Plant and Fungal Systematics 68(2): 462–474, 2023
DOI: https://doi.org/10.35535/pfsyst-2023-0027

ISSN 2544-7459 (print)
ISSN 2657-5000 (online)

New species, new records, and a checklist of *Coenogonium* (*Ostropales*: *Coenogoniaceae*) from Brazil

Dayane de Oliveira Lima[1], Lidiane Alves dos Santos[1], Isaias Oliveira Junior[1], André Aptroot[2], Robert Lücking[3] & Marcela Eugenia da Silva Cáceres[4*]

Article info

Received: 23 Aug. 2023
Revision received: 15 Dec. 2023
Accepted: 15 Dec. 2023
Published: 29 Dec. 2023

Associate Editor

Christian Printzen

Abstract. The genus *Coenogonium*, the only genus in the family *Coenogoniaceae*, is mostly found in tropical and subtropical regions. Approximately 100 species of *Coenogonium* are known worldwide, and about 52 species have been previously recorded from Brazil. Here, we describe four species as new to science from the Atlantic Forest in the states of Bahia, Minas Gerais, and Sergipe, and present a few new state records. The new species are *C. carassense*, *C. itabaianense, C. pilosum,* and *C. subtomentosum*. An annotated checklist of the species of *Coenogonium* from Brazil is also included.

Key words: Atlantic Forest, Caraça, *Coenogonium*, Itabaiana, Monte Pascoal, new species

Introduction

Coenogonium was first described more than two centuries ago by Ehrenberg (1820), with *Coenogonium linkii* as the type and only species at the time, as a delicate filamentous lichen with yellowish, gyalectoid apothecia, first collected in the state of Santa Catarina in southern Brazil. Sixty years later, Trevisan (1880) established the genus *Dimerella* to accommodate two crustose lichens with gyalectoid, yellowish apothecia, *D. lutea* and *D. diluta*. Given that taxonomy was largely based on morphology at the time, almost no connection was made between the two genera until the second half of the 20th century, when both genera were included in the *Gyalectaceae* due to their apothecia morphology (Santesson 1952; Poelt 1969; Vězda 1969; Henssen & Jahns 1974). Earlier, Zahlbruckner (1907) had included *Dimerella* as a synonym of *Microphiale* (because he erroneously considered the latter to have priority) with other crustose lichens in the family *Gyalectaceae*, whereas he joined *Coenogonium* and the entirely unrelated *Racodium* in the filamentous family *Coenogoniaceae*. Watson (1929a) placed *Microphiale* (and consequently its synonym *Dimerella*) in the crustose *Lecaniaceae* (based on the 1-septate ascospores), but did not treat *Coenogonium* (Watson 1929a, b). Notably, long before Santesson (1952) and even before Zahlbruckner (1907), Müller (1881) did note a close relationship between *Coenogonium* and *Biatorinopsis* (another synonym of *Dimerella*), and much later Malme (1937) considered *C. moniliforme* intermediate between the two genera.

Despite agreeing on the strong similarities between the two genera, these authors continued to keep *Dimerella* and *Coenogonium* separate because of their filamentous versus crustose thalli. On the other hand, various authors already pointed out that, in addition to the same trentepohlioid photobiont, *Dimerella* and *Coenogonium* showed no difference in apothecial characters, including the gyalectoid appearance with yellowish to reddish colors, the paraplectenchymatous excipulum, the unbranched, apically thickened paraphyses, the thin-walled asci, the typically I+ sordid-blue to greenish then brownish reaction of the hymenium, and the small, mostly 1-septate ascospores (Santesson 1952; Poelt 1969; Vězda 1969; Henssen & Jahns 1974; Lücking 1999; Rivas Plata et al. 2006; Lumbsch et al. 2011). After realizing that the filamentous taxa did not form a coherent unit, Lücking (1999) and Lücking & Kalb (2000) proposed to synonymize them formally under the older name *Coenogonium*, a solution that was subsequently supported by molecular phylogenetic and phenotype-based cladistic analyses (Kauff & Lutzoni 2002; Rivas-Plata et al. 2006; Gagarina 2008) and has

