straight, sometimes fistulose in main branches and very thick (33–65%). This species is probably very closely related to U. roccelina Motyka, a strictly saxicolous species occurring in the Neotropical Andes further north.

Usnea miliaria Taylor, Hook. London J. Bot., 6: 192. 1847. TYPE: CHILE. Arica, *Cumming* 1477 (G!, holotype).

The report of this species in Argentina (Osorio 1968) was based on misidentifications of *U. fastuosa* specimens. Therefore, this species is excluded from the Argentinian flora.

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LITERATURE CITED

- Brodo, I. M., S. Duran Sharnoff & S. Sharnoff. 2001. Lichens of North America. Yale University Press, New Haven, Connecticut.
- Cabrera, A. L. 1971. Fitogeografía de la República Argentina. Boletín de la Sociedad Argentina de Botánica 14: 1–42.
- Clerc, P. 1984. Contribution à la révision de la systématique des usnées (Ascomycotina, Usnea) d'Europe. I. Usnea florida (L.) Wigg. emend. Clerc. Cryptogamie, Bryologie et Lichénologie 5: 333–360.
 - —. 1987a. Systematics of the Usnea fragilescens aggregate, and its distribution in Scandinavia. Nordic Journal of Botany 7: 479–495.
 - —. 1987b. On the morphology of soralia in the genus *Usnea*. Bibliotheca Lichenologica 25: 99–102.

— . 1992. Some new or interesting species of de genus Usnea (Lichenized Ascomycetes) in de British Isles. Candollea 47: 513–526.

. 1997. Notes on the genus *Usnea* Dill. ex Adanson. Lichenologist 29: 209–215.

- . 1998. Species concepts in the genus *Usnea* (Lichenized Ascomycetes). Lichenologist 30: 321–340.
- ——. 2004. Notes on the genus *Usnea* Adanson. II. Bibliotheca Lichenologica 88: 79–90.
- ——. 2006. Synopsis of Usnea (lichenized Ascomycetes) from the Azores with additional information on the species in Macaronesia. Lichenologist 38: 191–212.
- 2007. Usnea. Pages 302–335. In T. H. Nash III, C. Gries & F. Bungartz (eds.), Lichen Flora of the Greater Sonoran Desert Region. Volume 3. Lichens Unlimited, Arizona State University, Tempe, Arizona.
- & M. A. Herrera Campos. 1997. Saxícolous species of Usnea subgenus Usnea (Lichenized Ascomycetes) in North America. The Bryologist 100: 281–301.
- Culberson, C. F. & K. Ammann. 1979. Standardmethode zur Dünnschichtchromatographie von Flechtensubstanzen. Herzogia 5: 1–24.
- De la Sota, E. R., G. E. Giudice, M. Ponce, J. P. Ramos & M. Arturi. 2004. Relaciones Fitogeográficas de la Flora Pteridofítica Serrana Bonaerense. Boletín de la Sociedad Argentina de Botánica 39: 181–194.
- Fos, S. & P. Clerc. 2000. The lichen genus *Usnea* on *Quercus* suber in Iberian cork–oak forests. Lichenologist 32: 67–88.
- Halonen, P., P. Clerc, T. Goward, I. M. Brodo & K. Wulff. 1998.Synopsis of de genus *Usnea* (Lichenized Ascomycetes) inBritish Columbia, Canada. The Bryologist 101: 36–60.

Herrera–Campos, M. A., P. Clerc & T. H. Nash. 1998. Pendulous species of *Usnea* from the temperate forests in Mexico. The Bryologist 101: 303–329.

- —, T. H. Nash & A. Zambrano García. 2001. Preliminary study of the Usnea fragilescens aggregate in Mexico. The Bryologist 104: 235–259.
- InfoStat. 2009. InfoStat versión 2009. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- James, P. W., P. Clerc & O. W. Purvis. 1992. Usnea. Pages 620–629. In O. W. Purvis, B. J. Coppins, D. L. Hawksworth, P. W. James & D. M. Moore (eds.), The Lichen Flora of Great Britain and Ireland. Natural History Museum Publications, London, UNited Kingdom.
- Lamb, I. M. 1958. La vegetación liquénica de los Parques Nacional Patagónicos. Anales de Parques Nacionales 7: 1–188.
- Motyka, J. 1936–1938. Lichenum generis *Usnea* studium monographicum pars systematica. 2 vols. Leopoli: privately printed.
- Ohmura, Y. 2001. Taxonomic study of the genus *Usnea* (lichenized Ascomycetes) in Japan and Taiwan. Journal of the Hattori Botanical Laboratory 90: 1–96.

—— & H. Kashiwadani. 2000. *Usnea subfloridana* Stirt. (Parmeliaceae) and its related species in Eastern Asia. Journal of Japanese Botany 75: 164–177.

