

The genera *Hypotrachyna* and *Remototrachyna* (Parmeliaceae, Ascomycota) in northeastern Argentina

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Abstract: Morphological, chemical and phylogenetic examination of the lichen genera *Hypotrachyna* and *Remototrachyna* (Parmeliaceae, Ascomycota) revealed the presence of 12 species in northeastern Argentina. Three of them, *H. osseoalba*, *H. subformosana*, and *R. costaricensis*, are recorded for the first time for the country. The known distribution range of other eight species in the region is also extended. Distribution and comments are presented for all species, and descriptions and illustrations for most relevant records. The phylogenetic relationships of the species of *Hypotrachyna* and *Remototrachyna* reported from northeastern Argentina are analyzed.

Keywords: lichens, dichotomous rhizines, taxonomy, phylogeny

INTRODUCTION

The genus *Hypotrachyna* (Vain.) Hale, as traditionally defined, is characterized by its foliose thallus, sublinear to linear lobes with subtruncate to truncate apices, usually eciliate, dichotomously branched rhizines evenly distributed over the black lower surface, bifusiform conidia, and simple, ellipsoid to subglobose, middle-sized ascospores (Hale, 1974; Sipman et al., 2009). It currently includes *Everniastrum* Hale, *Cetrariastrum* Sipman, and *Parmelinopsis* Elix & Hale, which were reduced to subgenera based on a phylogenetic analysis (Divakar et al., 2013). *Remototrachyna* Divakar & A. Crespo was segregated from *Hypotrachyna*, differing in the subirregular, wider lobes with rounded apices, shorter rhizines, a scleroplektenchymatous exciple, and larger ascospores (Divakar et al., 2010). It comprises only 20 species (Lücking et al., 2017), none of which have been previously reported from Argentina.

Hypotrachyna as currently defined comprises ca. 270 species (Lücking et al., 2017; Aptroot & Cáceres, 2018; Kirika et al., 2019; Lendemmer & Allen, 2019, 2020; Wang et al., 2020; Rodrigues et al., 2022), of which 36 are known in Argentina (Rodríguez et al., 2016; Calvelo & Liberatore, 2002; Adler & Calvelo, 2007a,b). Only seven were reported so far in the northeastern region of the country (Ferraro, 1981; Osorio, 1981;

Sipman et al., 2009; Michlig & Ferraro, 2012). Recent fieldwork by the authors provided many new specimens of *Hypotrachyna* s. l., which were studied and the results are here presented.

MATERIAL AND METHODS

Morphological and chemical examination

About 100 specimens from northeast Argentina deposited at CTES herbarium were studied (including additional samples from Salta province). Morphological analysis was carried out using standard stereoscopic and compound light microscopes. Apothecia and pycnidia were sectioned by hand with a razor blade for examination. Lichen substances were checked with spot tests with 10% potassium hydroxide (K) and sodium hypochlorite (C), UV fluorescence (360 nm), and TLC with solvents C and G following standard methods (Orange et al., 2010). Only representative specimens are cited below and the following abbreviations are used: PP – Provincial Park; NP – National Park; NSR – Natural Strict Reserve; YBR – Yaboty Biosphere Reserve. In “Distribution” new reports are marked with an asterisk (*). Descriptions and illustrations for most relevant records are presented.

Phylogenetic analyses

Fifteen sequences belonging to nine species were newly generated and analyzed together with 24

Table 1. Collection data and GenBank accession numbers of specimens used in this study. Newly generated sequences are indicated in bold.

Species	Locality	Collector (s) and collection number	Genbank accession no.	Reference
<i>Bulbothrix isidiza</i>	Argentina, Misiones	Michlig et al. 2842	OQ971988	This study
<i>B. regnelliana</i> (1)	Argentina, Corrientes	Michlig & Niveiro 2568	OQ971991	This study
<i>B. regnelliana</i> (2)	Argentina, Corrientes	Rodriguez et al. s/n	OQ971989	This study
<i>B. regnelliana</i> (3)	Argentina, Corrientes	Michlig et al. 2572	OQ971990	This study
<i>B. tabacina</i> (1)	Congo, Kahuri-Biega National Park	Mamush s/n	GQ919267	Divakar et al. (2010)
<i>B. tabacina</i> (2)	Kenya, Kakamega district	Crespo, Lumbsch & Divakar s/n	GQ919268	Divakar et al. (2010)
<i>B. viatica</i>	Argentina, Misiones	Michlig et al. 2781	OQ971992	This study
<i>Hypotrachyna bonariensis</i>	Argentina, Corrientes	Michlig & Niveiro 2681	OQ971986	This study
<i>H. dactylifera</i>	Bolivia, Aniceto Arce	Flakus 18584	KF380893	Divakar et al. (2013)
<i>H. dentella</i> (1)	Bolivia, Aniceto Arce	Flakus 18757	KF380894	Divakar et al. (2013)
<i>H. dentella</i> (2)	Bolivia, Aniceto Arce	Flakus 18528/1	KF380895	Divakar et al. (2013)
<i>H. horrescens</i> (1)	Spain, La Coruña	Carvallal s/n	AY581085	Blanco et al. (2004)
<i>H. horrescens</i> (2)	USA, North Carolina	Lendemmer 43931	MT482178	Lendemmer & Allen (2020)
<i>H. imbricatula</i> (1)	Costa Rica, Manzanillo	Molina s/n	DQ279502	Divakar et al. (2006)
<i>H. imbricatula</i> (2)	South Africa, W Cape	Crespo et al. s/n	DQ279503	Divakar et al. (2006)
<i>H. imbricatula</i> (3)	Bolivia, Nor Yungas	Flakus & Rodríguez 17234	KF380900	Divakar et al. (2013)
<i>H. imbricatula</i> (4)	Brazil, São Paulo	Benatti & Cintra 3159	KF380901	Divakar et al. (2013)
<i>H. immaculata</i>	Australia, Queensland	Louwhoff et al. s/n	AY611073	Blanco et al. (2004)
<i>H. intercalanda</i>	Argentina, Misiones	Michlig et al. 2776	OQ972000	This study
<i>H. livida</i> (1)	Brazil, São Paulo	Benatti & Cintra 3211	KF380904	Divakar et al. (2013)
<i>H. livida</i> (2)	Bolivia, Aniceto Arce	Flakus 18756	KF380905	Divakar et al. (2013)
<i>H. livida</i> (3)	Bolivia, Aniceto Arce	Flakus & Quisbert 19785	KF380906	Divakar et al. (2013)
<i>H. livida</i> (4)	Argentina, Salta	Argüello s/n	GQ919282	Divakar et al. (2010)
<i>H. minarum</i> (1)	Argentina, Misiones	Michlig et al. 2723	OQ971987	This study
<i>H. minarum</i> (2)	Islas Canarias, Tenerife	Crespo s/n	DQ279538	Divakar et al. (2006)
<i>H. osseoalba</i> (1)	China, Yunnan	Crespo et al. s/n	DQ279511	Divakar et al. (2006)
<i>H. osseoalba</i> (2)	China, Yunnan	Crespo et al. s/n	DQ279512	Divakar et al. (2006)
<i>H. osseoalba</i> (3)	South Africa, W Cape	Crespo et al. s/n	GQ919279	Divakar et al. (2010)
<i>H. pluriformis</i>	Brazil, São Paulo	Benatti & Cintra 3209	KF380902	Divakar et al. (2013)
<i>H. polydactyla</i> (1)	Argentina, Misiones	Michlig et al. 2788	OQ971999	This study
<i>H. polydactyla</i> (2)	Argentina, Misiones	Michlig et al. 2687	OQ971998	This study
<i>H. polydactyla</i> (3)	Kenya, W province	Divakar & Lumbsch s/n	GQ919283	Divakar et al. (2010)
<i>H. pustulifera</i> (1)	Argentina, Chaco	Michlig et al. 2240	OQ971996	This study
<i>H. pustulifera</i> (2)	Argentina, Formosa	Michlig et al. 2350	OQ971997	This study