[1] Programa de Pós-Graduação em Biologia de Fungos, CB, Universidade Federal de Pernambuco, Campus Universitário, 50670-901, Recife, PE, Brazil
[2] Laboratório de Botânica / Liquenologia, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Avenida Costa e Silva s/n, Bairro Universitário, CEP 79070-900, Campo Grande, Mato Grosso do Sul, Brazil
ORCID: 0000-0001-7949-2594
[3] Botanischer Garten und Botanisches Museum Berlin, Freie Universität Berlin, Königin-Luise-Straße 6–8, 14195 Berlin, Germany
ORCID: 0000-0002-3431-4636
[4] Departamento de Biociências, Universidade Federal de Sergipe, Av. Vereador Olimpio Grande, s/n, Bairro Centro, CEP 49500-000, Itabaiana, Sergipe, Brasil
ORCID: 0000-0002-5612-1309
* Corresponding author e-mail: mscaceres@academico.ufs.br

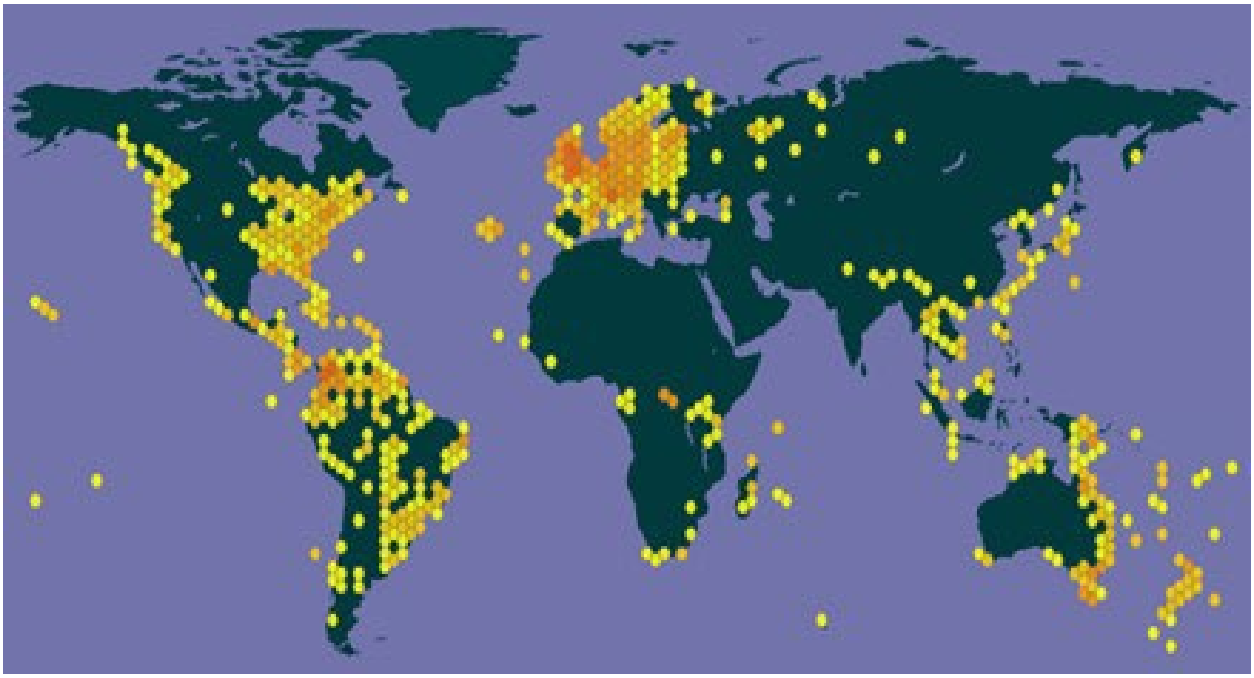

Figure 1. Records of *Coenogonium* from the GBIF portal https://www.gbif.org/species/2652125. Temperate records correspond mostly to *C. luteum* and *C. pineti* in the Northern Hemisphere, and to *C. implexum* in the Southern Hemisphere.

since been widely accepted, also because neither the filamentous nor the crustose taxa form monophyletic entities. Given that *Coenogonium* is not directly related to *Gyalecta*, the monogeneric family *Coenogoniaceae* has also been reinstated for this genus (Kauff & Lutzoni 2002).