- & H. Kanda. 2004. Taxonomic status of section *Neuropogon* in the genus *Usnea* elucidated by morphological comparisons and ITS rDNA sequences. Lichenologist 36: 217–225.
- Osorio, H. S. 1967. Contribution to the lichen flora of Uruguay III. Some additional new localities. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 4: 1–10.
 - . 1968. Contributions to the Lichen Flora of Argentina.
 I. Some Lichens from the Province of Buenos Aires.
 Bryologist 71: 285–286.
 - ——. 1980. Contribution to the lichen flora of Uruguay XIII. Lichens from Sierra Mahoma, San Jose Department. Phytologia 45: 217–220.
 - ——. 1981. Contribution to the lichen flora of Uruguay XVI. Lichens collected by Mariano B. Berro. Phytologia 47: 393–396.
 - —. 1982. Contribution to the lichen flora of Uruguay XVII. The scientific name of the "Yerba de la Piedra". Phytologia 52: 217–220.
 - —. 1987. Contributions to the Lichen Flora of Argentina. XVI. Lichens from Sierra de la Ventana, Buenos Aires Province. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 4: 1–11.
 - —. 1992. Contribution to the lichen flora of Uruguay.
 XXIV. Lichens from Sierra San Miguel, Rocha Department.
 Boletín de la Sociedad Argentina de Botánica 28: 37–40.
 - —. 1993. Contribution to the lichen flora of Uruguay. XXVI. Additions and corrections. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 5: 1–6.
 - —. 1995. Contribution to the lichen flora of Uruguay. XXVIII. Lichens from southern Rocha. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 5(103): 1–12.
 - —. 1996. Contribution to the lichen flora of Uruguay. XXIX. Lichens from Rivera Department. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 5: 1–5.
 - —. 1997. Contribution to the lichen flora of Brazil. XXXIV. Lichens from Laguna, Santa Catarina State. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 6: 1–4.
 - —. 2001. Contribution to the lichen flora of Uruguay. XXXIV. Lichens from Isla de Flores, Rio de la Plata. Comunicaciones Botánicas Museos Nacionales de Historia Natural y Antropología 6: 1–7.
 - 2005. Contribution to the lichen flora of Uruguay. XL.
 New or additional records. Comunicaciones Botánicas,
 Museo de Historia Natural y Antropología [Montevideo]
 6: 1–8.

- Øvstedal, D. O. & R. I. Lewis Smith. 2001. Lichens of Antarctica and South Georgia: A Guide to Their Identification and Ecology. Studies in Polar Research, Cambridge University Press, Cambridge, United Kingdom.
- Räsänen, V. 1939. De Usnea nova ex Argentinia. Borbasia 1: 115.
 ——. 1941. La Flora liquenológica de Mendoza (Argentina).
 Anales de la Sociedad Científica Argentina 131: 97–110.
- Rodriguez, J. M. & C. Estrabou. 2008. Usnea amblyoclada "barba de piedra" (Ascomycetes liquenizados) en Argentina. Boletín de la Sociedad Argentina de Botánica 43: 221–225.
- Stevens, G. N. 2004. Usneaceae. Pages 78–98 & 107–115. In P. M. McCarthy & K. Mallett (eds.), Flora of Australia. Volume 56A, Lichens 4. ABRS/CSIRO Australia, Melbourne, Australia.
- Swinscow, T. D. V. & H. Krog. 1974. Usnea subgenus Eumitria in in East Africa. Norwegian Journal of Botany 21: 165–185.
- ——— & ——. 1975. The Usnea undulata aggregate in East Africa. Lichenologist 7: 121–138.
- ——— & ———. 1976b. The *Usnea articulata* aggregate in East Africa. Norwegian Journal of Botany 23: 261–268.
- & . 1978. Pendulous species of Usnea in East Africa. Norwegian Journal of Botany 25: 221–241.
- & . 1979. The fruticose species of Usnea subgenus Usnea in East Africa. Lichenologist 11: 207–252.
- Truong, C., Bungartz, F. & P. Clerc. 2011. The genus *Usnea* in the tropical Andes and Galapagos Islands: species with a red–orange cortical or subcortical pigmentation. The Bryologist 114: xxx–xxx.
- Walker, J. 1985. The lichen genus Usnea subgenus Neuropogon. Bulletin of the British Museum (Natural History) Botany 13: 1–130.
- White, F. J. & P. W. James. 1985. A new guide to microchemical tecniques for the identification of lichen substances. Bulletin British Lichen Society 57(supl.): 1–41.
- Wirtz, N., C. Printzen, L. Sancho & H. T. Lumbsch. 2006. The phylogeny and classification of *Neuropogon* and *Usnea* (Parmeliaceae, Ascomycota) revisited. Taxon 55: 367–376.

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- **Supplementary Fig. S1.** Saxicolous lichen communities with *Usnea saxidilatata* in Central Andes, Western Argentina.
- Supplementary Fig. S2. Known distributions of saxicolous Usnea subgenus Usnea species in Argentina and Uruguay. Some dots on the maps may represent more than one locality. A. U. amblyoclada.
 B. U. densirostra. C. U. durietzii. D. U. exigua. E. U. fastuosa. F. U. hieronymii. G. U. lutii. H. U. saxidilatata.