Table 1. Continued.

Species	Locality	Collector (s) and collection number	Genbank accession no.	Reference
<i>H. pustulifera</i> (3)	Argentina, Chaco	Michlig et al. 2172	OQ971994	This study
<i>H. aff. pustulifera</i> (4)	Argentina, Formosa	Michlig & Niveiro 2371	OQ971995	This study
<i>Remototrachyna costaricensis</i> (1)	Argentina, Misiones	Michlig et al. 2090	OQ971993	This study
<i>R. costaricensis</i> (2)	Costa Rica, Volcán Arenal	Molina s/n	AY785269	Blanco et al. (2006)
<i>R. costaricensis</i> (3)	Cuba, Granma	Pérez Ortega s/n	GQ919274	Divakar et al. (2010)

sequences retrieved from GenBank, representing a total of 13 species of the genera *Hypotrachyna* and one of *Remototrachyna* from northeast Argentina, and four species of *Bulbothrix*, which were used as outgroup. Collection data and GenBank accession numbers of specimens used in this study are detailed in Table 1.

Total DNA extraction and PCR reactions were performed following Michlig et al. (2017). The ITS1+5.8S+ITS2 region of the nrDNA was amplified using the primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White et al., 1990). Forward and reverse regions were sequenced by Macrogen © (Seoul, South Korea), and both were assembled. Sequences were read and manually edited using Chromas v2.0 (McCarthy, 1996).

An automatic alignment was initially performed on the web through the site of the European Bioinformatics Institute (<https://www.ebi.ac.uk/Tools/msa/>; Madeira et al., 2022) with Muscle (Edgar, 2004), and then manually checked/edited in MEGA 5.0 (Tamura et al., 2011). Ambiguously aligned regions were removed using Gblocks v091b (Castresana, 2000), using options for a relaxed selection of blocks as recommended by the software for short alignments.

Phylogenetic relationships were estimated with maximum likelihood (ML) and Bayesian inference (BI) methods. For both, the appropriate nucleotide substitution model was selected with jModelTest v2.1.4 (Darriba et al., 2012) with AIC, AICc, and BIC, and a symmetrical model of nucleotide substitution (Zharkikh, 1994) including a discrete gamma distribution with six rate categories (SYM+G) was selected. ML analysis was performed with the online version of RAxML-NG v1.0.0 (Kozlov et al., 2019) with

a 1,000 bootstrap analysis. BI was performed with MrBayes v3.2.7 (Ronquist et al., 2012). Two simultaneous runs were done for 3,000,000 generations, saving every 500th sampled tree. The first 25% of the sampled trees were discarded as burn-in. With the remaining trees, a consensus tree showing the branch lengths and posterior probabilities of each clade, on a majority consensus tree, was constructed. Convergence of chains of each replicate was checked using Tracer v1.7.1 (Rambaut et al., 2018). Trees were visualized with FigTree v1.4.0 (Rambaut, 2012).