Coenogonium is a subcosmopolitan genus (Fig. 1), although most species are found in tropical and subtropical regions (Lücking 1999; Rivas-Plata et al. 2006; Ferraro & Michlig 2013; Kantvilas et al. 2018). It can be found on various substrates, such as tree bark, rocks, leaves, and even soil; indeed, *C. coppinsii* was the first *Coenogonium* described from this substrate, specifically from termite mounds (Aptroot & Caceres 2014).

Approximately 100 species of *Coenogonium* are known worldwide (Gagarina 2015; Lücking et al. 2017), with 52 species so far recorded for Brazil (Aptroot & Caceres 2018a). Earlier work carried out by Xavier Filho et al. (1983), with the objective to study the genus *Coenogonium* in Brazil, reported only the three most common filamentous species, widespread in tropical and subtropical forests, namely *C. leprieurii*, *C. moniliforme*, and *C. curvulum*. One of the first modern works on foliicolous lichens in Northeast Brazil, published by Cáceres & Lücking (2000), described one new species of *Coenogonium*, *C. flavoviride*, from this region. Another new species, the aforementioned *C. coppinsii*, was found in a Brejo de Altitude, a high-altitude tropical forest emerging from semiarid Caatinga vegetation (Xavier-Leite et al. 2014). Santos et al. (2019) furthered the study of foliicolous lichens from this forest type and reported a total of ten species. Six new records of *Coenogonium* from the Brazilian Amazonas (near Manaus) were listed by Cáceres & Aptroot (2016), out of 157 species identified for that area (*C. barbatillum*, *C. chloroticum*, *C. interplexum*, *C. leprieurii*, *C. linkii*, and *C. strigosum*). More recently, Aptroot & Souza (2021b) reported new records for Paraná State in Southern Brazil, namely *C. barbatum*, *C. strigosum*, and *C. subdentatum*. All of this data highlight that the diversity of this genus in Brazil had been much underestimated in the past. Beyond Brazil, several studies have revealed the discovery of new species of *Coenogonium* worldwide (Mateus et al. 2011; Ferraro & Michlig 2013; Joshi et al. 2015; Kalb et al. 2016).

Here, we describe four new *Coenogonium* species from the Brazilian Atlantic Forest in the states of Bahia, Minas Gerais, and Sergipe, based on molecular data and phenotypical characters. An annotated checklist is also presented with the stately distributions of species in Brazil.

Material and methods

Sampling of specimens was carried out in three states: Minas Gerais, Sergipe, and Bahia. Other specimens collected by other researchers were added, as well as samples already deposited at the ISE Herbarium. These samples include species from the States of Pernambuco, Rio de Janeiro, Sergipe, Bahia, and Paraíba.

Specimens were observed with a Leica EZ4 dissecting microscope and an Olympus SZX7 dissecting microscope, and pictures were taken with a Nikon DM3200 camera. Hand-made sections of ascomata and thallus were studied in water, 5% KOH (K), and/or Lugol's reagent (1% I_2) after pre-treatment with KOH (IKI) to observe microscopic characters of ascospores and algal cells.

Approximately, 100 specimens were selected for molecular study, based on different localities, morphology, and good condition of the sample with the aim of sequencing the entire ITS region. From each sample, about ten apothecia were taken from the thallus and transferred to an Eppendorf tube for the extraction. Genomic DNA was extracted using the Wizard® Genomic DNA Purification

Kit (Promega), following the manufacturer's protocols. REDExtract-N-Amp Plant PCR Sigma-Aldrich (St. Louis, Missouri, EUA) was used for the amplification of the target. PCR reactions of 20 µL were prepared by adding 10 µL of PCR MIX, 4 µL of sterile water, 1 µL of each primer at 10 µM concentration, and 4 µL of DNA. PCR products were checked for amplification on 2% agarose gels. The kit Wizard® SV Gel and PCR Clean-Up (Promega) was used to purify the amplified PCR products, following the manufacturer's instructions. The products were then sequenced by the genetics laboratory at the Universidade Federal de Pernambuco.

