

Caloplaca aptrootii (Teloschistaceae), a new blastidiolate species with a dark-brown squamulose thallus from the Bolivian Andes

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Abstract. *Caloplaca aptrootii* is described as a new species based on morphological, anatomical, and molecular evidence. Phylogenetic analyses of a three-locus dataset (ITS, nuLSU, and mtSSU) place it within *Caloplaca* s.str. in the subfamily *Caloplacoideae*. Morphologically, the species fits well within the current circumscription of the genus, being characterized by a thallus containing the Sedifolia-grey pigment rather than anthraquinones, lecanorine apothecia, and the presence of blastidia. It is, however, unusual in possessing a distinctly squamulose thallus. The new species most closely resembles *C. chlorina*, but differs in having a thicker, squamulose thallus, a thicker thalline cortex, a distinct epinecral layer, and larger ascospores. The species inhabits high Andean vegetation, where it grows on siliceous rock outcrops. Additionally, a revised checklist of crustose *Teloschistaceae* species known from Bolivia is presented, and the new combination *Lacrima erythrantha* is proposed. Further records of the latter species from Bolivia are provided.

Key words: biodiversity, lichen-forming fungi, new combination, new species, phylogeny, South America, tropical Andes, vegetative propagules

Introduction

The family *Teloschistaceae* is a cosmopolitan lineage of lichen-forming *Lecanoromycetes* that predominantly inhabits dry, open and well-exposed environments (e.g., Fletcher & Laundon 2009). The crustose taxa, which constitute the dominant growth form within the *Teloschistaceae*, are relatively well studied in Europe, Asia, North America, Australasia, and the polar regions, whereas, Africa and South America remain among the least explored areas with respect to the family's diversity (Arup et al. 2013). *Teloschistaceae* is currently represented in Bolivia by eighteen genera: *Aridoplaca*, *Athalia*, *Austroplaca*, *Caloplaca* s.str., *Cinnabaria*, *Huneckia*, *Josefpoeltia*, *Lacrima*, *Leproplaca*, *Rusavskia*, *Scutaria*, *Squamulea*, *Tayloriellina*, *Teloschistes*, *Xanthomendoza*, *Xanthoria*, *Wetmoreana* and *Wilketalia* (Wilk & Flakus 2017; Wilk et al. 2021; Wilk 2023; Wilk & Lücking 2024; Rodriguez-Flakus et al. 2025; and the present study). Further Bolivian lineages assigned to the genus *Caloplaca* s.lat. appear to represent distinct, undescribed genera; their formal delimitation and taxonomic placement require further study (Table 2 in Wilk et al. 2021). Twenty-four crustose species of *Teloschistaceae* have been reported from Bolivia to date (see Table 1 and literature cited

therein). *Wetmoreana texana* was previously reported from Bolivia by Wilk & Flakus (2017), but subsequent studies demonstrated that the Bolivian material represents recently described *W. variegata* Wilk & Lücking (Wilk & Lücking 2024). *Wetmoreana variegata*, *W. ochraceo-fulva* (Müll. Arg.) Wilk & Lücking, and *W. brouardii* (B. de Lesd.) Wilk & Söchting (the latter not yet recorded from Bolivia) are morphologically similar species that are often difficult to distinguish. Their taxonomy and nomenclature were comprehensively revised by Wilk & Lücking (2024), whereas, a detailed account of the diagnostic characters separating *W. ochraceo-fulva* and *W. brouardii* was presented by Wilk (2021).

In recent years, interest in the diversity and taxonomy of *Teloschistaceae* in South America has increased considerably. In addition to Bolivia (see above), the family has been comprehensively revised in the Galápagos Islands (Bungartz et al. 2020), while species occurring in the southern part of the continent, particularly Patagonia, have been the subject of a series of studies by Söchting, Arup and co-authors (Söchting & Arup 2021; Söchting et al. 2021, 2023). In addition, important contributions to the knowledge of South American *Teloschistaceae* have been provided by Aptroot and collaborators, mainly in studies focusing on the lichen biota of Brazil (Aptroot 2015; Aptroot & Cáceres 2016; Aptroot et al. 2017, 2021, 2022, 2023). Schumm and Aptroot (2019a–c) also published

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Table 1. Revised list of crustose *Teloschistaceae* species reported from Bolivia to date.

Current name	Name reported from Bolivia	Source	Substrat	Status
<i>Aridoplaca peltata</i> Wilk & Lücking	–	Wilk et al. 2021	on siliceous rocks	accepted
<i>Athallia holocarpa</i> (Hoffm.) Arup, Frödén & Söchting	<i>Caloplaca holocarpa</i> (Hoffm. ex Ach.) Wade	Feuerer et al. 1998	on bones	requires molecular confirmation
<i>Athallia pyracea</i> (Ach.) Arup, Frödén & Söchting	<i>Lecanora pyracea</i> (Ach.) Nyl.	Nylander 1861	on tree bark	requires molecular confirmation
<i>Austroplaca darbshirei</i> (C.W. Dodge & G.E. Baker) Söchting, Frödén & Arup	<i>Caloplaca darbshirei</i> (C.W. Dodge & G.E. Baker) Cretz.	Wilk & Flakus 2017	on siliceous rocks	accepted
‘ <i>Caloplaca</i> ’ <i>baueri</i> (Müll. Arg.) Zahlbr.	–	Wilk & Flakus 2017	on siliceous rocks	accepted
‘ <i>Caloplaca</i> ’ <i>brebissonii</i> (Fée) J. Sant. ex Hafellner & Poelt	<i>Lecanora brebissonii</i> (Fée) Nyl.	Nylander 1861; Hafellner & Poelt 1979; Feuerer et al. 1998; Wilk et al. 2021	on tree bark and wood	accepted
‘ <i>Caloplaca</i> ’ <i>chrysochroa</i> (Mont.) Zahlbr.	<i>Placodium chrysochroum</i> (Mont.) Nyl.	Nylander 1859	on humus-rich soil	taxonomic status uncertain (historical collection)
‘ <i>Caloplaca</i> ’ <i>cinnabarina</i> (Ach.) Zahlbr.	–	Wilk & Flakus 2017	on siliceous rocks	accepted
‘ <i>Caloplaca</i> ’ <i>crocea</i> (Kremp.) Hafellner & Poelt	<i>Callopisma xanthaspis</i> (Kremp.) Müll. Arg.	Malme 1926; Hafellner & Poelt 1979	on tree bark	accepted
‘ <i>Caloplaca</i> ’ <i>quadriculularis</i> (Nyl.) Zahlbr.	<i>Lecidea quadriculularis</i> Nyl.	Nylander 1859; Hafellner & Poelt 1979; Wilk et al. 2021	on tree bark	accepted
<i>Caloplaca stillicidiorum</i> (Vahl) Lynge s.lat.	<i>Caloplaca cerina</i> (Ehrh. ex Hedwig) var. <i>chloroleuca</i> (Sm.) Th. Fr.	Feuerer et al. 1998	no data available	specimen not seen
<i>Cinnabaria boliviana</i> Wilk & Lücking	–	Wilk et al. 2021	on strongly calcareous rocks	accepted
<i>Huneckia crocina</i> (Kremp.) Wilk	<i>Caloplaca crocina</i> (Kremp.) K. Wilk & R. Vargas	Wilk & Flakus 2017; Wilk 2021	on tree bark, rarely on wood	accepted
<i>Lacrima erythrantha</i> (Tuck.) Kukwa & Wilk	<i>Caloplaca erythrantha</i> (Truck.) Zahlbr.	Guzow-Krzemińska et al. 2019; Kosecka et al. 2022; this paper	on tree bark	accepted
<i>Leproplaca cirrochroa</i> (Ach.) Arup, Frödén & Söchting	<i>Placodium cirrochroum</i> (Ach.) Rabenh.	Nylander 1861	on rocks	specimen not seen, require confirmation (historical collection)
<i>Scutaria andina</i> (Räsänen) Söchting, Frödén & Arup	<i>Xanthoria andina</i> Räsänen	Gaya et al. 2012; Wilk et al. 2021	on tree bark	accepted
<i>Squamulea squamosa</i> (B. de Lesd.) Arup, Söchting & Frödén	<i>Caloplaca squamosa</i> (B. de Lesd.) Zahlbr.	Wilk & Flakus 2017	on siliceous rocks	accepted
<i>Squamulea subsoluta</i> (Nyl.) Arup, Söchting & Frödén s.lat.	<i>Caloplaca subsoluta</i> (Nyl.) Zahlbr. s.lat.	Wilk & Flakus 2017	on siliceous, rarely calcareous rocks	accepted
<i>Tayloriellina malmeana</i> Wilk	–	Wilk 2023	on tree bark	accepted
<i>Wetmoreana ochraceofulva</i> (Müll. Arg.) Wilk & Lücking	–	Wilk & Lücking 2024	on siliceous or calcareous rocks	accepted
<i>Wetmoreana rubra</i> Wilk & Lücking	–	Wilk & Lücking 2024	on strongly calcareous rocks	accepted
<i>Wetmoreana sliwae</i> Wilk & Lücking	–	Wilk & Lücking 2024	on siliceous rocks	accepted
<i>Wetmoreana variegata</i> Wilk & Lücking	all Bolivian specimens previously reported as <i>Caloplaca ochraceofulva</i> (Müll. Arg.) Jatta and <i>Caloplaca texana</i> Wetmore & Kärnefelt by Wilk & Flakus (2017) belong to <i>W. variegata</i> .	Wilk & Lücking 2024	on siliceous, rarely calcareous rocks	accepted
<i>Wilketalia citrinoides</i> (Wilk & Lücking) S.Y. Kondr.	<i>Andina citrinoides</i> Wilk & Lücking	Wilk et al. 2021	on siliceous rocks	accepted