RESULTS AND DISCUSSION

Phylogenetic analyses

The final ITS matrix included 39 sequences of 442 bp long, from 18 taxa. Since the topologies of the best ML tree and the Bayesian phylogenetic tree did not show any supported conflict, only the Bayesian tree with both support values is shown (Fig. 1). The three genera included in the analyses were recovered as monophyletic, with *Bulbothrix* as sister to the *Remototrachyna* + *Hypotrachyna* clade. The species of *Hypotrachyna* were grouped into one clade including three subclades (I, II, III). Subclade I includes *H. imbricatula* + *H. dentella*, with relationships partially unresolved; subclade II grouped species of *H.* subgen. *Parmelinopsis* (1/90); and finally, the larger subclade (III), which corresponded to *H.* subgen. *Hypotrachyna* and included most species here considered. Although this last subclade was highly supported (1/100), some relationships within were resolved as polytomies, and the species *H. livida*, *H. pustulifera*, and *H. polydactyla* were recovered as polyphyletic. They

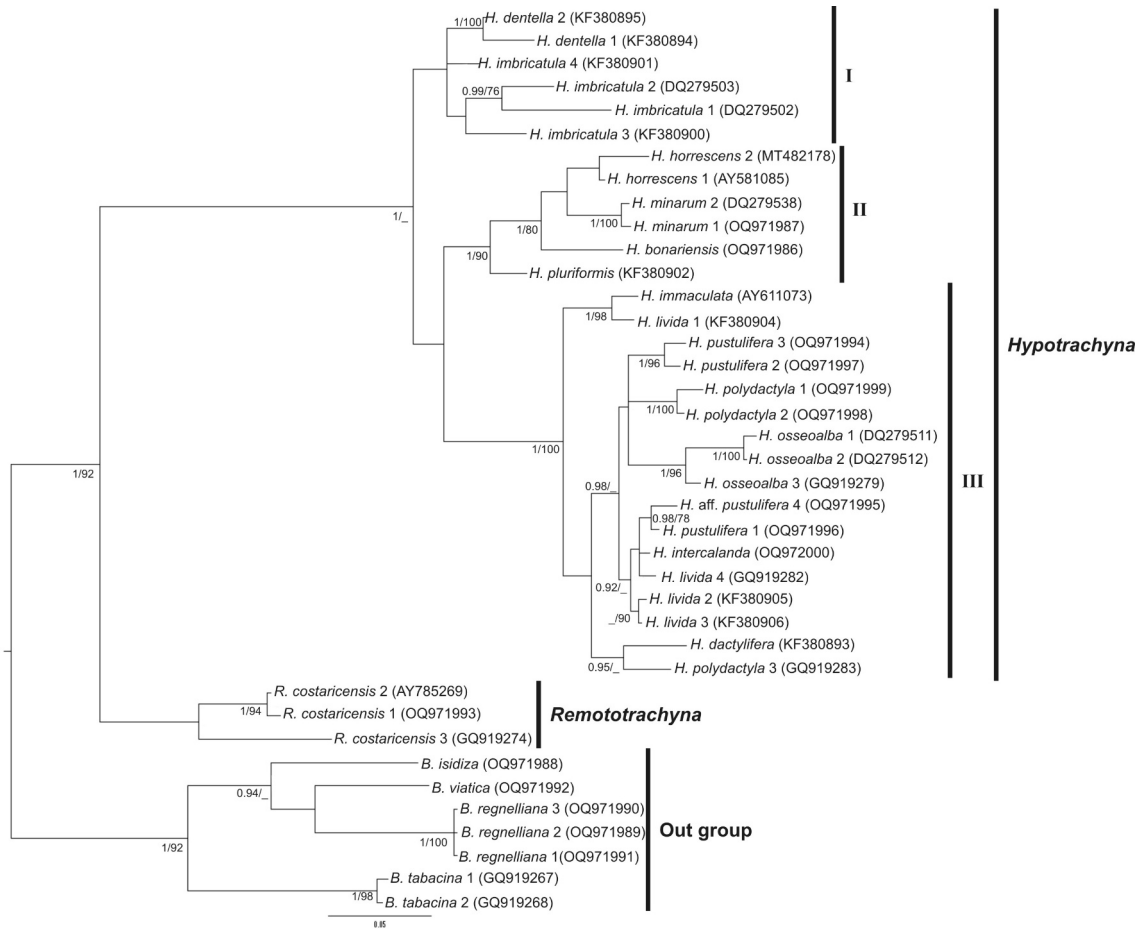


Fig. 1. Phylogenetic relationships inferred from the ITS1+5.8S+ITS2 region of the nrDNA. The tree is rooted using *Bulbothrix* as outgroup. The numbers on internal branches indicate posterior probabilities (≥ 0.9) from Bayesian inference and bootstrap (≥ 70) support from Maximum Likelihood analysis in the following format: BI-PP/ML-BP.

appear to be closely related and other loci are needed to distinguish between them.

The species

HYPOTRACHYNA BONARIENSIS (Adler & Elix) Divakar, A. Crespo, Sipman, Elix & Lumbsch

Phytotaxa 132(1): 33 (2013)

Distribution: Argentina: Buenos Aires (Adler & Elix, 1987), Cordoba (Rodriguez et al., 2016), Santiago del Estero (Adler, 2013), Corrientes*, and Misiones* provinces.

Comments: *Hypotrachyna bonariensis* lacks vegetative propagules, has narrow lobes with truncate apices, cortical atranorin, and 3-methoxy-2,4-di-O-methylgyrophoric and gyrophoric acids as main medullary substances (Adler & Elix, 1992). Species morphologically related are *H. damaziana* (Zahlbr.) Krog & Swinscow, and *H. neodamaziana* (Elix & J. Johnst.) Divakar, A. Crespo, Sipman, Elix & Lumbsch, which share the absence of vegetative propagules, but both differ chemically: *H. damaziana* contains also 5-O-methylhyascic acid and lacks umbilicinic acid (the latter present in

H. bonariensis), while *H. neodamaziana* lacks 3-methoxy-2,4-di-O-methylglyphoric (Adler & Elix, 1987). *Hypotrachyna damaziana* also differs in the larger ascospores (16–18 × 10–12 μm), whereas in *H. neodamaziana* the lobes are more highly branched (Elix & Johnston, 1986).