The newly generated sequences were combined with selected sequences of the genus from GenBank (Table 1). Sequences were assembled and edited manually using BioEdit 7.2.0 (Hall 1999) and aligned using MAFFT 7 (Katoh et al. 2009; Katoh & Standley 2013; Supplementary Table S1) and subsequently inspected manually. Maximum likelihood analyses were performed using the program RAxML v8.1.11 (Stamatakis 2006), with

Table 1. Specimens of *Coenogonium* used for the molecular phylogenetic analysis in this study. New sequences are indicated in boldface.

Species	Voucher	ITS accession number
Coenogonium carassense	**Brazil, D.O. Lima s.n (ise 52148)**	**1329IF_52148ISE**
Coenogonium carassense	**Brazil, D.O. Lima s.n (ise 52336)**	**1340IF_52336ISE**
Coenogonium carassense	**Brazil, D.O. Lima s.n (ise 52154)**	**1367IF_52154ISE**
Coenogonium carassense	**Brazil, D.O. Lima s.n (ise 52335)**	**1339IF_52335ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52111)**	**1370IF_52111ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52160)**	**1357IF_52160ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52206)**	**1356IR_52206ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52105)**	**1369IF_52105ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (is 52156)**	**1359IF_52156IS**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52204)**	**1363IF_52204ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52109)**	**1368IF_52109ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52073)**	**1328IF_52073ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52283)**	**1325IR_52283ISE**
Coenogonium cf. ***acrocephalum***	**Brazil, D.O. Lima s.n (ise 52205)**	**1362IF_52205ISE**
Coenogonium disjunctum	**Brazil, D.O. Lima s.n (ise 52157)**	**1358IR_52157ISE**
Coenogonium disjunctum	**Brazil, D.O. Lima s.n (ise 52146)**	**1360IF_52146ISE**
Coenogonium disjunctum	**Brazil, D.O. Lima s.n (ise 52280)**	**1327IF_52280ISE**
Coenogonium isidiatum	Russia, Chesnokov LE-L 14438	MH179135
Coenogonium isidiatum	Russia, Konoreva LE-L 14437	MH179136
Coenogonium isidiatum	Russia, Konoreva LE-L 14436	MH179137
Coenogonium isidiatum	Russia, Konoreva LE-L 14441	MH179138
Coenogonium isidiatum	Russia, Konoreva LE-L 14440	MH179139
Coenogonium leprieurii	**Brazil, D.O. Lima s.n (ise 52201)**	**1364IR_52201ISE**
Coenogonium luteolum	Portugal, personal: J. Malicek:14105	OQ366541
Coenogonium luteum	Austria, PRA-Vondrak 26140	OQ366542
Coenogonium luteum	AFTOL-ID 352	HQ650710
Coenogonium luteum	Portugal, personal: J. Malicek:14095	OQ366548
Coenogonium luteum	**Brazil, D.O. Lima s.n (ise 52341)**	**1308IF_52341ISE**
Coenogonium luteum	**Brazil, D.O. Lima s.n (ise 52212)**	**1314IF_52212ISE**
Coenogonium nepalense	**Brazil, D.O. Lima s.n (ise 53728)**	**1300IF_53728ISE**
Coenogonium pineti	Czech Republic, PRA-Vondrak 23798	OQ366550
Coenogonium pineti	Canada, BIOUG24047-G12	KT695346
Coenogonium pineti	Czech Republic, PRA-Palice 32241	OQ366551
Coenogonium pineti	Czech Republic, PRA-Palice 32447	OQ366552_
Coenogonium sp.	United Kingdom: Great Britain, personal: J. Malicek:Powell 4685	OQ366543
Coenogonium sp.	United Kingdom: Great Britain, PRA-Vondrak 19912	OQ366544
Coenogonium sp.	United Kingdom: Great Britain, PRA-00021373	OQ366546
Coenogonium sp.	United Kingdom: Great Britain, PRA-Vondrak 19844	OQ366545
Coenogonium sp.	United Kingdom: Scotland, Great Britain, personal: J. Malicek:12373	OQ366547
Coenogonium strigosum	**Brazil, D.O. Lima s.n (r 77099)**	**77099R**
Coenogonium subtomentosum	**Brazil, D.O. Lima s.n (ise 52293)**	**1321IF_52293ISE**
Coenogonium subtomentosum	**Brazil, D.O. Lima s.n (ise 52001)**	**1345IF_52001ISE**
Coenogonium subtomentosum	**Brazil, D.O. Lima s.n (ise 52253)**	**1336IF_52253ISE**
Coenogonium subtomentosum	**Brazil, D.O. Lima s.n (ise 52017)**	**1344IR_52017ISE**
Coenogonium tavaresianum	United Kingdom: Great Britain, PRA-Vondrak 19776	OQ366549
Gyalecta flotowii	Norway, O-L-203030	MK811730
Gyalecta geoica	Norway, O-L-200544	MK811956
Gyalecta jenensis	Czech Republic, PRA-JV23907	OL396595