a worldwide photographic catalogue of species belonging to *Caloplaca* s.lat.

The revised classification of the *Teloschistaceae* proposed by Arup et al. (2013) resulted in a narrower circumscription of *Caloplaca* s.str., to which the newly described species, *Caloplaca aptrootii*, belongs. According to Arup

et al. (2013), the genus comprises twelve accepted species, with *C. cerina* (Hedw.) Th. Fr. serving as the type species. The group was investigated in detail by Šoun et al. (2011), whose study revealed the presence of numerous cryptic lineages requiring further taxonomic evaluation. Members of *Caloplaca* s.str. are characterized by thalli

lacking anthraquinones, usually white to grey or blackish in color, lecanorine apothecia with orange discs, common occurrence of vegetative diaspores (soredia, blastidia and isidia), and the presence of the Sedifolia-grey pigment in the cortex and vegetative diaspores, except of soredia in *C. sterilis* Šoun, Khodos. & Vondrák, and presence of conspicuous paraplectenchymatous cortex, especially in the lower part of the apothecial margin (Šoun et al. 2011; Arup et al. 2013). The genus is distributed predominantly in the Northern Hemisphere, confirmed mostly from Europe, some from North America and Asia, and one from Australia (Šoun et al. 2011). Two species of *Caloplaca* s.str. have been reported from South America, *C. cerina* and *C. chlorina* (Osorio 1972; Aptroot et al. 2022), however, these records have not been confirmed using molecular data. None of the remaining species currently assigned to *Caloplaca* s.str. have been reported from the continent. Therefore, *C. aptrootii* represents the first molecularly confirmed record of a member of *Caloplaca* s.str. from South America.

Materials and methods

Taxon sampling and morphological studies

Our results are based mainly on fresh material collected from Bolivia and deposited at KRAM and LPB. Morphological and anatomical characters were examined using standard stereo- and compound microscopes (Nikon SMZ 800, Nikon Eclipse 80i DIC, Japan) following the methods outlined by Vondrák et al. (2013). Sections were prepared manually using a razor blade, or a Thermo Fisher Scientific Microm HM430 (USA) freezing microtome combined with a BFS-MP freezing stage and a BFS-3MP controller. Sections and squash mounts were examined in distilled water, 10% KOH (K) or Lactophenol Cotton Blue (LPCB; Fluka, no. 61335-100ML). All photomicrographs showing anatomical characters were made using transmitted differential interference contrast (DIC) microscopy. Amyloid reactions of anatomical structures were tested using Lugol's solution (I) (Fluka, no. 62650-1L-F), or with Lugol's solution preceded by a 10% KOH treatment (K/I). All measurements were made in distilled water. Ascospores measurements are presented as: arithmetic mean – standard deviation, *arithmetic mean*, and arithmetic mean + standard deviation, flanked by the minimal and maximal measurements in parentheses, the length/breadth ratio (l/b) and septum width/spore length ratio are presented in the same way, followed by the number of measurements (n). Hydrochloric acid was used to test for the presence of calcium carbonate (CaCO₃) in rock substrata.

DNA extraction, PCR amplification, and DNA sequencing

Fresh ascomata of lichen were removed from the host thallus and carefully cleaned in double-distilled water on a microscope slide under sterile conditions to remove any visible impurities, using ultra-thin tweezers and a razor blade. DNA was extracted from 5 clean ascomata, using

QIAamp DNA Investigator Kit (Qiagen, Germany), following the manufacturer's instructions. Primers used for PCR and sequencing were ITS1F+LR3 and mrSSU1+mrSSU3R, whereas, the amplification parameters and additional detailed information on PCR, visualization of amplicons and preparation of samples can be found in Rodríguez-Flakus & Printzen (2014) and Flakus et al. (2019). PCR amplicons were sequenced by Macrogen (Amsterdam, the Netherlands). The newly generated sequences were carefully checked, assembled and edited manually using Geneious Pro 8.0. (Biomatters Ltd) and deposited in GenBank. Information about all OTUs used in this study, including sequences downloaded from GenBank and newly obtained accession numbers, are provided in Table S1.

