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WHAT DO WE KNOW ABOUT BIOCRUST LICHENS IN ARGENTINA? A COMPREHENSIVE REVIEW AND NEW RECORDS

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Abstract. Filippini, E. R.; R. E. Díaz Dominguez, R. A. García, M. Gallinger & E. C. Mlewski. 2024. What do we know about biocrust lichens in Argentina? A comprehensive review and new records. *Darwiniana*, nueva serie 12(2): 220-236.

Lichens are among the most distinctive and colorful organisms found in biological soil crusts (biocrusts). Along with cyanobacteria, green algae, and bryophytes, they inhabit the top few millimeters of the soil surface, forming the living skin of the soil. They cover large areas of the planet's arid and semiarid regions, as well as degraded terrestrial ecosystems in other regions. Although global studies of biocrusts have tripled in the last two decades, South America remains one of the least studied continents. In Argentina, ecological studies of biocrusts are increasing, but knowledge of the taxonomic diversity of the lichens that comprise them remains limited. Therefore, it is crucial to increase studies on terrestrial lichens, which, although often inconspicuous, may be more abundant than previously thought. To contribute to the knowledge of biocrust lichens taxonomy in Argentina, we proposed to 1) perform a bibliographic review of the works that reported species lists to confirm and update the taxonomic nomenclature and distribution, and 2) expand knowledge in less studied regions through the study of specimens from central Argentina. The results reveal that between 2002 and 2022, 78 crust-forming lichen species were recorded in Argentina. The richest family was Verrucariaceae, along with Collemataceae, Peltulaceae, and Lichinaceae distributed in the northern, western, and central-southern regions of the country, mainly in the arid and semiarid areas of Mendoza, San Juan, Neuquén, and San Luis. The most common lichen species found in the crusts were *Placidium squamulosum*, *Endocarpon pusillum*, *Enchylium tenax*, *Peltula obscurans*, and *Psora decipiens*, in descending order. We have expanded this lichen diversity with three new species records for Argentina: *Gloeoheppia erosa*, *Heppia adglutinata*, and *Heteroplacidium divisum*, as well as the distribution of *Enchylium coccophorum*, *Peltula obscurans*, *Placidium squamulosum*, and *Psora icterica* in the central region of the country. In this way, we hope that this study can serve as a starting point for future research on lichen composition in soil crusts.

Keywords. Biocrust; *Gloeoheppia*; *Heppia*; *Heteroplacidium*; Verrucariaceae; semiarid.

Resumen. Filippini, E. R.; R. E. Díaz Dominguez, R. A. García, M. Gallinger & E. C. Mlewski. 2024. ¿Qué sabemos de los líquenes de biocostra de Argentina? Una revisión exhaustiva y nuevos registros. *Darwiniana*, nueva serie 12(2): 220-236.

Los líquenes se encuentran entre los organismos más distinguibles y coloridos de las costras biológicas de suelo (biocostras). Junto a cianobacterias, algas verdes y briofitas, habitan en el interior o en los milímetros superiores de la superficie del suelo, formando su piel viva. Cubren gran parte de

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las zonas áridas y semiáridas del planeta, así como ecosistemas terrestres degradados de otras regiones. Aunque globalmente los estudios de las biocostras se han triplicado en las últimas dos décadas, Sudamérica sigue siendo uno de los continentes menos estudiados. Particularmente, en Argentina, los estudios ecológicos sobre biocostras están aumentando, aunque el conocimiento sobre la diversidad taxonómica de líquenes que las componen sigue siendo limitado. Por lo tanto, es crucial incrementar estos estudios sobre los líquenes terrícolas que, aunque a menudo son inconspicuos, pueden ser más abundantes de lo que se pensaba anteriormente. Para contribuir al conocimiento taxonómico de los líquenes formadores de biocostra, nos propusimos: 1) realizar una revisión bibliográfica de los trabajos que reportaron listas de especies, con el fin de confirmar y actualizar la nomenclatura taxonómica y su distribución, y 2) ampliar el conocimiento en regiones menos estudiadas a través del estudio de ejemplares del centro de Argentina. Los resultados revelan que se han registrado 78 líquenes formando costra en Argentina entre el año 2002 y 2022. La familia más rica en especies fue Verrucariaceae, junto con Collemataceae, Peltulaceae y Lichinaceae, distribuidas en las regiones norte, oeste y centro-sur del país, predominantemente en áreas áridas y semiáridas de Mendoza, San Juan, Neuquén y San Luis. Las especies de líquenes más frecuentes en las costras fueron *Placidium squamulosum*, *Endocarpon pusillum*, *Enchylium tenax*, *Peltula obscurans* y *Psora decipiens*, en orden decreciente. Aumentamos esta diversidad de líquenes conocida agregando tres nuevos registros de especies para Argentina: *Gloeoheppia erosa*, *Heppia adglutinata*, *Heteroplacidium divisum*, así como ampliaciones de distribución de *Enchylium coccophorum, Peltula obscurans, Placidium squamulosum* y *Psora icterica* en el centro del país. De esta manera, esperamos que este estudio pueda servir como un punto de partida para futuras investigaciones sobre la composición de líquenes en las costras de suelo.

Palabras clave. Biocostra; *Gloeoheppia*; *Heppia*; *Heteroplacidium*; Verrucariaceae; semiárido.

INTRODUCTION

Biological soil crusts (biocrusts) are communities present across much of the world's arid and semiarid areas, as well as degraded terrestrial ecosystems in other regions (Weber et al., 2022). They are defined as a close association between soil particles and a variable proportion of autotrophic and heterotrophic organisms that inhabit the inner or upper few millimeters of the soil surface, forming the living skin of the soil (Bowker et al., 2018). The autotrophic organisms include cyanobacteria, green algae, lichens, and bryophytes, while the heterotrophic organisms include archaea, bacteria, and fungi (Belnap & Lange, 2003; Soule et al., 2009). Biocrusts contribute to carbon sequestration, nitrogen fixation, soil stability, erosion control, and ecohydrological processes, making them communities with multiple ecosystem functions. Notably, biocrust species exhibit a high degree of uniqueness in ecosystem functionality, meaning that each species has highly individualistic effects on multiple functions. Bowker et al. (2011) found that indicators of soil carbon, nitrogen, and phosphorus can be suppressed or promoted depending on the lichen or moss species present in the crust, suggesting that each species may effectively be a unique functional group. Some of these ecosystem functions may be threatened by biodiversity loss. For example, Finger-Higgens et al. (2022) reported a drastic decline in *Collema*-dominated biocrusts (N-fixing lichens) and their partial replacement by mosses (non-N-fixing organisms) over the last 60 years, associated with increasing summer temperatures. Therefore, maintaining species-rich biocrust communities is essential to preserving overall ecosystem functioning, and understanding the diversity of species that form biocrusts is key to understanding ecosystem processes.

Lichens are well-known components of biocrust communities. They integrate with other organisms, such as mosses and eukaryotic algae, after initial stabilization of the soil surface by cyanobacterial growth and the production of exopolysaccharides (Belnap & Lange, 2003). Biocrust lichens are typically terrestrial species with green algae or cyanobacterial photobionts, capable of aggregating and trapping soil particles through their hyphae, rhizohyphae, and rhizines that penetrate the substrate. They are also characterized by their small, usually squamulose, crustose, or subfruticose (sometimes foliose) thalli. Although they are among the most distinguishable and colorful organisms in biocrusts, knowledge about the diversity of lichens inhabiting these communities remains limited in most of the world's ecosystems, except in drylands where these communities have been studied extensively (Nash III et al., 2002, 2004; McCune & Rosentreter, 2007; Büdel et al., 2013).

While general interest in studying biocrusts has tripled in the last two decades, South America remains one of the least studied continents (Weber et al., 2022). Büdel (2001) published a review of biocrusts across various South American biomes, highlighting the scarcity of studies in Argentina,

particularly those focused on biocrust lichens. In recent years, Castillo-Monroy & Maestre (2011) discussed this gap of knowledge in the region, they assumed that the crusts of Argentina have been described, and highlighted the lack of studies on the ecology of these organisms. However, the taxonomic descriptions cited by the authors focus only on algae and cyanobacteria, not on lichens, making their conclusions incomplete.

Fortunately, in recent years, biocrusts have begun to attract the attention of ecologists in Argentina. Researchers are focusing on distribution patterns (García et al., 2015; Navas Romero et al., 2020), functionality (Garibotti et al., 2018; Aranibar et al., 2022), restoration (Navas Romero & Carretero, 2021), climatic and biotic interactions (Velasco Ayuso et al., 2020; Pissolito et al., 2021; Yahdjian et al., 2023), among other topics. As a result, the indirect contribution of these ecological studies may increase knowledge of the diversity of biocrust lichens. However, these records may require more exhaustive taxonomic studies for more reliable identifications.

In summary, although the understanding about the ecology of biocrust has advanced, the knowledge about the taxonomy of the biocrust lichen community remains limited. Therefore, it is crucial to conduct taxonomic studies of lichens, with special attention to the terricolous biocrust taxa, which although often inconspicuous, may be more abundant than previously thought. To contribute to the knowledge of biocrust lichen taxonomy in Argentina, we proposed to 1) perform a bibliographic review of studies that reported species lists to confirm and update taxonomic nomenclature and distribution, and 2) expand knowledge in less studied regions through the study of specimens from central Argentina.