GTRGamma and 1,000 bootstrap replicates. BLAST searches (NCBI) (https://www.ncbi.nlm.nih.gov, accessed on 01 February 2023) were performed for the newly generated sequences and after confirmation of their identity, the sequences were edited and contigs were assembled using BioEdit 7.2.0 and deposited in GenBank (Table S1). For the phylogenetic analysis, we retrieved from GenBank ITS rDNA sequences classified as *Coenogonium*, and then the newly generated sequences were added to the set of ITS sequences downloaded from GenBank, and aligned using MAFFT, with subsequent manual inspection.

Results

Sequenced specimens

We obtained ITS sequence data from approximately 26 specimens of the 100 in which extractions were performed, more than doubling the number of accessions now available for this genus. While the backbone of the tree is largely unsupported, the topology confirms earlier findings that the crustose and filamentous species of the genus do not form reciprocally monophyletic groups. Thus, a crustose taxon from Brazil identified as *Coenogonium luteum* forms as supported clade (82%) with a newly described filamentous species, *C. carassense*. Another well-supported clade (92%) also contains crustose (*C. luteum*, *C. nepalense*) and filamentous taxa (*C.* cf. *acrocephalum*, *C. disjunctum*, and the newly described *C. subtomentosum*). Thus, the merging of the genera *Coenogonium* and *Dimerella* (the latter containing the crustose species), formally proposed by Lücking & Kalb (2000), is supported.

Notably, even with the much-refined species concept provided by Rivas Plata et al. (2006), certain morphodemes are still polyphyletic or display cryptic speciation and require further attention. Thus, crustose forms