Phylogenetic analyses

All sequences generated were subjected to BLAST (Altschul et al. 1990) to verify potential fungal contamination and to reveal their general phylogenetic placement. The alignment comprising ITS sequences from representatives of all major lineages within the family *Teloschistaceae* sourced from Wilk et al. (2021) was initially used to determine the phylogenetic placement of the newly collected specimen (unpublished). Subsequently, a multilocus dataset based on three loci (ITS, nuLSU and mtSSU) was assembled for the subfamily *Caloplacoideae*, together with selected representatives of the remaining subfamilies *Teloschistoideae* and *Xanthorioideae*. Taxon sampling within *Caloplacoideae* was designed to be as comprehensive as possible, and included representatives of all currently recognized genera. Finally, a separate ITS dataset was prepared to assess the phylogenetic relationships among taxa of *Caloplaca* s.str. For this purpose, the taxonomic framework of Šoun et al. (2011) was followed, as this study comprehensively resolved the *C. cerina* group, including lineages potentially representing distinct genera. Alignments were generated for each locus using MAFFT v. 7 (Katoh et al. 2019), and then adjusted manually in AliView 1.17.1 (Larsson 2014). Taxon coverage differed among the three loci included in the multilocus dataset, comprising 102 terminals for ITS, 82 for nuLSU, and 88 for mtSSU, with a total of 102 terminals represented in the combined analysis. Ambiguously aligned regions were manually excluded in AliView, resulting in final alignments of 637 bp for ITS, 831 bp for nuLSU, and 862 bp for mtSSU. The final concatenated dataset, including all three loci, comprised 2,330 bp across 102 taxa. The ITS dataset of *Caloplaca* s.str. comprised 142 terminals and 944 bp. Phylogenetic analyses were conducted using the Maximum Likelihood (ML) method implemented in RAxML via the CIPRES Science Gateway (Miller et al. 2010). The GTRGAMMA substitution model was applied. For the multilocus dataset, the three regions corresponding to ITS, nuLSU, and mtSSU were treated as separate partitions, with model parameters estimated independently for each partition. Statistical support for nodes was assessed using 1,000 rapid bootstrap replicates. The resulting ML phylogenetic trees were visualized with Figtree v. 1.4.4 (Rambaut 2018) and Inkscape v. 1.4.3.

Results and discussion

Phylogenetic relationships

Phylogenetic analyses at the family level placed the newly collected specimen within the monophyletic and strongly supported clade *Caloplaca* s.str., as a clearly distinct evolutionary lineage (Fig. S1). The phylogenetic relationship of the newly collected taxon to other members of *Caloplaca* s.str. was not established. This species occupies an unsupported sister position to the Australian *C. hanneshtertelii* S.Y. Kondr. & Kärnefelt in (Fig. 1).

The phylogenetic position of *Caloplaca* s.str. is well resolved and the genus in question is closely related to *Leproplaca*, *Seiropora*, and *Variospora*, which is consistent with previous results (e.g., Arup et al. 2013). The phylogenetic relationships of the studied clade with other members of the subfamily *Caloplacoideae* are largely unclear. In recent years, many new genera have been described within the family *Teloschistaceae*, as well as in the subfamily *Caloplacoideae* (e.g., Bungartz et al. 2020; Frolov et al. 2023; Søchting & Arup 2024). Adopting a possibly comprehensive approach, the phylogeny of the given subfamily includes 31 known genera and 5 additional genera awaiting description (Fig. S1). The occurrence of five undescribed genera from South America demonstrates how insufficiently studied this biota is on this continent. The occurrence of the subfamily *Caloplacoideae* was recently reported for the first time

in South America by Aptroot and Cáceres (2016). To date, there has been no molecularly confirmed record of a representative of the genus *Caloplaca* s.str. from this continent. Therefore, this is the first such record. As of 2020, two species, *C. saviczii* I.V. Frolov, Himelbr., Stepanch., Konoreva & S. Chesnokov and *C. fluviatilis* Vondrák & I.V. Frolov, from the genus *Caloplaca* s.str. have been described (Vondrák et al. 2019; Frolov et al. 2021), but many more taxa await clarification of their taxonomic status, such as the *C. cerina* complex and the *C. stillicidiorum* complex (Šoun et al. 2011). Later authors divided these complexes into several clades (*C. cerina*: A–D clades; *C. stillicidiorum* (Vahl) Lynge: 1–6 clades) and discussed them in detail. The sequences of the discussed taxa were used in our analyses, and one clade, *C. stillicidiorum* ‘2’, was placed in a position separate from the rest of *C. stillicidiorum*, except for the Russian specimen (GenBank no. EU681283) (Fig. 1, Table S1).

Of the twelve accepted species included in the genus-level phylogeny (Fig. 1), four are exclusively saxicolous taxa, like the newly collected species, occurring on siliceous or calcareous rocks (these are *C. thracopontica* Vondrák & Šoun, *C. chlorina* (Flot.) Sandst., *C. subalpina* Vondrák, Šoun & Palice, and *C. isidiigera* Vězda), whereas the remaining species usually occur on bark, wood, plant debris, or mosses (Vondrák et al. 2008; Šoun et al. 2011). Most species occur in Europe, about half of them are also found in North America (with two species,

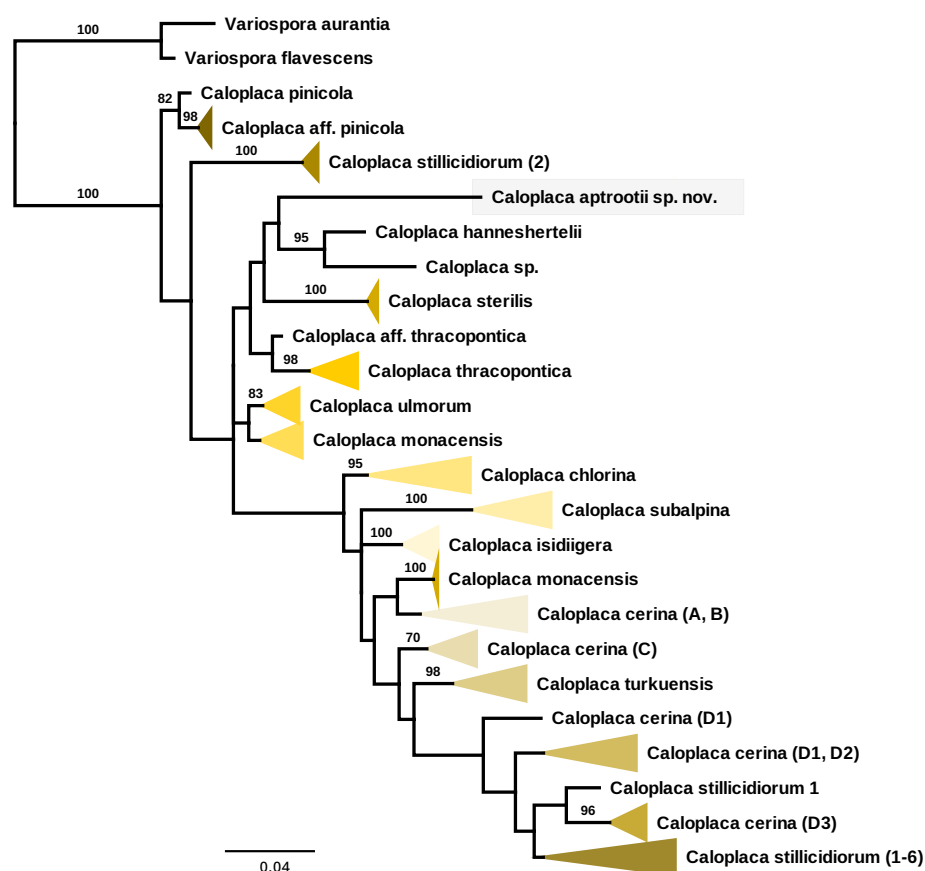


Figure 1. Phylogenetic relationships of *Caloplaca aptrootii* within *Caloplaca* s.str., inferred from maximum likelihood (ML) analyses of the nrITS dataset comprising 142 sequences. Clade designations of the *C. cerina* group (A–D) and the *C. stillicidiorum* group (1–6), as well as the selection of *Variospora aurantia* and *V. flavescentia* as outgroups, follow Šoun et al. (2011). Nodes with bootstrap support values $\geq 70\%$ were considered significantly supported. Scale bars indicate the number of nucleotide substitutions per site.