MATERIALS AND METHODS

First, a systematic review of the literature published between 2002 and 2022 was performed using the keywords "LICHEN", "BIOLOGICAL SOIL CRUST" and "ARGENTINA" in Scopus and Google Scholar. Additionally, articles reporting lists of lichen species recognized in the international literature as biocrust forming for the same period were included. After filtering the results to include only scientific articles that reported species, the taxonomic lists with geographical information were extracted. The nomenclature was updated according to Index Fungorum (https:// www.indexfungorum.org). For this group of articles, the topics and research questions addressed were also considered. The lower limit for search was the year 2002, following a previous review of biocrusts that highlighted the lack of studies on lichens in Argentina (Büdel, 2001).

The distribution of lichens was determined using the coordinates of the study sites and the aridity index (de Martonne, 1925). This approach allowed us to identify areas and provinces where biocrust-related research is concentrated, as well as regions that have not been studied but could potentially harbor these organisms due to their similar characteristics. Additionally, the species found in the literature review were listed by families, and their distribution was reported by Argentine provinces.

Specimens collected between 2022 and 2023 in north-western Córdoba (Chancaní and San Marcos Sierras), central and eastern La Rioja (Olta and La Rioja), and southern of Catamarca were examined. As an exploratory study, collections were made opportunistically in the field, visiting areas where biological soil crusts were likely to be present, with a focus on maximizing the diversity found at each site. The 45 biocrust samples collected were transported in rigid containers to preserve the mineral substrate and then maintained in Petri dishes under natural light conditions. Voucher specimens were stored in the herbarium of the Institute of Biological and Technological Research (LUTI) in Córdoba, Argentina. The lichen thalli were examined under a stereoscopic microscope (Optika SZM-LED2) and photographed with an Olympus Tough GT-3 camera. Observations of reproductive structures and thallus organization were performed using freehand sections, which were subsequently mounted in 5% KOH and examined under a Motic B1 microscope. Spore length and width (minimum N=5, maximum N=10) and cortex thickness (N=10 per thallus section) were measured. Data are expressed as minimum-maximum ranges in micrometers (µm). Descriptions are presented first for upper external morphology, followed by thallus anatomy (upper cortex, photobiont, medulla, and lower cortex), lower external morphology, and finally reproductive structures. Spot tests with reagents K (KOH) and C (NaClO) were performed when necessary.

The following bibliography was consulted for species identification: Schultz & Büdel (2002), Rosentreter et al. (2007), Breuss (2010), Prieto et al. (2012), Marques et al. (2013), and Candan & Schultz (2015). Based on the examination of these new specimens, their distribution in Argentina has been revised, taking into account previous citations under other names after reviewing the synonymy with Calvelo & Liberatore (2002), The Consortium of Lichen Herbaria (https://lichenportal.org/portal/) and Global Biodiversity and Facility (https://www.gbif.org/es/). Finally, the taxonomic novelties were added to the list of biocrust lichen species reported in the literature.

RESULTS

Between 2002 and 2022, 12 scientific articles and three theses have been published addressing the diversity of biocrust lichens in Argentina (Table 1). According to the reviewed articles, there are 78 records of biocrust lichens in Argentina. Twenty-three of these taxa are identified at the genus level and 55 at the species level (Table 2). The first biocrust-related studies to report lichen composition were by Scutari et al. (2002 and 2004) in the Patagonian steppe near Puerto Madryn (Chubut). The authors first studied the composition of the lichen community growing on grasslands, and then analyzed how the lichen community was structured in response to livestock pressure to identify bioindicators of trampling impact. They identified ten crust forming lichen species from a wide variety of families including Acarosporaceae, Collemataceae, Lecanoraceae, Lecanoraceae, Megasporaceae, Physciaceae, Teloschistaceae, and Verrucariaceae. Regarding

Table 1. Studies of biocrust lichen species reported in Argentina. The table includes the authors, year of publication, provinces studied, number of lichen species recorded, study titles, and the main approaches used. Theses are indicated with an asterisk.

Authors	Year	Provinces	N# species	Titles	Approaches
Scutari et al.	2002	CHU	9	New records of soil-associated lichen from north-eastern Patagonia (Chubut, Argentina)	Taxonomy
Scutari et al.	2004	CHU	7	Soil-associated lichens in rangelands of north-eastern Patagonia. Lichen groups and species with potential as bioindicators of grazing disturbance	Ecology
Prieto et al.	2008a	JU, SA	6	New records in the lichen family Verrucariaceae (Ascomycota) from Argentina	Taxonomy
Prieto et al.	2008b	JU	1	A new species of *Anthracocarpon* (Verrucariaceae) from Argentina	Taxonomy
Gómez et al.	2012	ME	13	Biological soil crust recovery after long-term grazing exclusion in the Monte Desert (Argentina). Changes in coverage, spatial distribution, and soil nitrogen	Ecology
Tabeni et al.	2014	ME	7	Grazing effects on biological soil crusts and their interaction with shrubs and grasses in an arid rangeland	Ecology
García et al.	2015	ME	6	Multiscale effects on biological soil crusts cover and spatial distribution in the Monte Desert	Ecology
Garibotti et al.	2018	SL	10	Linking biological soil crust attributes to the multifunctionality of vegetated patches and interspaces in a semiarid shrubland	Functional ecology
Corvalán Videla*	2019	ME	35	Diversidad florística y funcional de las costras biológicas de suelo en el Desierto del Monte Central, y su efecto en la funcionalidad del ecosistema	Functional ecology
Guiamet et al.	2019	LR	3	Bioreceptivity of archaeological ceramics in an arid region of northern Argentina	Biodeterioration
Navas Romero*	2019	ME, SJ	14	Funciones ecosistémicas y atributos ecológicos de las costras biológicas en ecosistemas semiáridos-áridos-hiperáridos del centro-oeste de la argentina	Ecology
Garibotti & Polo	2021	SL	11	Divergence among biological soil crust communities developing under different environmental conditions	Ecology
García*	2022	ME	6	Costra Biológica del Suelo como potencial herramienta para restaurar sistemas degradados del Desierto del Monte Central, Argentina	Restoration ecology
Aranibar et al.	2022	ME	6	Functional responses of biological soil crusts to simulated small precipitation pulses in the Monte desert, Argentina	Functional ecology
Bustos et al.	2022	NE	15	Microhabitat-specific differences on the composition and function of biological soil crust communities	Functional ecology

the latter family, Prieto et al. (2008a, b) provided new records of lichen species for northern Argentina, from the provinces of Salta and Jujuy, and even described a new species, *Anthracocarpon andinum* (Verrucariaceae). Subsequent research in the arid and semiarid regions of western Argentina focused on the functional ecology of crusts (Garibotti et al., 2018; Aranibar et al., 2022; Bustos et al., 2022), their restoration in degraded environments (García, 2022), and their role in the biodeterioration of archaeological ceramics (Guiamet et al., 2019). Most of the records of lichen species were obtained from these ecological studies, with two theses on biocrusts in Mendoza and San Juan being particularly significant, as they provided the most comprehensive lists of lichens (Corvalán Videla, 2019; Navas Romero, 2019).

Of the total number of biocrust lichen species (78) in Argentina, the highest species richness was recorded in Mendoza (52), followed by San Juan (17), Neuquén (12), San Luis (11), and Chubut (9) while Salta (4), Jujuy (3) and La Rioja (2) recorded lower richness. To date, no papers have been published on biocrust lichen species from other provinces. More than 90% of these species reported for Argentina belong to arid and semiarid areas of the country, except for *Anthracocarpon andinum*, *Catapyrenium pilosellum*, and *Heteroplacidium acarosporoides* (Jujuy and Salta), which were recorded only in dry sub-humid areas (Fig. 1, Table 2).

The richest family was Verrucariaceae with 22% of the species and together with Collemataceae, Lichinaceae and Peltulaceae grouped almost 50% of the species cited for Argentina. The most frequent lichen species the articles reviewed, were *Placidium squamulosum*, *Endocarpon pusillum*, *Enchylium tenax*, *Peltula obscurans*, and *Psora decipiens*, listed in decreasing order of frequency. These species are common in both arid and semiarid areas.

In addition to the diversity of biocrust lichens reported in the literature in the last 20 years and from the material examined, in this work we add three new species records for Argentina and expand the distribution of four species in the central region of the country. The taxonomic novelties are described below, accompanied by descriptions of the diagnostic characters, geographical distribution, and images of the species.

Taxonomic treatment

Gloeoheppia erosa (J. Steiner) Marton, in Marton & Galun, *Israel J. Bot.* 30(3): 144. 1982 [1981].

Thallus squamulose to subgelatinous, squamules 1 to 3 mm wide, with rimose sometimes sorediate margins (Fig. 2A). Thallus ecorticate and homomerous, very thin, light brown, pale. Medulla contains spaces and densely reticulated hyphae that penetrate the substrate. Photobiont cyanobacterial, unicellular, Chroococcoid-type. Apothecia urceolate (sunken), disc reddish. Asci cylindrical, containing 8 spores per ascus, spores are simple, hyaline, measuring 10-13 x 5-10 µm. Pycnidia: not seen. Spot tests negative.

References. See Henssen (1995) for a description of the species.

Geographic distribution and habitat. Spain, Greece, Yemen, Israel, and Jordan. This species is reported for the first time in Argentina (Fig. 2), located in humid microsites, near a riverside.