Specimens studied: Argentina. Corrientes, San Cosme, road to Santa Ana, near the poultry farm, 27°27'28.83"S, 58°41'25.11"W, alt. 71 m, on fence post, 21 Sep. 2011, A. Michlig & N. Niveiro 2681; Misiones, San Ignacio, Teyū Cuaré PP, de la Selva trail, Isla Toro viewpoint, 27°16'55.2"S, 55°35'40.1"W, alt. 155 m, 22 May 2009, A. Michlig & N. Niveiro 1707; San Pedro, YBR, Moconá PP, around the Marcio Ayres biological station, 27°9'13.2"S, 53°54'4.7"W, alt. 318 m, 26 May 2009, A. Michlig & N. Niveiro 1888; YBR, Esmeralda PP, road to the pine forest, 26°53'40"S, 53°52'42"W, alt. 318 m, on *Syagrus romanzoffiana*, 15 May 2008, A. Michlig et al. 827.

HYPOTRACHYNA DACTYLIFERA (Vain.) Hale

Smithsonian Contributions to Botany 25: 30 (1975)

Distribution: America (Nash et al., 2002). In South America: Bolivia, Brazil, Chile, Colombia, Paraguay, Venezuela, Uruguay (Sipman et al., 2009), and Argentina. In Argentina: Cordoba, Misiones, San Luis (Sipman et al., 2009), Corrientes (Michlig & Ferraro, 2012), and Salta* provinces.

Comments: *Hypotrachyna dactylifera* is characterized by the sublinear lobes, the upper surface with isidioid dactyls, sometimes branched, which do not form soredia, cortical atranorin, and substances of the lividic acid complex in the medulla (Sipman et al., 2009). Among *Hypotrachyna* species in northeast Argentina, it is morphological and chemically similar to *H. pustulifera*, which differs in the pustules that become sorediate (Sipman et al., 2009) and *H. polydactyla* (see comments below).

Specimens studied: Argentina. Corrientes, Mburucuyá, Mburucuyá NP, Maizal paddock, on trees in palm groove of *Butia yatay*, 17 Oct. 2006, L. Ferraro et al. 8188. Salta, Santa Victoria, Los Toldos, El Nogalar Reserve, 24 Apr. 2009, L. Ferraro 8995.

HYPOTRACHYNA IMBRICATULA (Zahlbr.) Hale (Fig. 2A)

Smithsonian Contributions to Botany 25: 30 (1975)

Thallus mineral gray, subcoriaceous, corticolous, moderately adnate, 3–4 cm diam.; lobes sublinear, irregular to anisotomically dichotomously branched, 1–2 mm wide, contiguous to slightly imbricate, with subrounded apices; margin entire to crenate, eciliate. Upper surface shiny, smooth, mostly continuous, with some irregular cracks, weakly maculate; maculae punctiform, laminal; isidiate. Isidia cylindrical, simple to little branched, with brown apex, eciliate, firm to caducous. Medulla white. Lower surface black, shiny, smooth, moderately rhizinate, with a narrow, dark brown marginal zone, shiny, smooth to slightly rugose, papillate; rhizines black, simple to dichotomously branched (2–3 times branched), evenly distributed. Apothecia absent. Pycnidia absent.

Chemistry: Cortex K+ yellow, UV– (atranorin, major); medulla K+ yellow, C–, KC+ orange, UV+ bluish white (barbatic acid, major; 4-O-demethylbarbatic acid, major; obtusatic acid, minor; and norobtusatic acid, minor).

Distribution: America, Asia, and Oceania (Sipman et al., 2009). In South America: Bolivia, Brazil, Chile, Colombia, Ecuador, French Guiana, Guyana, Surinam, Peru, Venezuela (Eliasaro et al., 1998; Sipman et al., 2009), and Argentina. In Argentina: Chubut (Calvelo & Liberatore, 2002) and Misiones* provinces.

Comments: *Hypotrachyna imbricatula* is characterized by the sublinear lobes, cylindrical isidia, cortical atranorin, and medullary barbatic acid and related substances (Sipman et al., 2009). Among the related species, *H. steyermarkii* (Hale) Hale shares the same chemistry and has also cylindrical isidia, but they are ciliate and turn lobulate and procumbent (Hale, 1975; Sipman et al., 2009). *Hypotrachyna dentella* (Hale & Kurok.) Hale, cited for the region by Sipman et al. (2009), is morphologically similar to *H. imbricatula*, but it differs chemically as it contains echinocarpic acid together with the barbatic acid aggregate.

Specimen studied: Argentina. Misiones, San Pedro, YBR, Moconá PP, near Camping, 27°9'13.1"S, 53°54'5.2"W, alt. 333 m, 26 May 2009, A. Michlig & N. Niveiro 1906.

HYPOTRACHYNA INTERCALANDA (Vain.) Hale

Smithsonian Contributions to Botany 25: 42 (1975)

Distribution: Brazil (Eliasaro et al., 1998) and Argentina. In Argentina: Misiones province (Sipman et al., 2009).

Comments: *Hypotrachyna intercalanda* lacks vegetative propagules and has sublunar lobes, an emaculate upper surface, cortical atranorin, and olivetoric and anziaic acids as medullary substances (Eliasaro et al., 1998). It is morphologically similar to *H. livida*, which is also present in the region, although that species produces substances of the lividic acid complex in the medulla (Eliasaro et al., 1998). *Hypotrachyna pluriformis* (Nyl.) Hale also lacks vegetative propagules but it differs by having subirregular lobes, often convex, and gyrophoric acid as main medullary compound (Sipman et al., 2009). Although it was cited from Misiones province (Osorio, 1981), no material of this species from the region was available for confirmation.