C. pinicola H. Magn. and *C. ulmorum* (Fink) Fink, known exclusively from this continent), while some occur in Asia or polar regions. One species, *C. hanneshtertelii*, is known only from Australia (Kärnefelt & Kondratyuk 2004; Vondrák et al. 2008; Šoun et al. 2011).

Taxonomy

Caloplaca aptrootii Wilk & Flakus, sp. nov. (Fig. 2)

MycoBank MB 864504

Diagnosis: Differs from *C. chlorina* in having a distinctly squamulose and thicker thallus, a thicker thalline cortex, a distinct epinecral layer, often $\pm$ concave apothecia, non-blastidiolate apothecial margins, and longer ascospores.

Type: Bolivia, Dept. La Paz, Prov. Camacho, near road Wila Kala – Huarina, 15°24'36"S, 69°04'28"W, 4,277 m, open high Andean vegetation with sandstone rocks, on siliceous sandstone, 5 Jun. 2017, A. Flakus 29598 (KRAM L-75315 – holotype, LPB – isotype).

Etymology. Named in honor of André Aptroot on the occasion of his 65th birthday.

Description. Thallus squamulose, irregular in outline, $\pm$ loosely attached to the substrate, pale to dark brown, mainly epruinose, up to about 10 cm wide, 0.5–2 mm thick; squamules stipitate, surface coarsely and irregularly bullate, single convex areoles present at the thallus periphery; photobiont chlorococcoid, cells 6–14 μ m diam. Blastidia present, on the surface and margins of squamules, soon covering large parts of the thallus, blackish/bluish, 25–35(–50) μ m diam., containing 1–4(–8) photobiont cells, with a high content of Sedifolia-grey pigment (strongly K⁺ violet, C⁺ violet). Prothallus sometimes visible, distinct, dark grey, thin, of radiating hyphae. Upper cortex 20–80 μ m thick, hyaline, slightly greyish in the upper part, with a low content of Sedifolia-grey pigment (slightly K⁺ violet, C⁺ violet), paraplectenchymatous, composed of thick-walled cells. Epinecral layer conspicuous, 5–20 μ m thick. Apothecia frequent, mostly scattered, rounded, sometimes curling inwards and undulate, sessile from the beginning, lecanorine, 0.4–1 mm diam. Disc $\pm$ concave, rarely plane, yellowish orange, K⁺ purple, epruinose, surface uncracked. Apothecial margin more or less prominent, rather thick, concolorous with thallus but usually blackish in the upper part and white pruinose especially in young apothecia, entire, without blastidia. Amphithecium (thalline exciple) well-developed, 65–110 μ m thick in the upper part, 120–180 μ m in the lower part, with distinct and thick cortex, 30–80 μ m thick, para- to prosoplectenchymatous, composed of thick-walled hyphae, hyaline, upper part dark greyish, especially near the epihymenium, containing Sedifolia-grey (K⁺ violet, C⁺ violet), algae abundant, algal layer continuous, composed of loosely arranged, thin-walled hyphae. Parathecium (proper exciple) strongly reduced, 5–15 μ m thick, prosoplectenchymatous, usually continuous with the lowermost part of the hypothecium, visible only in cross section and not discernible externally, upper part covered by Sedifolia-grey pigment rather than anthraquinones.

Epihymenium 5–20 μ m thick, interspersed with orange granules (K⁺ purple). Hymenium 80–120 μ m thick, hyaline. Hypothecium 30–80(–100) μ m thick, hyaline, prosoplectenchymatous in lower part. Paraphyses simple to somewhat branched, rarely anastomosed, $\sim$ 2 μ m broad, with apical cells widened to 4–6 μ m. Asci *Teloschistes*-type, 8-spored (sometimes 4–6 spores in mature asci), 52–75 $\times$ 10–20 μ m. Ascospores hyaline, polarilocular, broadly to narrowly ellipsoid, (10.0–)12.6–15.0–17.3(–20.0) $\times$ (4.5–)5.1–6.1–7.0(–8.0) μ m, ascospore septa (2.0–)2.8–3.8–4.7(–5.0) μ m wide, length/width ratio (1.4–)1.9–2.5–3.2(–4.0), septum width/spore length ratio (0.1–)0.19–0.25–0.31(–0.4) (n = 42). Pycnidia not seen.

Ecology and distribution. The species is known only from locus classicus where it grows on exposed siliceous sandstone boulders in the Bolivian Andes.

Notes. *Caloplaca aptrootii* is characterized by relatively thick, brown, squamulose, blastidiolate thallus, and evidently lecanorine apothecia with orange discs. The most similar species is *C. chlorina*, which differs from the newly described taxon in having an areolate, thinner thallus, up to 0.3(–0.5) mm thick, entirely lacking pruina, often with a bluish tinge, a thinner thalline cortex, up to 10(–30) μ m thick, and shorter ascospores, 10–15 μ m long (Šoun et al. 2011). *Caloplaca aptrootii* occupies an unsupported sister position to the Australian species *C. hanneshtertelii*. The latter species differs from *C. aptrootii* in having an areolate, grey, K[–] thallus with characteristic crater-like soralia, smaller apothecia, up to 0.5 mm in diameter, and a distinct ecology, as it occurs on tree bark (Kärnefelt & Kondratyuk 2004).

Saxicolous species are relatively rare within *Caloplaca* s.str. Besides *C. chlorina*, only *C. isidiigera*, *C. subalpina*, and *C. thracopontica* are known to exclusively inhabit rocky substrates (Vondrák et al. 2008; Šoun et al. 2011; Arup et al. 2013). *Caloplaca isidiigera* and *C. thracopontica* are readily distinguished from the new species by the presence of isidia and pustules or lobules, respectively, instead of blastidia. They further differ in their habitat and/or substrate preferences, occurring on calcareous and maritime rocks, respectively. *Caloplaca subalpina* differs in having an areolate thallus, up to 0.5 mm thick, smaller apothecia, up to 0.7 mm in diameter, and shorter ascospores, reaching 15 μ m in length (mean 11.5 μ m). Moreover, all of these species are clearly separated in the phylogenetic analyses (Fig. 1). To date, only *C. chlorina* has been reported from South America, although its occurrence has not yet been confirmed using molecular data (Aptroot et al. 2022). A previous report of *Caloplaca chlorina* from the Galápagos Islands was later shown to be based on a misidentification, with the material instead representing a species of *Oceanoplaca* (Bungartz et al. 2020).

Members of *Caloplaca* s.str. may be confused with a species-rich group of lichens characterized by grey to blackish thalli lacking anthraquinones and apothecia with yellow-orange to red discs. These taxa were formerly included in the *Caloplaca ferruginea* and *C. sideritis* groups of *Caloplaca* s.lat. (Magnusson 1944; Wetmore 1996), but are currently assigned to *Blastenia* (Arup et al.