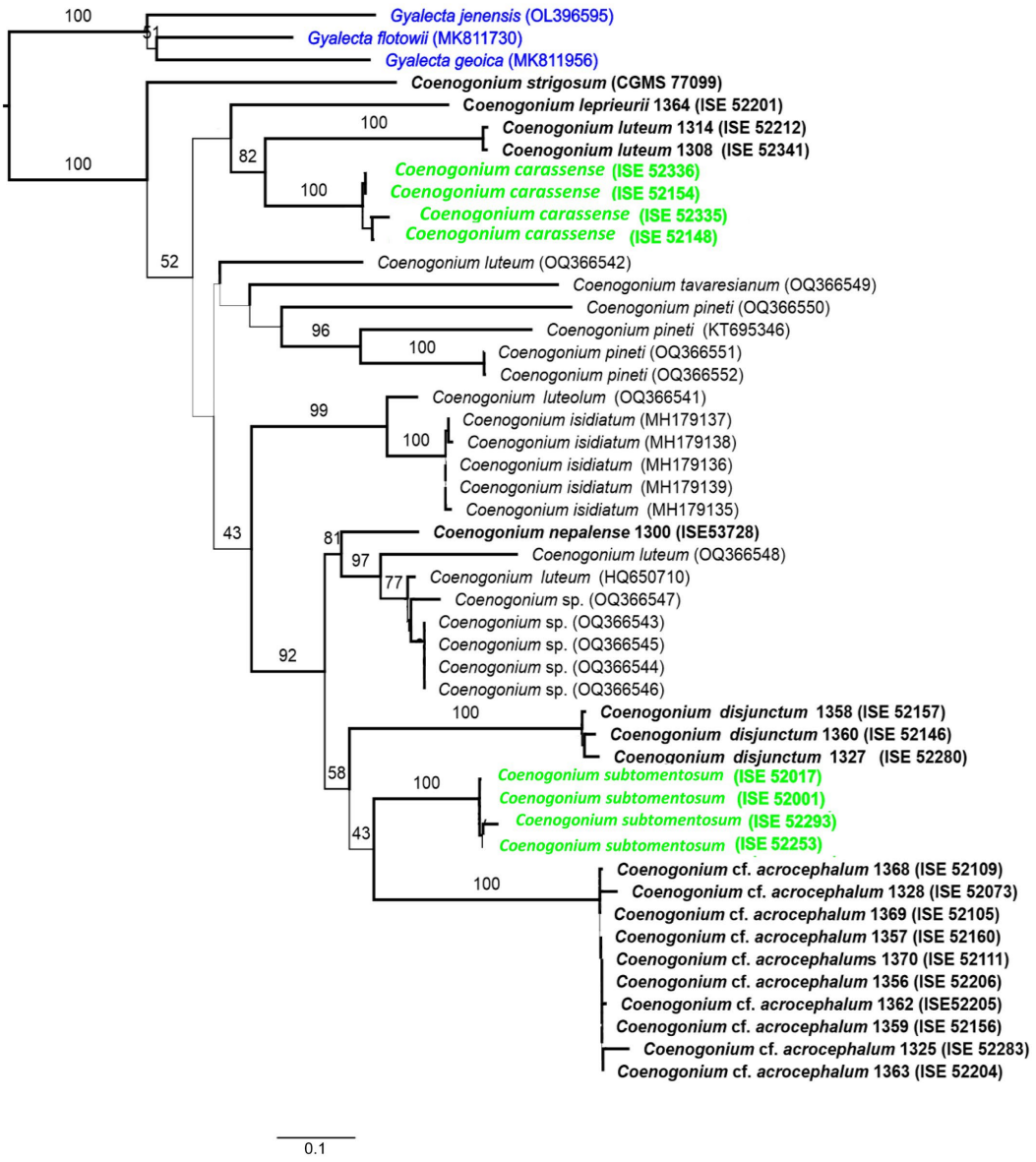

Figure 2. Best-scoring ML tree based on the analysis of ITS sequence data. Bootstrap support values are given above the branches. The new sequences generated in this study are indicated in bold and new species of *Coenogonium* are in green.

that agree with, or have been identified as, *C. luteum* appear in four clades in the tree and another crustose morphodeme, *C. pineti*, is split into three phylogenetically clearly distinct lineages (Fig. 2). *Coenogonium luteum* has been described from Great Britain, and so one of the two accessions from Austria (OQ366542) or Madeira (OQ366548) are more likely to represent that species, whereas those from the USA (HQ650710) and Brazil are possibly an undescribed taxon. *Coenogonium pineti* has been described from Central Europe; the three accessions from the Czech Republic (OQ366550, OQ366551, OQ366552) form two lineages, separated by one from Canada (KT695346) requiring further study.

Among these successfully sequenced specimens, two (*Coenogonium carassense* and *C. subtomentosum*) were considered new species according to the tree topology and morphological characters and are formally described below. Unfortunately, we did not obtain sequence data for the other two proposed new species, *C. itabaianense* and *C. pilosum*.

New species

Coenogonium carassense D.O. Lima, Aptroot, Lücking & M. Cáceres, sp. nov. (Fig. 3A–B)

MycoBank MB 851536

Diagnosis: Corticolous, filamentous *Coenogonium* similar to *C. leprieurii* and *C. linkii* in the flabelliform thallus; differing from *C. leprieurii* in the thallus spreading over the substrate, not vertically projecting, being composed of numerous smaller thalli, and the apothecia formed on the upper side, and from *C. linkii* additionally by the non-septate ascospores.

Type: Brazil, Minas Gerais: Catas Altas, Parque Natural Municipal, alt. 1200–1400 m, 20°06′S, 43°29′W, on tree in Atlantic rain forest, 17–25 May 2021, D.O. Lima & A. Aptroot 52148 (ISE – holotype; ABL – isotype).