Observation. *Gloeoheppia* is morphologically similar to *Heppia* sharing a squamulose thallus and urceolate apothecia (see below), it differs by lacking a cortex and containing a coccoid photobiont. In addition, the ecorticate and brittle thallus, along with the rimose margins, contribute to the studied material's tendency to disintegrate undergo significant changes in appearance after collection (Fig. 2B).

Specimens examined. ARGENTINA. **La Rioja**. Depto. Capital, Reserva Natural Urbana "Taku", 29° 26' 2.95" S; 66° 53' 17.40"O, 566 m, II-2022, *Filippini 5277* (LUTI).

Heppia adglutinata A. Massal., *Geneac. Lich.* (Verona): 8. 1854.

Thallus squamulose, light brown, pale (when dry) to olive green (when wet), smooth upper surface, without pruine. Squamules between 1 to 3 mm wide (sometimes peltate), with ascending edges that can be grouped to form thalli up to 1.5 cm in diameter (Fig. 2C). Soralia absent. Thallus heteromerous, upper cortex 61-73 µm thick, composed of a first layer of elongated anticlinal cells and followed by ovoid cells. Algal layer composed of cyanobacteria of the *Scytonema* type (filamentous), 25-79 µm thick. Lower cortex similar to the upper one but without anticlinal cells. Underside dark, brown to black. Apothecia urceolate, disc reddish to brown (Fig. 2D), generally one per squamule, sometimes 2, and exceptionally up to 10 when the squamules are grouped. Asci cylindrical, 8 simple spores per ascus, 10-15 x 6-8 µm. Pycnidia immersed, conidia fusiform, 2-3 x 1-2 µm. Spot tests negative.

References. See Henssen (1994) for a description of the species.

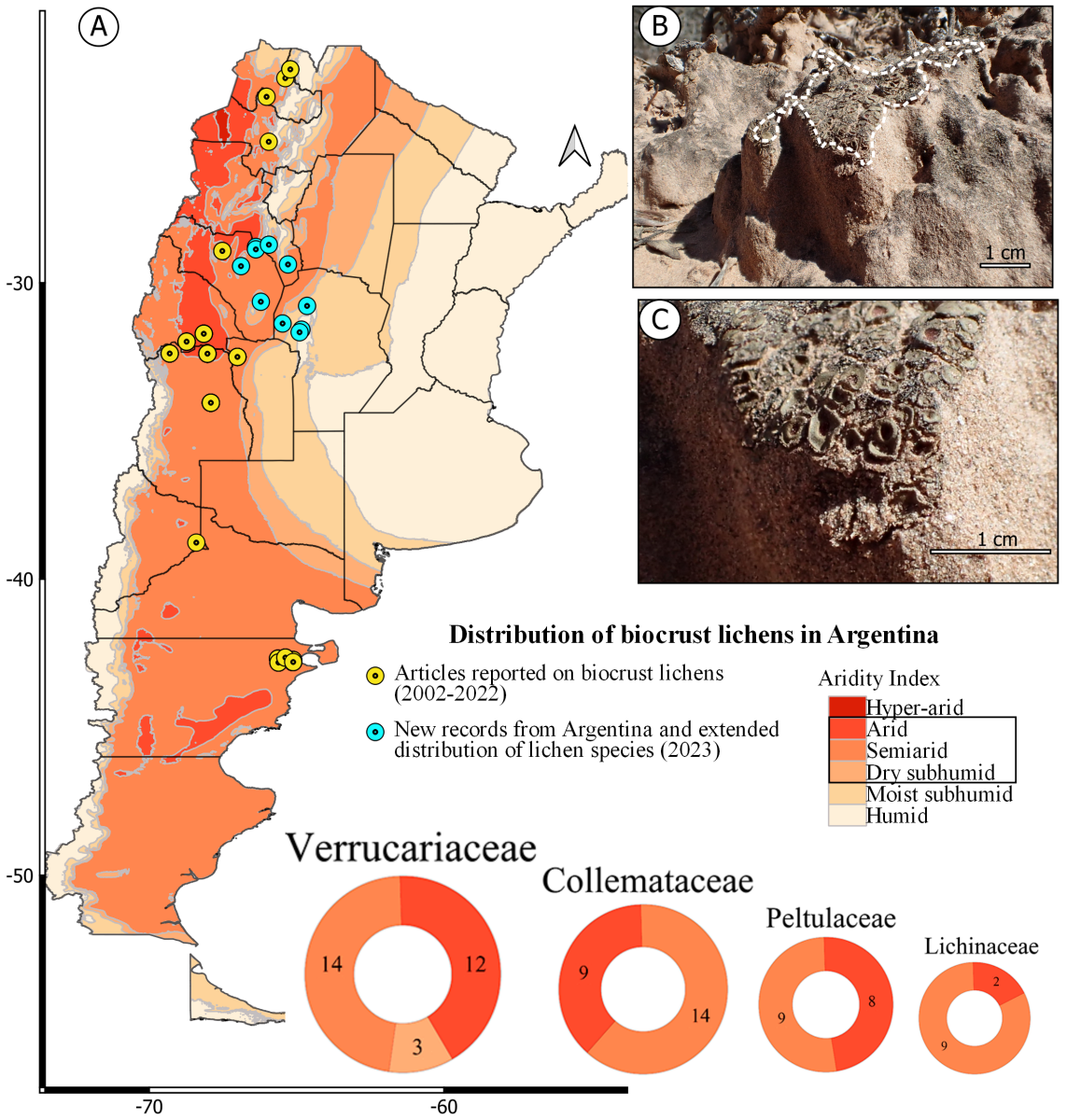

Fig. 1. Distribution of biocrust lichens in Argentina in relation to aridity. **A,** Map of species recorded between 2020-2022 and new records from Argentina (left). The donut charts show the occurrence of species grouped by family in the three regions where biocrust lichens have been reported (bottom). **B,** General aspect of a typical biocrust cover and **C,** detail of this biocrust composed of *Heppia adglutinata* and free-living filamentous cyanobacteria.

Geographical distribution and habitat. Southern Africa, Eastern Europe, Arabian Peninsula, Central, and North America. In South America, *H. adglutinata* has only been recorded in Ecuador (Jørgensen & Palice, 2015), and this is its first record for Argentina.

Observations. The *Scytonema*-type photobiont can also be observed as longer, free-living filaments among the squamules and between the soil particles and the underside of the thallus. However, inside the thallus, the filaments are not observed as such, but rather they appear folded, twisted, or fragmented within sheaths.

Table 2. Geographic distribution of biocrust lichens by provinces from Argentina. CA: Catamarca; CO: Córdoba; CHU: Chubut; JU: Jujuy; LR: La Rioja; ME: Mendoza; NE: Neuquén; SA: Salta; SJ: San Juan; SL: San Luis. New records from Argentina and species that extend their distribution are shown in bold.

Family	Species	CA	CO	CHU	JU	LR	ME	NE	SA	SJ	SL
Acarosporaceae	*Acarospora xanthophana* (Nyl.) Jatta			x							
	Acarospora sp.						x				
	Trimmatothelopsis terricola (H. Magn.) K. Knudsen & Lendemer							x			
Caliciaceae	*Buellia elegans* Poelt									x	
Candelariaceae	*Candelariella citrina* B. de Lesd.							x			
Collemataceae	*Blennothallia crispa* (Huds.) Otálora, P.M. Jørg. & Wedin						x				
	Collema sp.						x				
	Enchylium coccophorum (Tuck.) Otálora, P.M. Jørg. & Wedin	**X**	**X**	x			x			x	x
	Enchylium tenax (Sw.) Gray						x	x		x	x
	Enchylium sp.						x				
	Leptogium caespitosum (Taylor) Swinscow & Krog						x				
	Leptogium sp.						x				
	Scytinium sp.						x				
	Scytinium subaridum (P.M. Jørg. & Goward) Otálora, P.M. Jørg. & Wedin						x				
Gloeoheppiaceae	***Gloeoheppia erosa*** (J. Steiner) Marton					**X**					
	Gloeoheppia polyspora Henssen						x				
	Gloeoheppia turgida (Ach.) Gyeln.										x
	Gloeoheppia sp.						x				
Graphidaceae	*Diploschistes diacapsis* (Ach.) Lumbsch						x			x	
Heppiaceae	***Heppia adglutinata*** A. Massal.	**X**	**X**								
	Heppia lutosa (Ach.) Nyl.						x				
	Heppia sp.						x			x	
Lecanoraceae	*Lecanora* sp.						x			x	
	Lecidella sp.						x				
	Miriquidica scotopholis (Tuck.) B.D. Ryan & Timdal						x			x	
	Polyozosia dispersa (Pers.) S.Y. Kondr., Lőkös & Farkas			x							
Lecideaceae	*Lecidea* sp.						x				
Lichinaceae	*Lempholemma chalazanum* (Ach.) B. de Lesd.							x			
	Lempholemma sp.						x				
	Lichinella intermedia Henssen, Büdel & T.H. Nash					x					
	Lichinella stipatula Nyl.										x