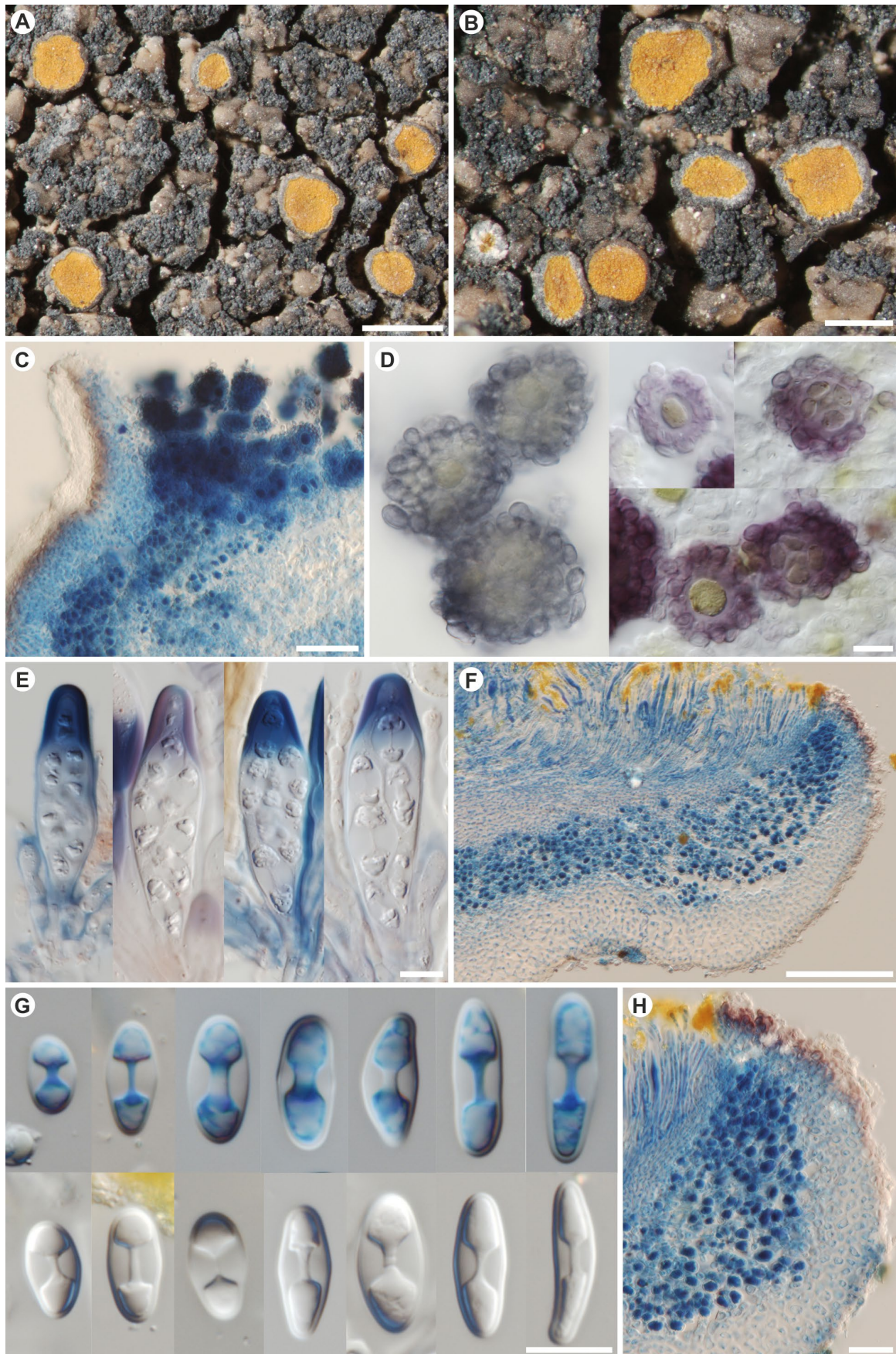


Figure 2. *Caloplaca aptrootii* (holotype). A, B – habit of greyish brown thallus with dark grey blastidia areas and ascomata, growing on sandstone; C – transversal section of thallus surface (visible epinecral and cortical layer) developing blastidia from algal layer (in LPCB); C – blastidia composed of algal cells tightly enclosed within an envelope of fungal hyphae, with Sedifolia-grey pigment (left in water, right in KOH); E – asci *Teloschistes*-like mounted in Lugol's solution pretreated by 10% KOH; F, H – transversal section of exciple in LPCB (H, showing Sedifolia-grey pigment in the outermost apical portion of the exciple); G – ascospores in LPCB (upper row) and water (lower row). Scales: A = 1 mm; B = 500 μ m; C = 50 μ m, D, E, G = 10 μ m; F = 100 μ m; H = 25 μ m.

2013; Vondrák et al. 2020). The most useful character distinguishing these lichen groups is the type of apothecia. *Blastenia* species possess biatorine or zeorine apothecia, whereas, *Caloplaca* s.str. is characterized by typically lecanorine apothecia. Additional distinguishing characters are discussed by Arup et al. (2013) and Vondrák et al. (2020).

Since crustose members of *Teloschistaceae* remain insufficiently studied in South America, additional representatives of *Caloplaca* s.str. are likely to occur on the continent. Therefore, our assessment was not restricted to species currently assigned to *Caloplaca* s.str., but also included other taxa that could potentially belong to this lineage. The newly collected material was compared with an extensive herbarium dataset, predominantly comprising South American specimens, including type material whenever available, as well as with published taxonomic treatments and original species descriptions from the South Hemisphere (e.g., Malme 1926; Magnusson 1950; Kondratyuk et al. 2012; Kantvilas 2016; Bungartz et al. 2020; and others). Based on the combined morphological, ecological, and molecular evidence, we conclude that the examined material represents a previously undescribed species, which is therefore described here as new to science.

Caloplaca aptrootii develops characteristic corticated vegetative propagules that may be accommodated within the broad concept of blastidia (e.g., Ryan et al. 2002). The term blastidium was originally introduced by Poelt (1980) for vegetative propagules produced by budding from the thallus, and was subsequently applied to structures morphologically intermediate between isidia and soredia (Tønsberg 1992; Giralt et al. 1995; Spribille et al. 2020). According to Vondrák et al. (2013), blastidia in *Teloschistaceae* members are rounded to irregular, 50–100 µm in diameter, rarely branched, ±constricted at the base, and not aggregated into soralia-like structures; they may possess a thin alveolate cortex. The propagules of *C. aptrootii* differ from the above-mentioned concepts in several respects. They are smaller, (25–)35–50 µm in diameter, and originate from the algal layer in a manner similar to soredia. Unlike typical soredia, they lack projecting hyphae and possess a compact, nearly paraplectenchymatous cortex composed of isodiametric cells. Initially consisting of a single photobiont cell, the propagules mature to contain 1–4(–8) algal cells surrounded by fungal hyphae. They occur in aggregated patches on the surface and margins of squamules, giving the thallus a sorediate/blastidiolate appearance.