Description. Thallus filamentous, flabelliform, forming flat, fan-shaped shelves of up to 3 cm diam., composed of individual, smaller thalli spreading over the substrate and intermingled with bryophytes, yellowish green, up to 10 mm long and broad; prothallus absent. Photobiont *Trentepohlia*, cells in distinct filaments, cylindrical, 40–60 × 10–12.5 µm. Apothecia on the upper surface, emerging between the individual thalli, sessile, rounded, 0.3–0.8 mm diam. and 100–150 µm high; disc flat to somewhat convex, pale yellow to yellow-orange; margin thin, not prominent, smooth, creme-colored. Excipulum paraplectenchymatous, with radiating cell rows, 30–60 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3–7 µm diam. Hypothecium 15–20 µm high, colorless. Hymenium 65–70 µm high, colorless, I+ blue then quickly sordid green then reddish brown. Asci 55–75 × 5–7 µm. Ascospores uniseriate, ellipsoid, non-septate, 5–7.5 × 2–2.5 µm, 2.5–3 times as long as broad. Pycnidia not observed.

Etymology. The epithet refers to the type locality.

Ecology and distribution. On tree bark in primary Atlantic rain forest; so far only known from the type locality.

Discussion. This species agrees with *C. leprieurii* and *C. linkii*, as well as some other species, in the flabelliform thallus and the uniseriate arrangement of the ascospores. However, whereas *C. leprieurii* and *C. linkii* form individual large thalli projecting from the substrate, in the new species the thallus is composed of numerous smaller thalli spreading over the substrate. In addition, the apothecia emerge on the upper side between the individual thalli, whereas in *C. leprieurii* and *C. linkii* they are formed on the underside. The ascospores of *C. carassense* are identical to those of *C. linkii*, whereas *C. leprieurii* also deviates by its non-septate ascospores (Rivas-Plata et al. 2006).

Among the hitherto sequenced species, the closest relative of the new taxon is a crustose species tentatively identified as *C. luteum* (Fig. 2). Unsupported sister to this clade is the only sequenced specimen of *C. leprieurii*, further supporting *C. carassense* as an undescribed species. Although common and widespread, no sequence data are yet available for *C. linkii*.

Additional material. BRAZIL. Minas Gerais: Same as the type, 52154; 52335; 52336 (ISE, ABL).

Coenogonium itabaianense D.O. Lima, Aptroot, Lücking & M. Cáceres, sp. nov. (Fig. 3C–D)

MycoBank MB 851537

Diagnosis: Corticolous filamentous *Coenogonium* similar to *C. interpositum* in the cushion-forming thallus, differing chiefly by the densely arranged filaments, giving the thallus an almost felty appearance, and by the comparatively broader, uniseriately arranged ascospores within the ascus (biseriate in *C. interpositum*).

Type: Brazil, Sergipe: Areia Branca, Parque Nacional de Itabaiana, alt. 100 m, 10°50′16″S, 37°25′14″W, on tree in Atlantic rain forest, 29 Oct. 2021, D.O. Lima 55063 (ISE – holotype; ABL – isotype).

Description. Thallus filamentous, prostrate, forming rather thick cushions with densely arranged, much branched filaments, giving the thallus an almost felty appearance, green to olive-green, up to 20 mm across; prothallus absent. Photobiont *Trentepohlia*, cells in distinct filaments, cylindrical, about 60 × 9–11 µm. Apothecia formed on the upper surface, 0.3–0.6 mm diam. and 100–150 µm high; disc pale yellowish, flat to slightly convex; margin thin, paler to cream-colored. Excipulum paraplectenchymatous, with radiating cell rows, 85–105 µm broad, colorless, I+ sordid yellow green; cells isodiametric and thin-walled, 3–7 µm diam. Hypothecium 12–15 µm high, colorless. Hymenium 60–70 µm high, colorless, I+ blue then quickly sordid green then reddish brown. Asci 15 × 9–10 µm. Ascospores uniseriate, ellipsoid, non-septate, 7.5 × 3.0–3.5 µm, 2–2.5 times as long as broad. Pycnidia not observed.

Etymology. The epithet refers to the type locality.

Ecology and distribution. On tree bark in primary Atlantic rain forest; so far only known from the type locality.