	Lichinella sp.						x				
	Peccania subnigra (B. de Lesd.) Wetmore							x			x
	Peccania sp.						x			x	
	Thallinocarpon nigritellum (Lettau) P.M. Jørg.						x				
Megasporaceae	*Aspicilia praecrenata* (Nyl.) Hue							x			
	Circinaria contorta (Hoffm.) A. Nordin, Savić & Tibell			x							
Pannariaceae	*Fuscopannaria* sp.						x				
Peltulaceae	*Peltula euploca* (Ach.) Poelt										x
	Peltula hassei (Zahlbr.) Büdel, Kauff & Bachran					x	x				
	Peltula obscurans (Nyl.) Gyeln.	**X**	**X**			**X**	x	x		x	x
	Peltula placodizans (Zahlbr.) Wetmore										x
	Peltula psammophila (Nyl.) Egea						x				
	Peltula radicata Nyl.						x				
	Peltula richardsii (Herre) Wetmore						x				
	Peltula sp.						x				
Pertusariaceae	*Porina* sp.						x				
	Sagedia mastrucata (Wahlenb.) A. Nordin, Savić & Tibell						x				
Physciaceae	*Phaeorrhiza nimbosa* (Fr.) H. Mayrhofer & Poelt							x			x
	Rinodina mucronatula H. Magn.			x							
Placynthiaceae	*Placynthium nigrum* Gray						x				
	Placynthium sp.						x				
Psoraceae	*Psora decipiens* (Hedw.) Hoffm.			x				x		x	
	Psora icterica (Mont.) Müll. Arg.	**X**	**X**				x			x	
	Psora tuckermanii R.A. Anderson						x			x	
	Psora sp.						x	x			
	Psorula rufonigra (Tuck.) Gotth. Schneid.						x				
Ramalinaceae	*Bibbya ruginosa* (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman						x				
	Thalloidima sedifolium (Scop.) Kistenich, Timdal, Bendiksby & S. Ekman									x	
	Toninia tristis (Th. Fr.) Th. Fr.									x	
Teloschistaceae	*Gyalolechia subbracteata* (Nyl.) Søchting, Frödén & Arup			x							
Trapeliaceae	*Placynthiella uliginosa* (Schrad.) Coppins & P. James						x				x
	Placynthiella sp.						x				

Verrucariaceae	*Agonimia tristicula* (Nyl.) Zahlbr.					x				
	Anthracocarpon andinum M. Prieto, Aragón & Breuss				x					
	Catapyrenium exaratum Breuss							x		
	Catapyrenium lachneum (Ach.) R. Sant.					x			x	
	Catapyrenium pilosellum Breuss				x					
	Clavascidium lacinulatum (Ach.) M. Prieto					x			x	
	Clavascidium sp.					x				
	Endocarpon pseudosubnitescens Breuss					x				
	Endocarpon pusillum Hedw.			x		x	x			x
	Endocarpon simplicatum (Nyl.) Nyl.					x				
	Endocarpon sp.					x				
	Heteroplacidium acarosporoides (Zahlbr.) Breuss							x		
	Heteroplacidium divisum (Zahlbr.) Breuss		**X**							
	Placidiopsis sp.					x				
	Placidium andicola (Breuss) Breuss				x			x		
	Placidium squamulosum (Ach.) Breuss		**X**	x		**X**	x	x	x	x
	Placidium sp.					x				
	Polyblastia sendtneri Kremp.					x				

Specimens examined. ARGENTINA. Prov. **Córdoba.** Depto. Pocho, Parque Provincial y Reserva Forestal Natural Chancaní, 31° 22’ 13.71” S; 65° 28’ 36.88” O, 348 m, II-2022, *Filippini 5275* (LUTI). Prov. **Catamarca**. Depto. Capayán, al norte de Huillapima por RN38, 28° 42’ 39.96” S; 65° 56’ 33.72” O, 443 m, IX-2023, *Filippini 5276* (LUTI).

Heteroplacidium divisum (Zahlbr.) Breuss, Ann. naturhist. Mus. Wien, 98B: 40, 1996.

Thallus squamulose, dark brown to light brown, more greenish when hydrated. Squamules 1-3 mm, with dark margins (Fig. 2E). Thallus heteromerous, cortex and medulla paraplectenchymatic, chlorococcoid type algal layer. Underside with hyaline rhizohyphae, some darker, that penetrate the substrate (visible under a magnifying glass). Perithecia laminal, abundant, subglobose, excipule dark brown to black, darker near the ostiole (Fig. 2F). Asci cylindrical to fusiform, 8 simple spores, 10-13 x 5-7 µm. Pycnidia laminal, conidia ellipsoid, 3-4 x 1-2 µm. Spot tests negative.

References. See Prieto et al. (2012) for a description of the species.

Geographical distribution and habitat. Southern Europe and China. This is the first record for Argentina.

Observations. *Heteroplacidium* is a segregate genus of *Placidium*, sometimes very difficult to differentiate macroscopically (Prieto et al., 2012). The most important morphological differences are that *Heteroplacidium* has laminar pycnidia, the medulla has isodiametric cells (paraplectenchyma), and no ricines. In *Placidium*, on the other hand, although the pycnidia may be laminar and/or marginal, the medulla is never completely paraplectenchymatous. Species included in *Heteroplacidium* generally have crustose to areolate thalli, except for some species such as *H. divisum* which form small squamules.

Specimens examined. ARGENTINA. Prov. **Córdoba**. Depto. Cruz del Eje, San Marcos Sierras, 30°47’9.22” S; 64°38’8.18”O, 652 m, X-2022, *Filippini 5282* (LUTI). Prov. **Córdoba**.

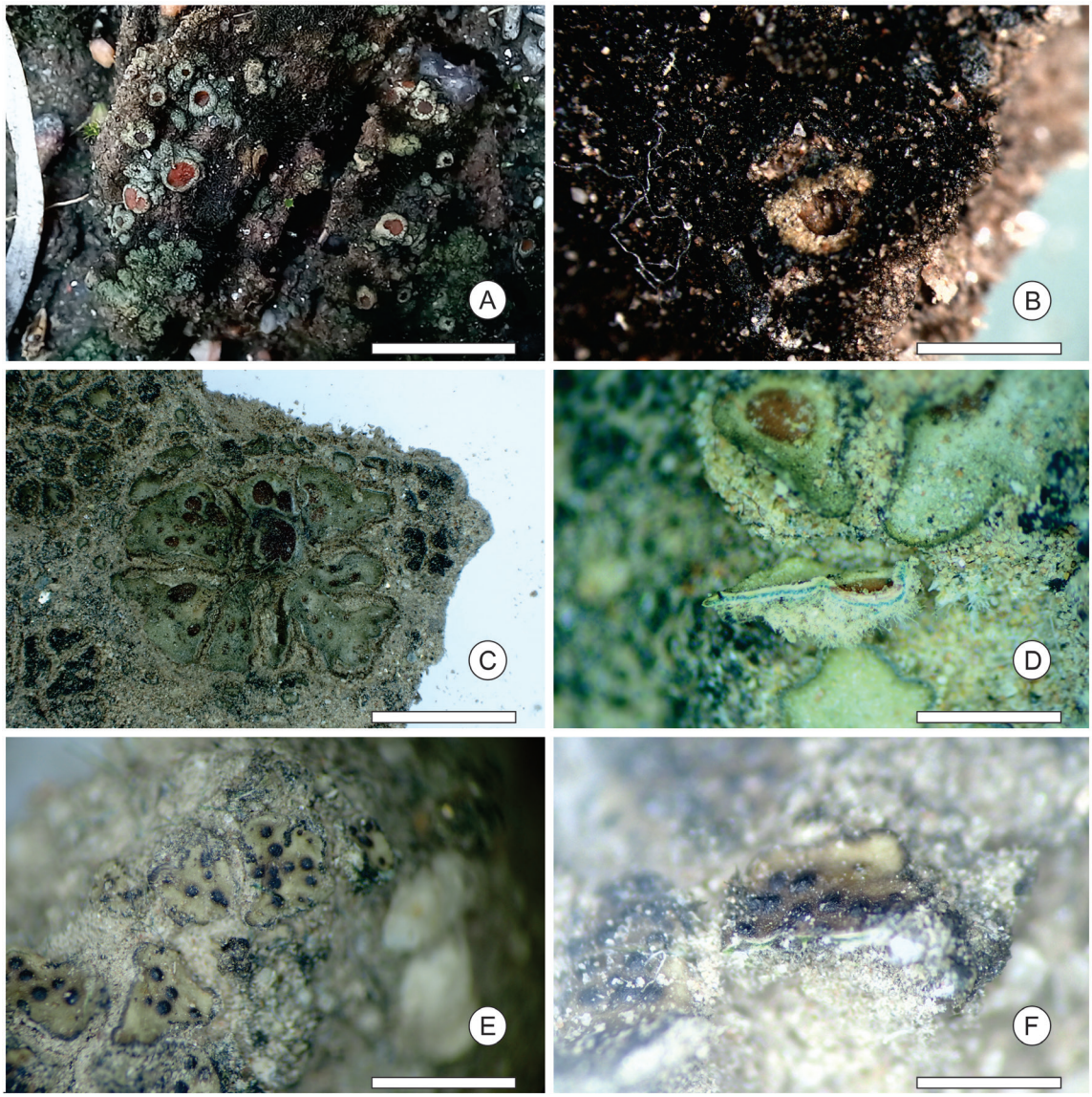

Fig. 2. Morphology of new records for Argentina of biocrust lichens. A-B, *Gloeoheppia erosa*. **A,** Appearance of the thallus before collection. **B,** Squamulae months after collection. C-D, *Heppia adglutinata*. **C,** Thallus morphology. **D,** Detail of urceolate apothecium. E-F, *Heteroplacidium divisum*. **E,** Thallus morphology. **F,** Detail of perithecia. Scales = A: 10 mm; B: 5 mm; C: 10 mm; D: 5 mm; E: 5 mm; F: 2 mm.