The anatomy of these propagules more closely resembles the goniocysts described by Sérusiaux (1985), reported from, e.g., *Bacidina mirabilis* (Vězda) Vězda and *Opegrapha lambinonii* Sérus. Similar corticated propagules, interpreted as goniocysts, corticated soredia or granules have also been reported from several unrelated lichen genera, including *Hertelidea printzenii* Rodr. Flakus, *Micarea prasina* Fr., *Placynthiella dasaea* (Stirt.) Tønsberg, *P. uliginosa* (Schr.) Coppins & P. James, *Lendemeriella sorocarpa* (Vain.) S.Y. Kondr., species of *Lichenomphalia*, *Vezdaea aestivalis* (Ohlert)

Tscherm.-Woess & Poelt, or *Lepraria glaucosorediata* Flakus & Kukwa (Sérusiaux 1985 and references therein; Tønsberg 1992; Kukwa & Flakus 2009; Rodríguez-Flakus 2020). The considerable morphological overlap among these structures highlights the need for further ontogenetic, anatomical, and ultrastructural studies to clarify their nature and terminology.

New combination

Lacrima erythrantha (Tuck.) Kukwa & Wilk, comb. nov.

MycoBank MB 864505

Basionym: *Lecanora erythrantha* Tuck., Proc. Amer. Acad. Arts Sci. 5: 402. 1862.

Type: Cuba, C. Wright 1857 (FH-T – holotype; see Wetmore, The Bryologist 110: 802. 2007).

≡ *Caloplaca erythrantha* (Tuck.) Zahlbr., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 111: 409. 1902.

Notes. Phylogenetic analyses recovered the two Bolivian specimens of *Caloplaca erythrantha* and the GenBank sequence FJ349101 (labelled as *C. erythrantha*) as a strongly supported (BS = 98) monophyletic clade within the *Lacrima* lineage, sister to the *sonorae–galapagoensis* clade and clearly separated from the *epiphora–aphanotripta* clade (Fig. S1). *Lacrima erythrantha* is a highly variable taxon that may represent a species complex. Additional studies are needed to assess its morphological and genetic diversity and to delimit species boundaries (see also Wetmore 2007).

The sequenced specimen of *Lacrima erythrantha* was recently reported from Bolivia by Guzow-Krzemińska et al. (2019). Here, we formally establish its systematic position and provide additional Bolivian records of this probably widespread South American species.

Exsiccate seen. K. Kalb, *Lichenes Neotropici* 55 (B).

Specimens examined. BOLIVIA, Dept. Chuquisaca, Prov. Belisario Boeto, close to Padilla between Nuevo Mundo and Santa Rosa, 18°57'12"S, 64°16'37"W, 1,790 m, transition between Boliviano-Tucumano forests and dry interandean vegetation, on tree bark, 16 Jul. 2015, Kukwa 16254 (KRAM, LPB, UGDA). Dept. Cochabamba, Prov. Quillacollo, East Cordillera, area of Inkarraya-Sipesipe, 17°29'25"S, 66°22'09"W, 3,146 m, semidesert Inter-Andean Valleys, rocky and shrubby slope, sunny place, E exposition, 17 Dec. 2004, K. Wilk 3270, 3257, 3191, 3189, 3187 (KRAM, LPB). Dept. La Paz, Province Franz Tamayo, Madidi National Park, San Martín – Cumbre to the north-west of Azariamas, 14°09'26"S, 68°43'50"W, 1,296 m, mountain humid forest, 25 May 2006, K. Wilk 5605 (LPB). Dept. Santa Cruz, Prov. Cordillera, Parque Nacional y Área Natural de Manejo Integrado Kaa-Iya del Gran Chaco, Charata village near campamento de guardaparques, 18°28'05"S, 62°05'43"W, 307 m, Chaqueño forest, 2 Dec. 2010, A. Flakus 20144a (KRAM, LPB). Dept. Tarija, Prov. Aniceto Arce: close to la Mamora between Tarija and Bermejo, 22°09'51"S, 64°40'03"W, 1,320 m, disturbed Tucumano-Boliviano forest with Tillandsia, 27 Jul. 2015, A. Flakus 27310 & P. Rodríguez (KRAM, LPB), M. Kukwa 16782 (LPB, UGDA); Seranía de Propiedad Arnold, 22°13'19"S, 64°33'41"W, 1,309 m, Tucumano-Boliviano montane forest, 24 Nov. 2010, A. Flakus 18849 (KRAM, LPB); Filo de Sidras, near campamento de

quardaparques, 2 hours by car of Tarija, 22°14'50"S, 64°33'28"W, 1,064 m, Tucumano-Boliviano submontane forest, 22 Nov. 2010, A. Flakus 18540, 18570 (KRAM, LPB); Prov. Burnet O'Connor, close to Soledad, old road between Entre Ríos and Chuquisaca, 21°39'45"S, 64°07'22"W, 1,750 m, Boliviano-Tucumano forest with shrubs and *Alnus acuminata*, on *Alnus acuminata*, 31 Jul. 2015, M. Kukwa 16939a (LPB, UGDA).

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Supplementary electronic materials

Figure S1. Phylogenetic placement of *Caloplaca aptrootii* within the family *Teloschistaceae*, inferred from maximum likelihood (ML) analyses of the combined ITS, nuLSU and mtSSU dataset for 102 terminals. *Letroitia vulpina* and *Brigantiaea* sp. were used to root the tree. Nodes with bootstrap support values $\geq 70\%$ were considered significantly supported. Scale bars indicate the number of nucleotide substitutions per site. [Download file](#)

Table S1. Voucher data and GenBank accession numbers for the sequences included in this study. Newly generated sequences are shown in bold. Column B: species used to determine the phylogeny of the family (Fig. S1). Column C: species used to determine the phylogeny of the genus (Fig. 1). [Download file](#)