Selected specimens studied: Argentina. Misiones, Guaraní, YBR, Caá-Yarí PP, surroundings of forest rangers' house, 26°52'19.6"S, 54°13'33.8"W, alt. 526 m, 10 Dec. 2011, A. Michlig et al. 2776; San Ignacio, Teyú Cuaré PP, de la Selva trail, 23 May 2009, A. Michlig & N. Niveiro 1748; San Pedro, YBR, Moconá PP, around the Visitor's Center, 27°9'12.8"S, 53°54'0.3"W, alt. 314 m, 25 May 2009, A. Michlig & N. Niveiro 1802; Esmeralda PP, road to the pine forest, 26°53'40"S, 53°52'42"W, alt. 318 m, 15 May 2008, A. Michlig et al. 819.

HYPOTRACHYNA LIVIDA (Taylor) Hale

Smithsonian Contributions to Botany 25: 45 (1975)

Distribution: North (Nash et al., 2002; Sipman et al., 2009) and South America. In South America: Bolivia, Brazil, Ecuador, Paraguay, Uruguay, Venezuela (Sipman et al., 2009; Gerlach & Eliasaro, 2012), and Argentina. In Argentina: Buenos Aires (Calvelo & Liberatore, 2002), Catamarca (Rodriguez et al., 2016), Cordoba (Adler & Elix, 1992; Estrabou et al., 2006), Jujuy (Adler & Elix, 1992), Corrientes (Ferraro, 1981), and Misiones* provinces.

Comments: *Hypotrachyna livida* lacks vegetative propagules and has sublunar lobes, sometimes elongate, cortical atranorin, and substances of the lividic acid complex in the medulla (Sipman et al., 2009; Gerlach & Eliasaro, 2012). *Hypotrachyna palmarum* (Lynge) Hale, *H. degelli* (Hale) Hale, and *H. intercalanda* are similar species, all of them lacking vegetative propagules, but clearly differing in medullary chemistry. The first produces colensoic and norcolensoic acids as main medullary compounds, while *H. degelli* and *H. intercalanda* produce alectoronic and olivetoric acids, respectively (Sipman et al., 2009).

Specimens studied: Argentina. Corrientes, Mburucuyá, Mburucuyá NP, Camping, 18 Feb. 2006, A. Michlig & N. Niveiro 9, Che-Roga trail, in hygrophilous forest, 6 Apr. 2007, A. Michlig & N. Niveiro 345. Misiones, San Ignacio, Teyú Cuaré PP, de la Selva trail, in an open environment, shortly before the rainforest, 23 May 2009, A. Michlig & N. Niveiro 1771, 1773.

HYPOTRACHYNA MINARUM (Vain.) Krog & Swinscow

Lichenologist 19(4): 420 (1987)

Distribution: Africa, America, Asia, Europe, and Oceania (Elix, 1994). In South America: Bolivia, Brazil, Colombia, Venezuela [Hale (1976), as *Parmelina dissecta* (Nyl.) Hale; Gerlach & Eliasaro, 2014], and Argentina. In Argentina: Jujuy (Adler & Elix, 1992), and Misiones* provinces.

Comments: *Hypotrachyna minarum* has a densely isidiate upper surface, with eciliate isidia, cortical atranorin, and gyrophoric and 5-O-methylhiassic acid as main medullary compounds (Adler & Elix, 1992; Eliasaro & Adler, 2000). Among related species are *H. appalachensis* Lendemer & J. L. Allen, *H. horrescens* (Taylor) Krog & Swinscow, *H. mcMulliana* Lendemer & J. L. Allen, and *H. neohorrescens* Jungbluth, Marcelli & A. P. Lorenz. These species deviate because they all produce 3-methoxy-2,4-di-O-methylgyrophoric acid (Lendemer & Allen, 2020; Rodrigues et al., 2022), not detected in our material studied, except for *H. appalachensis*, which differs from *H. minarum* by having high concentrations of 4,5-di-O-methylhiassic acid (Lendemer & Allen, 2020), which was found in traces in the material studied. Among them, only *H. horrescens* was cited from the region

(Osorio, 1981), but, unfortunately, no material from this species was available for confirmation.

Selected specimens studied: Argentina. Misiones, General Manuel Belgrano, San Antonio NSR surroundings, in INTA's property, in *Araucaria angustifolia* forestry, 26°2'14.2"S, 53°47'24.8"W, alt. 526 m, 29 May 2009, A. Michlig & N. Niveiro 2034; Campiña de América, school, 26°16'50.6"S, 53°42'19.4"W, alt. 805 m, in rainforest, 9 Dec. 2011, A. Michlig et al. 2723; Guaraní, YBR, Caá-Yari PP, meters before forest rangers' house, 26°52'19.6"S, 54°13'33.8"W, alt. 526 m, 27/III/2010, A. Michlig et al. 2478; San Pedro, YBR, Esmeralda PP, road to the pine forest, 26°53'40"S, 53°52'42"W, alt. 318 m, 15 May 2008, A. Michlig et al. 759; Moconá PP, Piedra Bugre wharf, 27°9'13"S, 53°54'4"W, 16 May 2008, A. Michlig et al. 888.

HYPOTRACHYNA OSSEOALBA (Vain.) Y. S. Park & Hale (Fig. 2B)

Taxon 38: 88 (1989)

Thallus mineral gray, subcoriaceous, corticolous, moderately adnate to substrate, 2.5 cm diam.; lobes sublinear, anisotomically dichotomously branched, 0.75–1.5 mm wide, contiguous to slightly imbricate, with subtruncate to truncate apices; margin entire, eciliate. Upper surface shiny, smooth, continuous to slightly rugose and irregularly cracked centrally, emaculate, pustulate. Pustules subapical to submarginal, occasionally laminal, mainly on lateral lobes, turning soreciate; soredia subgranular to granular. Medulla white, sometimes with yellow-orange patches in the lower part. Lower surface black, shiny, smooth, moderately rhizinate, with a narrow, dark brown marginal zone in some areas, shiny, smooth, papillate, or rhizinate; rhizines black, simple to dichotomously branched (3–4 times branched), evenly distributed, projecting beyond the margins. Apothecia absent. Pycnidia absent.