Depto. Pocho, Parque Provincial y Reserva Forestal Natural Chancaní 31° 22' 11.07"S; 65° 28' 18.58"O, 354 m, IX-2023, *Filippini 5283* (LUTI).

Enchylium coccophorum (Tuck.) Otálora, P.M. Jørg. & Wedin, Fungal Diversity 64(1): 286 (2013).

Thallus subfruticose, black, 3-5 (10) mm in diameter, formed by flattened, ascending and branched branches (Fig. 3A); branches 0.5-1 (2) mm long, narrow at the base, dark green-olive, becoming wider and black in the distal part (shaped like an inverted triangle), sometimes with a coralloid appearance. Thallus homomerous, the upper cortex composed of a single row of cells. Photobiont cyanobacterial, short chains of

Nostoc, less than 10 cells. Apothecia marginal, dark, disc convex with thalline margin (Fig. 3B). Asci clavate, 8 spores per asci, fusiform with acute ends, 1-septate, 12-14 x 3.5-4.5 µm. Pycnidia marginal, conidia bacilliform, 5-6 x 1.5-2 µm. Spot tests negative.

References. See Jørgensen (2007) for a description of the species.

Geographical distribution and habitat. North and South America, Europe, Arabian Peninsula and Socotra, eastern Africa, India, Oceania, and Australasia. In Argentina, it was previously recorded for Mendoza, Río Negro (Calvelo & Liberatore, 2002) without mentioning its presence in biocrust. Later, this species was recorded forming biocrust in Chubut, Mendoza, San Juan, and San Luis (Scutari et al., 2004; Gómez et al., 2012; Tabeni et al., 2014; Garibotti et al., 2018; Corvalán Videla, 2019; Navas Romero, 2019; Garibotti & Polo, 2021; Aranibar et al., 2022). This is the first record for Catamarca and Córdoba.

Observations. *Enchylium coccophorum* can be confused with the species of *Lempholemma* (Lichinales) previously cited for Argentina in crusts since both groups present dark to black, subfruticose thallus, composed of flattened and erect branches, with *Nostoc* as the cyanobiont and marginal apothecia. The distinction between *Enchylium* and *Lempholemma* lies in the spores: in the former are 1-septate and fusiform (with acute ends), while in *Lempholemma* they are simple and globose (Cannon et al., 2020).

Specimens examined. ARGENTINA. Prov. **Catamarca**. Depto. Capayán, al norte de Huillapima por RN 38, 28° 42’ 39.96”S; 65° 56’ 33.72”O, 443 m, IX-2023, *Filippini 5284* (LUTI). Prov. **Córdoba**. Depto. Pocho, Parque Provincial y Reserva Forestal Natural Chancaní, 31° 22’ 13.71”S; 65° 28’ 36.88”O, 348 m, II-2022, *Filippini 5285* (LUTI).

Placidium squamulosum (Ach.) Breuss, Annln naturh. Mus. Wien, Ser. B, Bot. Zool. 98(Suppl.): 39 (1996)

Thallus squamulose, pale brown, non-sorediate (Fig. 3C-D). Squamules 1 to 5 mm wide with darker margins, completely adhered to the substrate by a network of hyphae concolorous with lower cortex (brown). Thallus heteromerous, epinecral layer present, upper cortex paraplectenchymatic, chlorococcoid type algal layer, medulla and lower cortex distinguishable. Perithecia lamellar, excipule concolorous with the thallus, sometimes darker. Asci cylindrical, 8 spores per asci, spores simple, globose, uniseriate, hyaline, thin-walled, 14-17 x 5-9 µm. Pycnidia laminal, conidia ellipsoid, 2-3 x 1-2 µm. Spot test negative.

References. See Breuss (1993) for a description of the species.

Geographical distribution and habitat. *Placidium squamulosum* is a cosmopolitan species, common in arid areas of North and South America, Europe, Asia, Africa, and Australasia. It was previously recorded in Argentina for Catamarca, Córdoba, Jujuy, Mendoza, Neuquén, San Juan, and Salta (Breuss, 1992; Calvelo & Liberatore 2002) as a terricolous species. Its presence as a biocrust lichen was also confirmed in Chubut, Mendoza, Neuquén, Salta, and San Juan (Scutari et al., 2002, 2004; Prieto et al., 2008a b; Gómez et al., 2012; Tabeni et al., 2014; Corvalán Videla, 2019; Navas Romero, 2019; Bustos et al., 2022), and in Córdoba and La Rioja thanks to our field collection, resulting in the first record for the latter province.

Observations. It is important to highlight that *P. squamulosum* in the study area presents great variability in the color and size of the squamules, which can be associated with sites with higher solar exposure. Furthermore, *P. squamulosum* is observed forming groups of numerous squamules, growing among a network of cyanobacteria, which together cover a large part of the biological soil crust, without another lichen species among them.

Specimens examined: ARGENTINA. Prov. **Córdoba.** Depto. Pocho, Parque Provincial y Reserva Forestal Natural Chancaní, 31° 22’ 13.71” S; 65° 28’ 36.88” O, 348 m, II-2022, *Filippini 5280* (LUTI). Prov. **La Rioja.** Depto. General Belgrano, Olta, 29° 26’ 2.4” S; 66° 53’ 16.8” O, 560 m, II-2022, *Filippini 5281* (LUTI).

Peltula obscurans (Nyl.) Gyeln., *Feddes Repert. Spec. Nov. Regni veg.* 38: 308 (1935)

Thallus squamulose, olive brown, peltate, non-sorediate. Squamules 1 to 5 mm wide, sometimes with dark and ascending margins, held by a central cord of rhizohyphae (umbilicus). Thallus with thin upper cortex, algal layer composed of coccal cyanobacteria of the *Chroococcodiopsis* type. Apothecia immersed in the thallus, one per squamule, with a thalline margin, disc reddish-brown, becoming darker in older squamules. Hyaline hymenium, brown epihymenium K-. Asci polisporate (more than 50 spores per asci), spores simple, hyaline, globose to ellipsoidal, 5-7 x 2-3 µm (Fig. 3H).