References

- Altschul, S. F., Gish, W., Miller, W., Myers, E. W. & Lipman, D. J. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215: 403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2)
- Aptroot, A. 2015. Holarctic and Caribbean crustose lichens collected by López Figueras in Venezuela. *Glalia* 7: 1–18.
- Aptroot, A. & Cáceres, M. E. S. 2016. Two new lecanoroid *Caloplaca* (*Teloschistaceae*) species from gneiss inselbergs in equatorial Brazil, with a key to tropical lecanoroid species of *Caloplaca* s.lat. *The Lichenologist* 48: 201–207. <https://doi.org/10.1017/S0024282916000049>
- Aptroot, A., Gumboski, E. L. & Cáceres, M. E. S. 2017. Ocean view: a first assessment of the littoral, crustose lichen biota of south Brazil. *The Lichenologist* 49: 597–605. <https://doi.org/10.1017/S0024282917000512>
- Aptroot, A., dos Santos, L. A. & Cáceres, M. E. S. 2021. Saxicolous Lichens in the Semi-Arid Caatinga in Brazil Show Substratum Shifts. *Cryptogamie, Mycologie* 42: 181–189. <https://doi.org/10.5252/cryptogamie-mycologie2021v42a11>
- Aptroot, A., de Souza, M. F., Cáceres, M. E. S., dos Santos, L. A. & Spielmann, A. A. 2022. New lichen records from Brazil. *Archive for Lichenology* 31: 1–51.
- Aptroot, A., dos Santos, L. A., Júnior, I. O. & Cáceres, M. E. S. 2023. The saxicolous and terricolous lichens of northeastern Brazil, with special reference to the Vale do Catimbau in Pernambuco. *Folia Cryptogamica Estonica* 60: 21–30. <https://doi.org/10.12697/fce.2023.60.04>
- Arup, U., Søchting, U. & Frödén, P. 2013. A new taxonomy of the family *Teloschistaceae*. *Nordic Journal of Botany* 31: 16–83. <https://doi.org/10.1111/j.1756-1051.2013.00062.x>
- Bungartz, F., Søchting, U. & Arup, U. 2020. *Teloschistaceae* (lichenized *Ascomycota*) from the Galapagos Islands: a phylogenetic revision based on morphological, anatomical, chemical, and molecular data. *Plant and Fungal Systematics* 65: 515–576. <https://doi.org/10.35535/pfsyst-2020-0030>
- Feuerer, T., Ahti, T. & Vitikainen, O. 1998. Lichenological investigations in Bolivia. In: Marcelli, M. P. & Seaward, M. R. D. (eds), *Lichenology in Latin America: History, current knowledge and applications*, pp. 71–86. CETESB, Sao Paulo.
- Flakus, A., Etayo, J., Miadlikowska, J., Lutzoni, F., Kukwa, M., Matura, N. & Rodriguez-Flakus, P. 2019. Biodiversity assessment of ascomycetes inhabiting *Lobariella* lichens in Andean cloud forests led to one new family, three new genera and 13 new species of lichenicolous fungi. *Plant and Fungal Systematics* 64(2): 283–344. <https://doi.org/10.2478/pfs-2019-0022>
- Fletcher, A. & Laundon, J. R. 2009. *Caloplaca*. In: Smith, C. W., Aptroot, A., Coppins, B. J., Fletcher, A., Gilbert, O. L., James, P. W. & Wolseley, P. A. (eds), *The Lichens of Great Britain and Ireland*. London: The British Lichen Society, Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, pp. 245–273.
- Frolov, I. V., Vondrák, J., Konoreva, L. A., Chesnokov, S. V., Himelbrant, D. E., Arup, U., Stepanchikova, I. S., Prokopiev, I. A., Yakovchenko, L. S. & Davydov, E. A. 2021. Three new species of crustose *Teloschistaceae* in Siberia and the Far East. *The Lichenologist* 53: 233–243. <https://doi.org/10.1017/S0024282921000177>
- Frolov, I. V., Prokopiev, I. A. & Konoreva, L. A. 2023. *Neoplaca mirabilis*, a new genus and a new epigeic species containing naphthopyrans from the family *Teloschistaceae*. *The Lichenologist* 55: 443–450. <https://doi.org/10.1017/S0024282923000567>
- Gaya, E., Högnabba, F., Holguin, Á., Molnar, K., Fernández-Brime, S., Stenroos, S., Arup, U., Søchting, U., van den Boom, P., Lücking, R., Sipman, H. J. M. & Lutzoni, F. 2012. Implementing a cumulative supermatrix approach for a comprehensive phylogenetic study of the *Teloschistales* (*Pezizomycotina*, *Ascomycota*). *Molecular Phylogenetics and Evolution* 63: 374–387. <https://doi.org/10.1016/j.ympev.2012.01.012>
- Giralt, M., Mayrhofer, H. & Sheards, J. W. 1995. The corticolous and lignicolous sorediate, blastidiate and isidiolate species of the genus *Rinodina* in southern Europe. *The Lichenologist* 27(1): 3–24. <https://doi.org/10.1006/lich.1995.0002>
- Guzow-Krzemińska, B., Flakus, A., Kosecka, M., Jabłońska, A., Rodriguez-Flakus, P. & Kukwa, M. 2019. New species and records of lichens from Bolivia. *Phytotaxa* 397(4): 257–279. <https://doi.org/10.11646/phytotaxa.397.4.1>
- Hafellner, J. & Poelt, J. 1979. Die Arten der Gattung *Caloplaca* mit pluriloculären Sporen (*Meroplacis*, *Triophthalmidium*, *Xanthocarpia*). *Journal of the Hattori Botanical Laboratory* 46: 1–41.
- Kantvilas, G. 2016. A synopsis and key for the lichen genus *Caloplaca* (*Teloschistaceae*) on Kangaroo Island, with the description of two new species. *Journal of the Adelaide Botanic Gardens* 29: 53–69.
- Katoh, K., Rozewicki, J. & Yamada, K. D. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Brief Bioinform* 20: 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Kärnefelt, I. & Kondratyuk, S. Y. 2004. Contribution to the lichen genus *Caloplaca* (*Teloschistaceae*) from Australia. *Bibliotheca Lichenologica* 88: 255–265.