Chemistry: Upper cortex K–, UV+ yellow (lichexanthone, major/minor); medulla K+ yellow turning brownish, C– or + pale yellow, KC+ orange, UV– (lividic acid, major; oxyphysodic acid, minor; 4-O-methylphysodic acid, minor/trace; physodic acid, minor/trace; pigmentosin A, trace).

Distribution: Africa, America, Asia, and Oceania (Sipman et al., 2009). In South America: Brazil, Colombia, Ecuador, Guyana, and Venezuela (Sipman et al., 2009; Gerlach & Eliasaro, 2012), and Argentina. In Argentina*: Misiones and Salta provinces.

Comments: *Hypotrachyna osseoalba* is characterized by the soredia arising from pustules, cortical lichexanthone, and the lividic acid complex in the medulla (Sipman et al., 2009; Gerlach & Eliasaro, 2012). Besides *H. osseoalba*, the only other species with lichexanthone in the area is *H. subformosana*, which shares the medullary chemistry but differs in having capitate soralia instead of pustules (Sipman et al., 2009).

Specimens studied: Argentina. Misiones, General Manuel Belgrano, Campiña de América, cemetery surroundings, 26°16'28.71"S, 53°42'56.12"W, alt. 811 m, on palm tree, 9 Dec. 2011, A. Michlig et al. 2504; Guaraní, Predio Guaraní, 26°54'59"S, 54°12'18"W, route 15, between guests housing and Papel Misionero, 28 Apr. 1999, S. Tressens et al. 6205; San Pedro, YBR, Moconá PP, around the Marcio Ayres biological substation, 27°9'13.2"S, 53°54'4.7"W, alt. 318 m, A. Michlig & N. Niveiro 1893. Salta, Santa Victoria. Baritú NP, shortly after the entry to the rustic camping area "El Ukumar", in an open environment, 22°25'39.2"S, 64°44'20.6"W, alt. 1118 m, 21 Apr. 2009, A. Michlig et al. 1239.

HYPOTRACHYNA POLYDACTYLA (Krog & Swinscow) T. H. Nash

Bryologist 88: 20 (1985)

Distribution: Africa, North (Nash, 1985; Sipman et al., 2009) and South America. In South America: Brazil (Eliasaro et al., 1998) and Argentina. In Argentina: Cordoba (Sipman et al., 2009), Entre Rios (Adler & Calvelo, 2007b), and Misiones* provinces.

Comments: *Hypotrachyna polydactyla* is characterized by sublinear lobes, closed and non-soreciate dactyls, which turn flattened and crescent-shaped, cortical atranorin, and substances of the lividic acid complex in the medulla (Eliasaro et al., 1998; Sipman et al., 2009). Another species in the region with dactyls and similar chemistry is *H. dactylifera*, but it differs in the isidioid dactyls (Sipman et al., 2009).

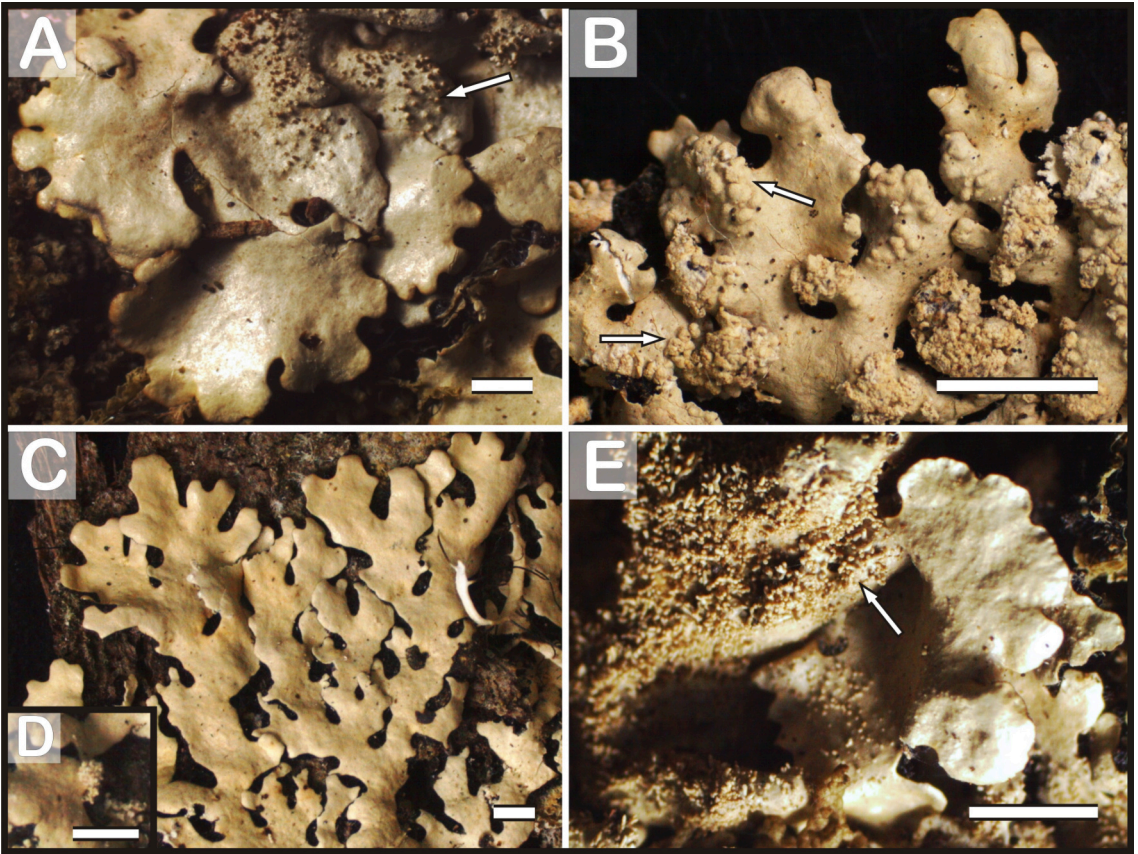


Fig. 2. Most relevant records: A – *Hypotrachyna imbricatula*, part of the thallus showing isidia (arrow); B – *H. osseocalba*, part of the thallus with sorediate pustules (arrows); C – *H. subformosana*, part of the thallus; D – *H. subformosana*, detail of a sororium; E – *Remototrachyna costaricensis*, portion of the thallus showing isidia (arrow). Scale bars: A–D = 1 mm; E = 0.5 mm.