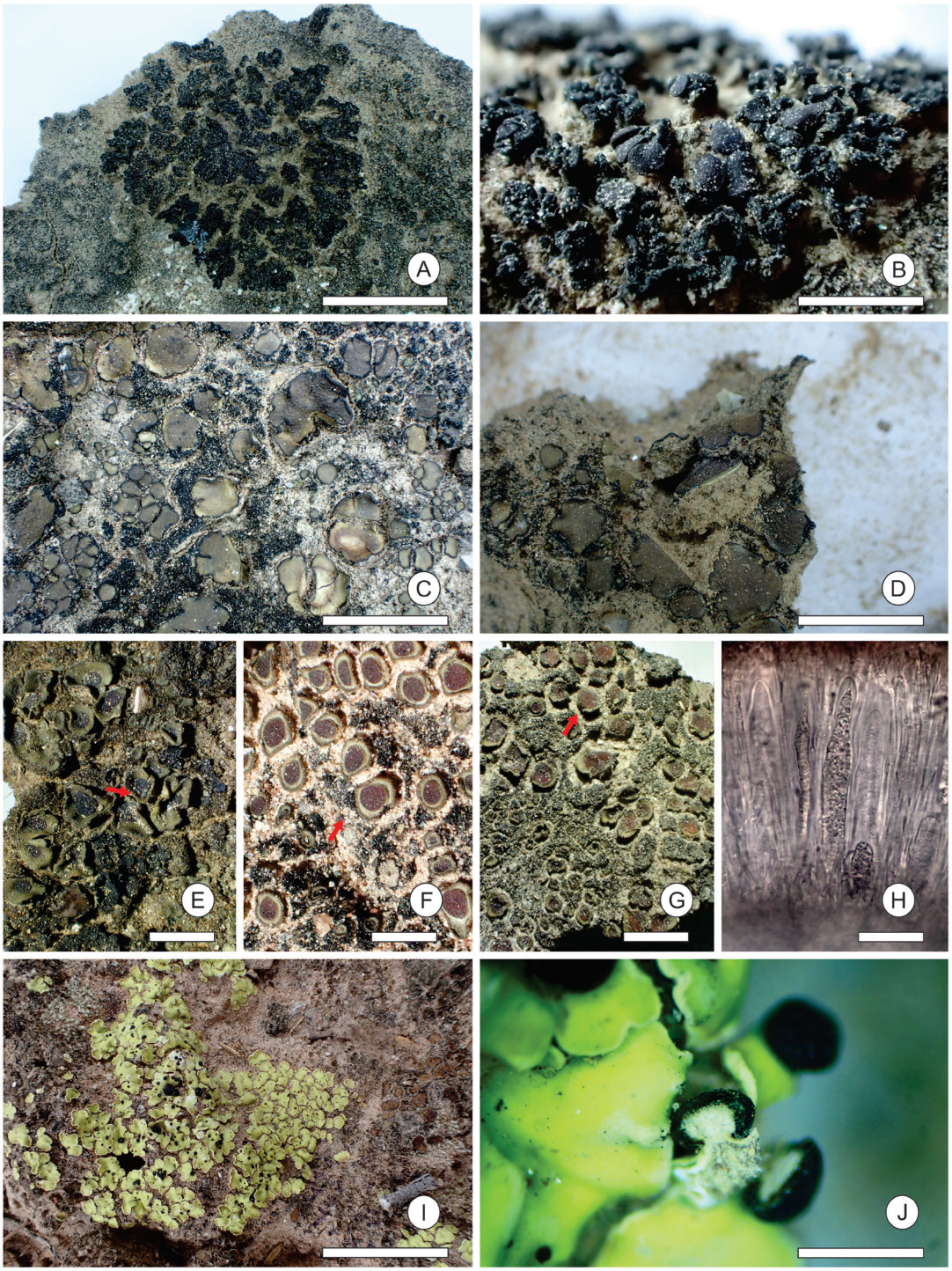

Fig. 3. Morphology of lichens in biocostra that we extend the known distribution in this work. Morphology of lichens in biocrust that we extend the known distribution in this work. A-B, *Enchylium coccophorum*. **A,** Thallus morphology. **B,** Marginal apothecia. C-D, *Placidium squamulosum*. **C,** Thallus morphology. **D,** Detail of perithecia. E-H, *Peltula obscurans*. **E-G,** Morphological diversity of thalli. **H,** Polysporous asci. I-J, *Psora icterica*. **I,** Thallus morphology. **J,** Mature apothecium (convex and emarginate). Scales = A: 5 mm; B: 2 mm; C-G: 10 mm; H: 30 µm; I: 20 mm; J: 2 mm.

References. See Wetmore (1970) for a description of the species.

Geographical distribution and habitat. Europe, Africa, North and South America, Asia and Australia. In Argentina, *P. obscurans* was previously recorded for Río Negro (Calvelo & Liberatore, 2002) and confirmed as a boicrust lichen in Mendoza, Neuquén, San Juan, and San Luis (Garibotti et al., 2018; Corvalán Videla, 2019; Guiamet et al., 2019; Navas Romero, 2019; Garibotti & Polo, 2021; Bustos et al., 2022). This is the first record of the species for Catamarca, Córdoba, and La Rioja.

Observations. *Peltula obscurans* is characterized by a broad morphological variability (Egea, 1989). The examined material reflects differences in the shape, size, and color of the squamules, as well as the margin of the apothecium disc (Fig. 3E-G). For example, in some specimens, the margins of the oldest squamules rise away from the substrate and even retract, resembling *P. crispatula*. In other specimens, the squamules with a darker margin are formed almost entirely by the apothecium, with a reddish to brownish disc. However, all these morphotypes share a squamulose thallus, never inflated, lacking soredia, rounded squamules, and attached to the substrate by rhizohyphae (or umbilicus). Inicially, three varieties were proposed: *deserticola*, *hassei* and *obscurans* (Wetmore, 1970), but currentyly, *Peltula hassei* is treated as a species and, the other varieties require further research to be treated as monophyletic entities (Marques et al., 2013). Since this genus is one of the most common in soil crusts in the studied region, future molecular analyzes may provide greater clarity on the identity of the morphotypes.

Specimens examined. ARGENTINA. Prov. **Córdoba**. Depto. Pocho, Parque Provincial y Reserva Forestal Natural Chancaní, 31° 22' 13.71" S; 65° 28' 36.88" O, 348 m, II-2022, *Filippini 5278* (LUTI). Prov. **La Rioja**. Depto. General Belgrano, Olta, 29° 26' 2.4" S; 66° 53' 16.8" O., 560 m, II-2022, *Filippini 5279* (LUTI).

Psora icterica (Mont.) Müll. Arg., Flora, Regensburg 71: 45 (1888)

Thallus squamulose, yellowish bright yellow to yellowish brown due to the presence of rhizocarpic acid, formed by confluent squamules, 3 to 5 mm wide and with somewhat ascending margins of lighter a color (Fig. 3I). Upper surface usually dull, although it sometimes shows localized rust in some parts. Thallus heteromerous, with a chlorococcoid-type algal layer. Apothecia laminar, lecideine, brown to black, and convex when mature (Fig. 3J). Asci with 8 spores. Spores simple, ellipsoid, 15-20 x 7-8 µm.

References. See Brodo et al. (2001) for a description of the species.

Geographical distribution and habitat. *Psora icterica* is a species with a wide American distribution (North and South), occurring in both desert environments and montane forests, even above 2000 m a.s.l., on soils, rock, and moss. In Argentina, *P. icterica* was previously recorded for Córdoba, Corrientes, Buenos Aires, Mendoza, and Rio Negro (Calvelo & Liberatore, 2002), and confirmed as a boicrust lichen in Mendoza and San Juan (Navas Romero, 2019). This is the first reference of the *P. icterica* as biocrust lichen, growing on shallow soil in rocky areas of the Sierras Grandes (Córdoba) and the first record for Catamarca, associated with low shrub "jarillales" (*Larrea* spp.) with high sun exposure.

Observations. *Psora icterica* is easily recognized in the field by its distinctive bright yellow pigment, contrasted with dark reddish-brown to black apothecia, which resembles species with areolate thalli such as *Acarospora* spp.

Specimens examined. ARGENTINA. Prov. **Catamarca**. Depto. Capayán, al sur de El Quemado por RN 60 29°32'48.3" S; 65°34'48.8" O, 226 m, VII-2023, *Filippini, 5286, 5287* (LUTI). Prov. **Córdoba**. Depto. San Alberto, al norte de RN 34 31°23'41.91" S; 65°25'24.41" O, 2230 m, III-2021, *Filippini 5288* (LUTI). Prov. **Córdoba**. Depto. San Alberto, al oeste de RN 34 31°40'6" S; 64°54'2.23" O, 1793 m, III-2020, *Filippini, 5289* (LUTI).

DISCUSSION AND CONCLUSIONS

Biocrust studies are relatively new in Argentina, and many do not explore the specific components of biocrusts in depth due to their ecological focus. Consequently, most of the knowledge about lichens as part of biocrusts is even more recent. This bias can be attributed to the fact that the term "biocrust" began to be used worldwide in the late 1990s, initially referring to "black crusts" (dominated by cyanobacteria) without considering other components (Weber et al., 2022). Later, the term expanded to a global definition based on a comprehensive review of their taxonomy, habitat, physical structure, and function (Belnap & Lange, 2003). By the time the term biocrust became widespread, lichenology was already a developing discipline in Argentina, at least in terms of taxonomy, but there was no

particular focus on whether lichens growing on soil could form part of biocrusts. In fact, there are no studies on the diversity of terricolous lichens in Argentina.

This study has compiled all known biocrust lichen species and added three new species for Argentina. Many of these species were previously recorded in Argentina by Calvelo & Liberatore (2002), who provided a valuable update on the lichens of Argentina, citing more than 1600 species. Since their list did not include information on substrates or habitats, it is challenging to determine how many of these species could inhabit soil environments. Overall, there is a significant need for more taxonomic studies on terricolous lichens in Argentina.

Over time, studies of biocrust lichens in Argentina have focused primarily on an ecological perspective. In recent years, research questions have shifted to focus on the composition and distribution patterns of biocrust lichens (García et al., 2015; Corvalán Videla, 2019), their interaction with vascular vegetation (Garibotti et al., 2018), their response to erosion by fire (Perazzo & Rodríguez, 2019) and livestock (Gómez et al., 2012), among other aspects. This broadened perspective has enhanced our knowledge of the most abundant species in the various environments studied so far. This shift explains why much of the specimen recognition in ecological work has been done at the genus level (Table 2). Many lichen species, and even some biocrust-forming genera, can be distinguished only by microscopic characters such as asci shape, spore shape and size, photobiont type, and specialized hyphae for fixation, among other features.

Conversely, when specialists have identified biocrust lichens, more precise species identification has been achieved, and a high family richness has been recorded (Table 2, Scutari et al., 2002, 2004). Therefore, macroscopic observations (already challenging due to the small size of the thalli) may underestimate the diversity of biocrust lichens in Argentina. This underscores the need to intensify taxonomic studies (morpho-anatomical, chemical, and molecular DNA sequencing) of these crust forming organisms.

In Argentina, the biocrust lichen species recorded so far belong mainly to the families Verrucariaceae, Collemataceae, Lichinaceae, and Peltulaceae, and are distributed in the north, west, and south-central regions of the country, particularly in arid and semiarid areas (Fig. 1). Our observations broadly support those of Bowker et al. (2017), who related the presence of many of these families to arid ecosystems around the world. According to these authors, climate is the main driver of the alpha and beta diversity of biocrusts in arid areas, which aligns with our results.

While a concentration of species reports in certain areas is expected (Bowker et al., 2017; Manzitto-Tripp et al., 2022), our results show that all families are nonetheless well represented across a wide range of localities throughout the country (Fig. 1). This could be attributed to the ecological nature of the studies, which aimed to associate biocrust lichen communities with environmental and anthropogenic factors (Table 1). Mendoza was the province with the highest reported diversity, which was expected given that most of the studies were conducted there. This indicates a greater sampling effort in this locality, similar to the explanation provided by Manzitto-Tripp et al. (2022). Additionally, La Rioja, Salta, and Jujuy were the provinces with the lowest reported diversity, reflecting the lowest sampling effort as studies focused on terricolous lichen species that could be related to biodeterioration and on the family Verrucariaceae (Table 1).