- Kondratyuk, S. Y., Elix, J. A., Kärnefelt, I. & Thell, A. 2012. An artificial key to Australian *Caloplaca* species (Teloschistaceae, Ascomycota). *Bibliotheca Lichenologica* 108: 141–160.
- Kosecka, M., Kukwa, M., Jabłońska, A., Flakus, A., Rodriguez-Flakus, P., Ptach, L. & Guzew-Krzemińska, B. 2022. Phylogeny and ecology of *Trebouxia* photobionts from Bolivian lichens. *Frontiers in Microbiology* 13: 779784. <https://doi.org/10.3389/fmicb.2022.779784>
- Kukwa, M. & Flakus, A. 2009. *Lepraria glaucosorediata* sp. nov. (Stereocaulaceae, lichenized Ascomycota) and other interesting records of *Lepraria*. *Mycotaxon* 108: 353–364. <https://doi.org/10.5248/108.353>
- Larsson, A. 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 22: 3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Magnusson, A. H. 1944. Studies in the ferruginea-group of the genus *Caloplaca*. Göteborgs Kungl Vetenskaps- och Vitterhets-Samhälles Handlingar Sjätte Följden Ser B. 3(1): 1–71.
- Magnusson, A. H. 1950. Lichens from Uruguay. *Meddelanden från Göteborgs Botaniska Trädgård* 18: 213–237.
- Malme, G. O. A. 1926. Lichenes blasteniospori Herbarii Regnelliani. *Arkiv för Botanik* 20A: 1–51.
- Miller, M. A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Nylander, W. 1859. Lichenes in regionibus exoticis quibusdam vigenes exposit synoptici enumerationibus. *Annales des Sciences Naturelles, la botanique* 11: 205–264.
- Nylander, W. 1861. Additamentum ad lichenographiam Andium Bolivensium. *Annales des Sciences Naturelles, la botanique* 15: 365–382.
- Osorio, H. S. 1972. Contribution to the lichen flora of Uruguay. VII. A preliminary catalogue. *Comunicaciones Botánicas del Museo de Historia Natural de Montevideo* 4(56): 1–46.
- Poelt, J. 1980. *Physcia opuntiella* spec. nov. und die Lebensform der Sprossenden Flechten. *Flora* 169: 23–31. [https://doi.org/10.1016/S0367-2530\(17\)31162-3](https://doi.org/10.1016/S0367-2530(17)31162-3)
- Rambaut, A. 2018. Figtree v1.4.4. [accessed 30 Sept. 2022] <http://tree.bio.ed.ac.uk/software/figtree/>
- Rodriguez-Flakus, P. 2020. Non-saxicolous lecideoid lichens in southern South America. *Phytotaxa* 476(1): 1–73. <https://doi.org/10.11646/phytotaxa.476.1.1>
- Rodriguez-Flakus, P. & Printzen, C. 2014. *Palicella*, a new genus of lichenized fungi and its phylogenetic position within *Lecanoraceae*. *The Lichenologist* 46(4): 535–552. <https://doi.org/10.1017/S0024282914000127>
- Rodriguez-Flakus, P., Kukwa, M., Etayo, J., Lücking, R., Meneses, R. I., Rivas Plata, E., Stanton, D., Truong, C., Vargas, R. & Flakus, A. 2025. Preliminary catalogue of lichens and lichenicolous fungi from Bolivia. Version 1.6. <https://bio.botany.pl/lichens-bolivia>
- Ryan, B. D., Bungartz, F. & Nash, T. H. III. 2002. Morphology and anatomy of the lichen thallus. In: Nash, T. H. III, Ryan, B. G., Gries, C. & Bungartz, F. (eds), *Lichen flora of the Greater Sonoran Desert Region I*. Lichens Unlimited, Arizona State University, Arizona, pp. 8–23.
- Schumm, F. & Aptroot, A. 2019a. *Images of the lichen genus Caloplaca. Volume 1. Caloplaca adelphoparasitica – Caloplaca crenularia*. Books on Demand, Norderstedt.
- Schumm, F. & Aptroot, A. 2019b. *Images of the lichen genus Caloplaca. Volume 2. Caloplaca crenularia – Caloplaca holocarpa*. Books on Demand, Norderstedt.
- Schumm, F. & Aptroot, A. 2019c. *Images of the lichen genus Caloplaca. Volume 3. Caloplaca holocarpa – Caloplaca pulicarioides*. Books on Demand, Norderstedt.
- Sérusiaux, E. 1985. Goniocysts, goniocystangia and *Opegrapha lambinonii* and related species. *The Lichenologist* 17: 1–25. <https://doi.org/10.1017/S0024282985000032>
- Søchting, U. & Arup, U. 2021. *Austroplaca sibirica* (lichenized Ascomycota, Teloschistaceae) – a bipolar lichen with an austral origin documented by molecular data. *Graphis Scripta* 33: 12–16.
- Søchting, U. & Arup, U. 2024. Revision of *Marchantiana* (Calopla-coideae, Teloschistaceae) – a misconceived lichen genus. *Plant and Fungal Systematics* 69(2): 135–148. <https://doi.org/10.35535/pfsyst-2024-0013>
- Søchting, U., Søgaard, M. Z., Sancho, L. G. & Arup, U. 2021. The lichen genus *Villophora* (Teloschistaceae, Ascomycota). *The Lichenologist* 53: 245–255. <https://doi.org/10.1017/S0024282921000141>
- Søchting, U., Sancho, L. G. & Arup, U. 2023. The lichen genera *Gondwania* and *Transdrakea* gen. nov. (Teloschistaceae) – speciation in three southern continents. *Plant and Fungal Systematics* 68: 304–319. <https://doi.org/10.35535/pfsyst-2023-0015>
- Šoun, J., Vondrák, J., Søchting, U., Hrouzek, P., Khodosovtsev, A. & Arup, U. 2011. Taxonomy and phylogeny of the *Caloplaca cerina* group in Europe. *The Lichenologist* 43(2): 113–135. <https://doi.org/10.1017/S0024282910000721>
- Spribile, T., Fryday, A. M., Pérez-Ortega, S., Svensson, M., Tønsberg, T., Ekman, S., Holien, H., Resl, P., Schneider, K., Stabentheiner, E., Thüs, H., Vondrák, J. & Sharman, L. 2020. Lichens and associated fungi from Glacier Bay National Park, Alaska. *The Lichenologist* 52(2): 61–181. <https://doi.org/10.1017/S0024282920000079>
- Tønsberg, T. 1992. The sorediate and isidiate, corticolous, crustose lichens in Norway. *Sommerfeltia* 14: 1–331. <https://doi.org/10.2478/som-1992-0002>
- Vondrák, J., Šoun, J., Hrouzek, P., Říha, P., Kubásek, J., Palice, Z. & Søchting, U. 2008. *Caloplaca subalpina* and *C. thracopontica*, two new saxicolous species from the *Caloplaca cerina* group (Teloschistales). *The Lichenologist* 40(5): 375–386. <https://doi.org/10.1017/S0024282908007871>
- Vondrák, J., Frolov, I., Arup, U. & Khodosovtsev, A. 2013. Methods for phenotypic evaluation of crustose lichens with emphasis on Teloschistaceae. *Chornomorski Botanical Journal* 9: 382–405. <https://doi.org/10.14255/2308-9628/13.93/6>
- Vondrák, J., Frolov, I., Davydov, E. A., Yakovchenko, L., Maliček, J., Svoboda, S. & Kubásek, J. 2019. The lichen family Teloschistaceae in the Altai-Sayan region (Central Asia). *Phytotaxa* 396: 1–66. <https://doi.org/10.11646/phytotaxa.396.1.1>
- Vondrák, J., Frolov, I., Košnar, J., Arup, U., Veselská, T., Halıcı, G., Maliček, J. & Søchting, U. 2020. Substrate switches, phenotypic innovations and allopatric speciation formed taxonomic diversity within the lichen genus *Blastenia*. *Journal of Systematics and Evolution* 58(3): 295–330. <https://doi.org/10.1111/jse.12503>
- Wetmore, C. M. 1996. The *Caloplaca sideritis* group in North and Central America. *Bryologist* 99(3): 292. <http://dx.doi.org/10.2307/3244301>
- Wetmore, C. M. 2007. Notes on *Caloplaca cerina* (Teloschistaceae) in North and Central America. *The Bryologist* 110: 798–807. [https://doi.org/10.1639/0007-2745\(2007\)110\[798:NOCCTI\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2007)110[798:NOCCTI]2.0.CO;2)
- Wilk, K. 2021. *Calogaya miniata* comb. nov., *Huneckia crocina* comb. nov., and new neotropical records of *Wetmoreana brouardii*. *Mycotaxon* 136(2): 387–400. <https://doi.org/10.5248/136.387>
- Wilk, K. 2023. New species of *Tayloriellina* (lichenized Ascomycota, Teloschistaceae) from Bolivia. *Phytotaxa* 616(2): 183–188. <https://doi.org/10.11646/phytotaxa.616.2.8>
- Wilk, K. & Flakus, A. 2017. Eight *Caloplaca* species newly recorded from Bolivia, including *C. crocina* comb. nov. *Mycotaxon* 132: 125–140. <https://doi.org/10.5248/132.125>
- Wilk, K. & Lücking, R. 2024. Quantitative integrative taxonomy informs species delimitation in Teloschistaceae (lichenized Ascomycota): the genus *Wetmoreana* as a case study. *IMA Fungus* 15: 9. <https://doi.org/10.1186/s43008-024-00140-1>
- Wilk, K., Pabijan, M., Satuga, M., Gaya, E. & Lücking, R. 2021. Phylogenetic revision of South American Teloschistaceae (lichenized Ascomycota, Teloschistales) reveals three new genera and species. *Mycologia* 113: 278–299. <https://doi.org/10.1080/00275514.2020.1830672>