Specimens studied: Argentina. Misiones, General Manuel Belgrano, Campiña de América, school, 26°16'32.4"S, 53°41'56.3"W, alt. 822 m, on fence post, 9 Dec. 2011, A. Michlig et al. 2687; Guaraní, YBR, Caá-Yarí PP, surroundings of forest rangers' house, 26°52'19.6"S, 54°13'33.8"W, alt. 526 m, 10 Dec. 2011, A. Michlig et al. 2788.

HYPOTRACHYNA PUSTULIFERA (Hale) Skorepa

Phytologia 53(4): 445 (1983)

Distribution: America (Nash et al., 2002; Sipman et al., 2009). In South America: Brazil (Eliasaro et al., 1998; Sipman et al., 2009) and Argentina. In Argentina: Chaco, Misiones (Sipman et al.,

2009), Corrientes (Sipman et al., 2009; Michlig & Ferraro, 2012), and Formosa* provinces.

Comments: *Hypotrachyna pustulifera* has sublinear to subirregular lobes, the upper surface with pustules that become sorediate, cortical atranorin, and lividic acid and related substances in the medulla (Nash et al., 2002; Sipman et al., 2009). In the material studied, soredia originate from nodular tubercles, which sometimes enlarge and crumble apically and form soredia. *Hypotrachyna immaculata* (Kurok.) Hale is a similar species, and it can be distinguished by the soralia which do not arise from pustules (Sipman et al., 2009). Material cited as *H. immaculata* for the region (Ferraro, 1981) was studied here and was reidentified as

H. pustulifera. However, *H. immaculata* might be present in the area (Sipman et al., 2009).

Selected specimens studied: Argentina. Chaco, Comandante Fernández, Nat. Route N° 95, between Presidencia Roque Sáenz Peña and Tres Isletas, kilometers before the junction with Prov. Route N° 44, 26°33'44.4"S, 60°18'26.6"W, alt. 108 m, in a *Schinopsis balansae* forest, 11 Feb. 2010, A. Michlig & N. Niveiro 2172; General Güemes, Prov. Route N° 9, between Miraflores and Las Hacheras, in front of the Productive Development Center–Miraflores, 25°29'34.8"S, 61°1'11.1"W, alt. 138 m, 11 Feb. 2010, A. Michlig & N. Niveiro 2240; San Fernando, Parque Norte Caraguatá, Nicolás Avellaneda Route km 15.8, 1500 m northwards, 13 Apr. 2008, A. Michlig & N. Niveiro 553. Corrientes, Saladas, Route 12, 33.5 km south of the drift to a Empedrado, in "monte", camping surroundings, 27 Dec. 1983, L. Ferraro et al. 2849. Formosa, Laishi, Herradura, Municipal Camping, 26°30'46.6"S, 58°17'5"W, alt. 82 m, 12 Feb. 2010, A. Michlig & N. Niveiro 2371; Pirané, Prov. Route N° 1, between Mayor Villafañe and San Francisco de Laishi, 26°12'16.8"S, 58°59'47.3"W, alt. 73 m, 12 Feb. 2010, A. Michlig & N. Niveiro 2350.

HYPOTRACHYNA SUBFORMOSANA Hale ex Elix, T. H. Nash & Sipman (Fig. 2C–D)

Flora Neotropica 104: 153 (2009)

Thallus mineral gray to gray-green, subcoriaceous, corticolous, moderately to tightly adnate, 2.5–5 cm diam.; lobes sublinear, anisotomically dichotomously branched, 0.8–1.2 mm wide, contiguous to slightly imbricate, with subrounded to subtruncate apices; margin entire, eciliate. Upper surface shiny, smooth to slightly rugose at center, continuous, emaculate, sorediate. Soralia submarginal, occasionally laminal, confluent, capitate to orbicular; soredia farinose to subgranular. Medulla white, sometimes partially orange pigmented in some areas. Lower surface black, shiny, slightly rugose, moderately to densely rhizinate, with a narrow marginal zone pale brown, papillate or rhizinate; rhizines dichotomously branched, up to 4 times branched, black, evenly distributed, sometimes projecting beyond the margins. Apothecia absent. Pycnidia absent.

Chemistry: Upper cortex K–, UV+ yellow (lichexanthone, major/minor); medulla K+ yel-

low turning reddish brown, C– or + pale yellow, KC+ yellow or orange turning reddish brown, UV– (lividic acid, major; oxyphysodic acid, major/minor; 4-O methylphysodic acid, minor/trace; colensoic acid, minor/trace; physodic acid, trace).

Distribution: Oceania and America (Sipman et al., 2009). In South America: Bolivia, Brazil, Venezuela (Flakus et al., 2012; Aptroot & Cáceres, 2018), and Argentina. In Argentina*: Misiones and Salta provinces.