Studies on biocrust lichen species are found in the arid and semiarid regions of Patagonia and northwestern Argentina, leaving a knowledge gap in other areas such as the central part of the country, even in less arid zones. This gap is particularly important given the regional processes of soil degradation and loss of ecosystem services in these less arid areas (Cingolani et al., 2013; Fernández et al., 2023). In the central region, biological crust could contain a high diversity of lichens, as observed in some protected areas of the Arid Chaco, where cattle exclusion has allowed for the development of highly diverse lichen communities at the morphospecies level (Filippini, pers. obs.). This is reflected in the species of Verrucariaceae and Peltulaceae, which are remarkably similar in appearance, sharing color and thalli morphology (Fig. 3). Many of the species found in the semiarid regions of central Argentina are new records for Catamarca, La Rioja, and Córdoba, with some even being new citations for the country. Biocrust lichens were also reported on degraded soils in the Sierras Grandes (Córdoba), a dry subhumid region. This suggests that the environmental conditions necessary for soil lichens to form crusts can be quite heterogeneous. These taxonomic updates, together with their detailed descriptions, aim to enhance the understanding of lichens and to assist ecological studies in refining species identification and obtaining more comprehensive diversity lists.

Among the species studied, it is observed that they all share the characteristics of being small in size with a scaly morphology, which has been associated with arid environments, as this would allow them to resist extreme environmental conditions (Leppik et al., 2015; Matos et al., 2015).

We also found that most species have dark

colored thalli, except for *P. icterica*, which is yellow due to the presence of rhizocarpic acid. Both dark and yellow-colored lichens have been observed in species inhabiting areas with high solar radiation (Barreno Rodríguez & Pérez-Ortega, 2003; Armstrong, 2017). In addition, most species have fixation structures, such as hyphae or rhizohyphae, which help bind soil particles together in environments with unconsolidated soil. This process creates a more stable substrate, facilitating colonization and crust formation. Species like *P. obscurans*, *P. escuamulosum*, *H. divisum*, and *G. erosa* not only exhibit these fixation structures but also have a squamulose morphology that further supports their ability to colonize soils, particularly in hot and arid areas (Budel & Scheidegger, 2008; Matos et al., 2015).

With almost 80% of Argentina's territory occupied by arid and semiarid areas (Ganem et al., 2022), the lack of information on biocrust composition in large areas may be due to the relative scarcity of specialists. As a result, biocrust lichens may be much more abundant than previously thought. We hope that this study can serve as a starting point for further research on these organisms.

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AUTHORS' CONTRIBUTIONS

ERF designed the research, collected, and identified the field material. REDD, RAG, MG, and CEM collaborated in the collection and identification of the material. All authors participated in the discussion and writing of the article.

BIBLIOGRAPHY

Armstrong, R. A. 2017. Adaptation of lichens to extreme conditions. In Shukla, V.; S. Kumar & N. Kumar (eds.) *Plant adaptation strategies in changing environment,* Springer.

Aranibar, J. N.; M. J. Repetur, V. R. García, R. E. Dazat, M. E. C. Videla & P. E. Villagra. 2022. Functional responses of biological soil crusts to simulated small precipitation pulses in the Monte desert, Argentina. *Geoderma* 410: 115660. DOI: https://doi.org/10.1016/j.geoderma.2021.115660

Barreno Rodríguez, E. & S. Pérez-Ortega. 2003. *Líquenes de la reserva natural integral de Muniellos, Asturias*. KRK ediciones.

Belnap, J. & O. L. Lange (eds.). 2003. *Biological soil crusts: structure, function and management. Ecological Studies*. Springer, Berlin. DOI: https://doi.org/10.1007/978-3-642-56475-8.

Bowker, M. A.; R. L. Mau, F. T. Maestre, C. Escolar & A. P. Castillo-Monroy. 2011. Functional profiles reveal unique ecological roles of various biological soil crust organisms. *Functional Ecology* 25: 787-795. DOI: https://doi.org/10.1111/j.1365-2435.2011.01835.x

Bowker, M. A.; B. Büdel, F. Maestre, A. Antoninka & D. Eldridge. 2017. Bryophyte and Lichen Diversity on Arid Soils: Determinants and Consequences; In B. Steven (ed.), *The Biology of Arid Soils*. Berlin, Boston: De Gruyter. DOI: https://doi.org/10.1515/9783110419047-005

Bowker, M. A.; S. C. Reed, F. T. Maestre & J. E. David. 2018. Biocrusts: the living skin of the earth. *Plant Soil* 429: 1-7. DOI: https://doi.org/10.1007/s11104-018-3735-1

Breuss, O. 1993. Catapyrenium (Verrucariaceae) species from South America. *Plant Systematics and Evolution* 185: 17-33.

Breuss, O. 2010. An Updated World-Wide Key to the Catapyrenioid Lichens (Verrucariaceae). *Herzogia* 23(2): 205-16. DOI: https://doi.org/10.13158/heia.23.2.2010.205

Brodo, I. M.; S. D. Sharnoff & S. Sharnoff. 2001. Lichens of North America. Yale University Press, New Haven and London.

Büdel, B. 2001. Biological Soil Crusts of South America. In J. Belnap & O. L. Lange (eds.), *Biological Soil Crusts: Structure, Function, and Management*. Springer-Verlag Berlin Heidelberg.

Büdel, B. & C. Scheidegger. 2008. Thallus morphology and anatomy. In T. H. Nash, III (eds.), *Lichen biology*. Cambridge University Press.

Büdel, B.; M. Vivas & O. L. Lange. 2013. Lichen species dominance and the resulting photosynthetic behavior of Sonoran Desert soil crust types (Baja California, Mexico). *Ecology Process* 2: 6. DOI: https://doi.org/10.1186/2192-1709-2-6

Bustos, M. J.; I. A. Garibotti; N. Cech; M. C. Navarro; M. Gonzalez Polo & P. Satti. 2022. Microhabitat-specific differences on the composition and function of biological soil crust communities. *Plant and Soil* 479: 663–677. doi:10.1007/s11104-022-05556-5.

Calvelo, S. & S. Liberatore. 2002. Catálogo de los Líquenes de la Argentina. *Kurtziana* 29(2): 7-170.

Candan, M. & M. Schultz. 2015. New and Additional Records

of Cyanolichens from Turkey. *Herzogia* 28(2): 359-69. DOI: https://doi.org/10.13158/heia.28.2.2015.359.

Cannon, P.; M. A. G. Otálora, A. Košuthová, M. Wedin, A. Aptroot, B. Coppins & J. Simkin. 2020. Peltigerales: Collemataceae, including the genera *Blennothallia*, *Callome*, *Collema*, *Enchylium*, *Epiphloea*, *Lathagrium*, *Leptogium*, *Pseudoleptogium*, *Rostania* and *Scytinium*. *Revisions of British and Irish Lichens* 2: 1-38. DOI: https://doi.org/10.34885/174

Castillo-Monroy, A. P. & F. T. Maestre. 2011. La costra biológica del suelo: Avances recientes en el conocimiento de su estructura y función ecológica. *Revista Chilena de Historia Natural* 84: 1-21.

Cingolani, A. M.; M. V. Vaieretti, M. A. Giorgis, N. La Torre, J. I. Whitworth-Hulse & D. Renison. 2013. Can Livestock and Fires Convert the Sub-Tropical Mountain Rangelands of Central Argentina into a Rocky Desert?. *The Rangeland Journal* 35(3): 285-97. DOI: https://doi.org/10.1071/RJ12095

Consortium of Lichen Herbaria. 2024. http//:lichenportal.org/portal/index.php. Accessed on July 12.

Corvalán Videla, M. E. 2019. Diversidad florística y funcional de las costras biológicas de suelo en el Desierto del Monte Central, y su efecto en la funcionalidad del ecosistema. Tesis Doctoral. Universidad Nacional de Cuyo, Argentina.

de Martonne, E., editor. 1925. The New Edition of de Martonne's Physical Geography. Geographical Review 15:336–337.

Egea, J. M. 1989. Los Géneros *Heppia* y *Peltula* (Líquenes) En Europa Occidental y Norte de África. *Bibliotheca Lichenologica* 31: 1-122.

Fernández, D. S.; M. E. Puchulu, C. M. Rostagno, L. La Manna, A. R. Becker, M. Del T. Grumelli, & H. F. Schiavo. 2023. Agricultural Land Degradation in Argentina. In: Pereira, P.; M. Muñoz-Rojas, I. Bogunovic & W. Zhao (eds.), *Impact of Agriculture on Soil Degradation I: Perspectives from Africa, Asia, America and Oceania* 120: 1-47. The Handbook of Environmental Chemistry. Cham: Springer International Pub. DOI: https://doi.org/10.1007/698_2022_917

Finger-Higgens, R.; M. C. Duniway, S. Fick, E. L. Geiger, D. L. Hoover, A. A. Pfennigwerth, M. W. Van Scoyoc & J. Belnap. 2022. Decline in biological soil crust N-fixing lichens linked to increasing summertime temperatures. *Proceedings of the National Academy of Sciences* 119(16): e2120975119. DOI: https://doi.org/10.1073/pnas.2120975119

Ganem, K. A.; Y. Xue, A. A. Rodrigues, W. Franca-Rocha, M. T. Oliveira, N. S. Carvalho, E. Y. T. Cayo, M. R. Rosa, A. C. Dutra & Y. E. Shimabukuro. 2022. Mapping South America's Drylands through Remote Sensing—A Review of the Methodological Trends and Current Challenges. *Remote Sensing* 14(3): 736. DOI: https://doi.org/10.3390/rs14030736

García, V.; J. Aranibar & N. Pietrasiak. 2015. Multiscale effects on biological soil crust cover and spatial distribution in the Monte Desert. *Acta Oecologica* 69: 35-45. DOI: https://doi.org/10.1016/j.actao.2015.08.005

García, V. R. 2022. Costra Biológica del Suelo como potencial herramienta para restaurar sistemas degradados del Desierto del Monte Central, Argentina. Tesis Doctoral. Universidad Nacional de Cuyo, Argentina.