Comments: *Hypotrachyna subformosana* is characterized by having sublinear lobes, capitate and laminal soralia that produce farinose soredia, cortical lichexanthone, and the substances of the lividic acid complex in the medulla (Sipman et al., 2009). Other sorediate species with cortical lichexanthone are *H. adaffinis* Sipman, *H. subaffinis* (Zahlbr.) Hale, and *H. virensica* Elix, T. H. Nash & Sipman, although they all differ chemically (Sipman et al., 2009).

Specimens studied: Argentina. Misiones, San Pedro, YBR, Moconá PP, Piedra Bugre wharf, 16 May 2008, A. Michlig et al. 893, 991, 995. Salta, Santa Victoria, El Nogalar de los Toldos Nat. Reserve, in front of the beginning of Santa Victoria, in *Podocarpus* forest, on *Podocarpus* sp., 22°16'46.6"S, 64°42'35.0"W, alt. 1677 m, 23 Apr. 2009, A. Michlig et al. 1483.

HYPOTRACHYNA SUBPUSTULIFERA Elix

Mycotaxon 47: 108 (1993)

Distribution: Africa, Oceania, and America (Nash et al., 2002; Sipman et al., 2009). In South America: Brazil, Colombia, Venezuela (Sipman et al., 2009), and Argentina. In Argentina: Corrientes, Cordoba (Rodríguez et al., 2016), and Formosa* provinces.

Comments: *Hypotrachyna subpustulifera* is characterized by the sorediate pustules, very narrow lobes (0.5–1 mm), cortical atranorin, and the lividic acid-physodic acid chemosyndrome as medullary compounds (Elix, 1993). Other species with dactyls or pustules in northeast Argentina with similar chemistry are *H. dactylifera*, *H. polydactyla*, and *H. pustulifera*, the latter being the most morphologically related, as it also produces pustules that become sorediate (Elix, 1993). However, all of them differ

in the wider lobes (Elix, 1993; Sipman et al., 2009).

Specimens studied: Argentina. Corrientes, Mburucuyá, Mburucuyá NP, Yatay trail, on a fence post, 20/VII/06, A. Michlig et al. 119, Santa Teresa ranch, 20/VII/2006, A. Michlig et al. 196. Formosa, Bermejo, Prov. Route N° 9, between Sumayén and El Aibal, 24°22'0.5"S, 61°38'19.7"W, alt. 169 m, in an *Aspidosperma quebracho-blanco* forest, 18 Apr. 2009, A. Michlig et al. 1119.

REMOTOTRACHYNA COSTARICENSIS (Nyl.) Divakar & A. Crespo (Fig. 2E)

American Journal of Botany 97(4): 586 (2010)

Thallus mineral gray, subcoriaceous, corticolous, moderately adnate, 2–8 cm diam.; lobes subirregular, anisotomically dichotomously to irregularly branched, 1.2–3 (3.5) mm wide, contiguous to slightly imbricate, with subtruncate to subrounded apices; margin entire to slightly crenate, eciliate. Upper surface shiny, smooth, continuous to sometimes irregularly cracked, weakly maculate; maculae punctiform, laminal; isidiate. Isidia cylindrical, generally simple, sometimes little branched, sometimes with colored apex, eciliate, firm. Medulla white. Lower surface black, shiny, smooth to slightly rugose, densely rhizinate, with a narrow, pale to dark brown marginal zone; rhizines dichotomously branched, several times (up to 4–5) branched, black, dense towards the margins, projecting beyond the margin, evenly distributed. Apothecia strongly concave, 0.6–5.5 mm diam., sessile, submarginal to laminal, margin crenulate, amphithecium isidiate; disc imperforate, pale brown, epruinose; ascospores ellipsoid, (5) 6–8 (9) × 3–5 µm. Pycnidia absent.

Chemistry: Upper cortex K+ yellow, UV– (atranorin, major/minor); medulla K–, C–, KC–, UV– (non-identified fatty acids, all minor).

Distribution: America, Africa, Asia, Europe, and Oceania (Sipman et al., 2009; Masson et al., 2015). In South America: Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela (Eliasaro et al., 1998; Sipman et al., 2009), and Argentina. In Argentina*: Misiones province.

Comments: *Remototrachyna costaricensis* is characterized by the subirregular lobes, dense isidia on the upper surface, white medulla,

dense rhizines, and fatty acids in the medulla (Hale, 1975; Nash et al., 2002). Other isidiate species of the genus are *R. consimilis* (Vain.) Flakus, Kukwa & Sipman, *R. kowaensis* (Asahina) A. Crespo & Divakar, *R. rhabdiformis* (Kurok.) Divakar & A. Crespo, and *R. sipmaniana* Kukwa & Flakus, although they differ chemically. *Remototrachyna rhabdiformis* produces norstictic acid as main medullary substance, while the others produce protocetraric acid together with other substances (Sipman et al., 2009; Flakus et al., 2012).

Specimens studied: Argentina. Misiones, General Manuel Belgrano, San Antonio NSR surroundings, in INTA's property, in *Araucaria angustifolia* forestry, 26°2'14.2"S, 53°47'24.8"W, alt. 526 m, 29 May 2009, A. Michlig & N. Niveiro 2090, 2096; San Pedro, YBR, Moconá PP, entry of Chachi trail, 27°10.8'53"S, 53°54'3.1"W, alt. 326 m, 24 May 2009, A. Michlig & N. Niveiro 1785.

ACKNOWLEDGMENTS

We are grateful to the Administración de Parques Nacionales (APN) and the Ministerio de Ecología, Recursos Naturales Renovables y Turismo (MERNRYT) of Misiones for collection permits; and P. Jungbluth, J. Lendemmer, and D. Masson for providing bibliography. This research was funded by the Agencia de Promoción Científica, Tecnológica y de Innovación, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Secretaría General de Ciencia y Técnica (UNNE), and the MERNRYT (Proyecto Araucaria XXI). The reviewers of the manuscript are also thanked for their valuable suggestions to improve the manuscript.

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