Garibotti, I. A.; M. Gonzalez Polo & S. Tabeni. 2018. Linking biological soil crust attributes to the multifunctionality of vegetated patches and interspaces in a semiarid shrubland. *Functional Ecology* 32: 1065-1078. DOI: https://doi.org/10.1111/1365-2435.13044

Garibotti, I. A. & Gonzalez Polo, M. 2021. Divergence among biological soil crust communities developing under different environmental conditions. *Journal of Vegetation Science* 32(1): e12987. DOI: https://doi.org/10.1111/jvs.12987

Gómez, D. A.; J. N. Aranibar, S. Tabeni, P. E. Villagra, I. A. Garibotti & A. Atencio. 2012. Biological soil crust recovery after long-term grazing exclusion in the Monte Desert (Argentina). Changes in coverage, spatial distribution, and soil nitrogen. *Acta Oecologica* 38: 33-40. DOI: https://doi.org/10.1016/j.actao.2011.09.001

Guiamet, P. S.; D. M. Soto & M. Schultz. 2019. Bioreceptivity of archaeological ceramics in an arid region of northern Argentina. *International Biodeterioration & Biodegradation* 141: 2-9. DOI: https://doi.org/10.1016/j.ibiod.2018.10.003

Henssen, A. 1994. Contribution to the morphology and species delimitation in *Heppia* sensu stricto (lichenized Ascomycotina). *Acta Botanica Fennica* 150: 57-73.

Henssen, A. 1995. The New Lichen family Gloeoheppiaceae and its Genera *Gloeoheppia*, *Pseudopeltula* and *Gudelia* (Lichinales). *The Lichenologist* 27(4): 261-290. DOI: https://doi.org/10.1006/lich.1995.0025

Jørgensen, P. M. 2007. Collemataceae. *Nordic Lichen Flora* 3: 14-42.

Jørgensen, P. M. & Z. Palice. 2015. Additions to the Cyanolichens of the Andes. *Herzogia* 28(1): 285-87. DOI: https://doi.org/10.13158/heia.28.1.2015.285

Leppik, E.; I. Jüriado, A. Suija & J. Liira. 2015. Functional ecology of rare and common epigeic lichens in alvar grasslands. *Fungal Ecology* 13: 66-76.

Manzitto-Tripp, E. A.; J. C. Lendemer & C. M. McCain. 2022. Most lichens are rare, and degree of rarity is mediated by lichen traits and biotic partners. *Diversity and Distributions* 28(9): 1810-1819.

Marques, J.; M. Schultz & G. Paz-Bermúdez. 2013. A *Peltula* Nyl. Diversity Hotspot in North-East Portugal, with One Species New to Science and Three Species New to Mainland Europe. *The Lichenologist* 45(4): 483-96. DOI: https://doi.org/10.1017/S0024282913000261

Matos, P.; P. Pinho, G. Aragón, I. Martínez, A. Nunes, A. M. Soares & C. Branquinho. 2015. Lichen traits responding to aridity. *Journal of Ecology* 103(2): 451-458.

McCune, B. & R. Rosentreter. 2007. Biotic Soil Crust Lichens of the Columbia Basin: Monographs in North American Lichenology. 1. *Northwest Lichenologists*, Corvallis, Oregon.

Nash III, T. H.; B. D. Ryan, C. Gries & F. Bungartz (eds). 2002. Lichen Flora of the Greater Sonoran Desert Region. 1. Lichens Unlimited, School of Life Sciences, Arizona State University, Tempe, Arizona.

Nash III, T. H.; B. D. Ryan, P. Diederich, C. Gries & F. Bungartz (eds). 2004. Lichen Flora of the Greater Sonoran Desert Region. 2. Lichens Unlimited, School of Life Sciences, Arizona State University, Tempe, Arizona.

Navas Romero, A. L. 2019. Funciones ecosistémicas y atributos ecológicos de las costras biológicas en ecosistemas semiáridos-áridos-hiperáridos del centro-oeste de la Argentina. Tesis Doctoral, Universidad Nacional de Cuyo, Argentina.

Navas Romero, A. L.; E. Martínez Carretero & M. Herrera Moratta. 2021. Restauración de costras biológicas del suelo: pasado, presente y futuro. *Multequina* 30(2): 25-47.

Perazzo, A. & J. Rodríguez. 2019. Impacto del fuego sobre la vegetación no vascular del suelo: un caso de estudio en los bosques de *Polylepis australis* (Rosaceae) del centro de Argentina. Lilloa 56:67-80. DOI: https://doi.org/10.30550/j.lil/2019.56.2/6

Pissolito, C.; I. Garibotti, & R. Villalba. 2021. Inter-annual climatic variability modulates biotic interactions on early *Nothofagus pumilio* community development. *Plant Ecology & Diversity* 14:65-80.

Prieto, M.; G. Aragón & I. Martínez. 2008a. New records in the lichen family Verrucariaceae (Ascomycota) from Argentina. *Boletín de la Sociedad Argentina de Botánica* 43(3-4): 205-210.

Prieto, M.; G. Aragón, I. Martínez & O. Breuss. 2008b. A new species of *Anthracocarpon* (Verrucariaceae) from Argentina. *The Bryologist* 111(1): 128-132.

Prieto, M.; I. Martínez, G. Aragón, C. Gueidan & F. Lutzoni. 2012. Molecular phylogeny of *Heteroplacidium*, *Placidium*, and related catapyrenioid genera (Verrucariaceae, Lichen-Forming Ascomycota). *American Journal of Botany* 99(1): 23-35. DOI: https://doi.org/10.3732/ajb.1100239

Rosentreter, R.; M. Bowker & J. Belnap. 2007. A field guide to biological soil crusts of western U.S. drylands: Common lichens and bryophytes. *Bureau of Land Management* 1-104.

Schultz, M. & B. Büdel. 2002. Key to the Genera of the Lichinaceae. *The Lichenologist* 34(1): 39-62. DOI: https://doi.org/10.1006/lich.2001.0367

Scutari, N. C.; B. Doris Diez & H. T. Lumbsch. 2002. New records of soil-associated lichens from north-eastern Patagonia (Chubut, Argentina). *Mycotaxon* 83: 369-383.

Scutari, N. C.; M. B. Bertiller & A. L. Carrera. 2004. Soil-associated lichens in rangelands of north-eastern Patagonia. Lichen groups and species with potential as bioindicators of grazing disturbance. *The Lichenologist* 36(6): 405-412. DOI: https://doi.org/10.1017/S0024282904014008

Soule, T.; I. J. Anderson, S. L. Johnson, S. T. Bates & F. Garcia-Pichel. 2009. Archaeal populations in biological soil crusts from arid lands in North America. *Soil Biology and Biochemistry* 41(10): 2069-2074. DOI: https://doi.org/10.1016/j.soilbio.2009.07.023

Tabeni, S.; I. A. Garibotti, C. Pissolito & J. N. Aranibar. 2014. Grazing effects on biological soil crusts and their interaction with shrubs and grasses in an arid rangeland. *Journal of Vegetation Science* 25(6): 1417-25. DOI: https://doi.org/10.1111/jvs.12204

Velasco Ayuso, S.; G. R. Oñatibia, F. T. Maestre & L. Yahdjian. 2020. Grazing pressure interacts with aridity to determine the development and diversity of biological soil crusts in Patagonian rangelands. *Land Degradation & Development* 31(4): 488-499.

Weber, B.; J. Belnap, B. Büdel, A. J. Antoninka, N. N. Barger, V. Bala Chaudhary, A. Darrouzet-Nardi, D. J. Eldridge, A. M. Faist, S. Ferrenberg, C. A. Havrilla, E. Huber-Sannwald, O. M. Issa, F. T. Maestre, S. C. Reed, E. Rodriguez-Caballero, C. Tucker, K. E. Young, Y. Zhang, Y. Zhao, X. Zhou & M. A. Bowker. 2022. What is a biocrust? A refined, contemporary definition for a broadening research community. *Biological Reviews* 97(5): 1768-85. DOI: https://doi.org/10.1111/brv.12862

Wetmore, C. M. 1970. The lichen family Heppiaceae in North America. *Annals of the Missouri Botanical Garden* 57: 158-209.

Yahdjian, L.; L. J. Carboni, S. Velasco Ayuso & G. R. Oñatibia. 2023. Intensification of livestock farming in times of climate change. The challenges of domestic grazing in the drylands of the Argentine Patagonia. *Mètode Science Studies Journal* 13: 25-31.