Discussion. This species is similar to *Coenogonium interpositum* in forming cushion-shaped, prostrate thalli over the substrate. However, its filaments are much more

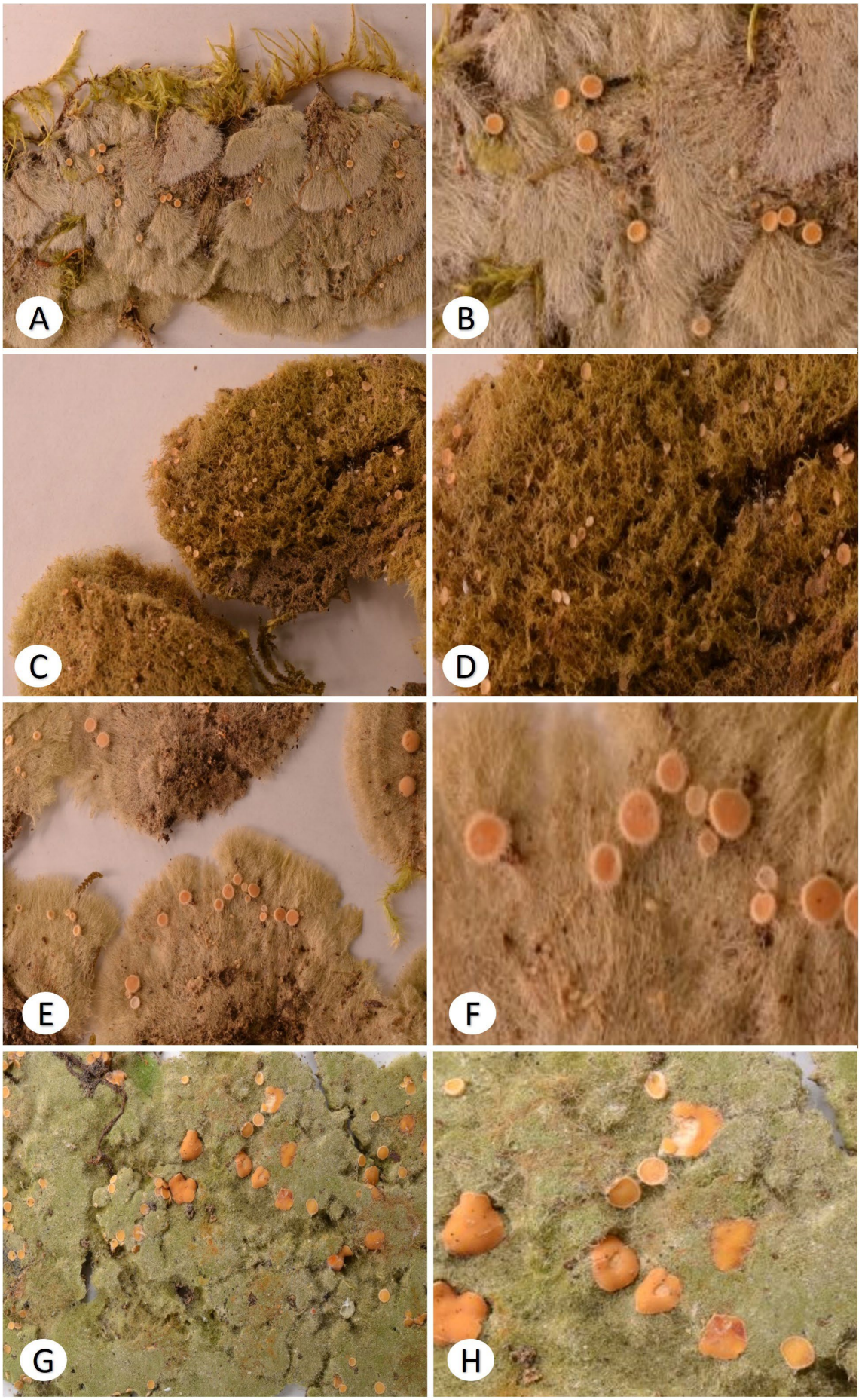

Figure 3. A–B – *Coenogonium carassense*, thallus with apothecia; C–D – *Coenogonium itabaianense*, thallus with apothecia; E–F – *Coenogonium pilosum*, thallus with apothecia; G–H – *Coenogonium subtomentosum*, thallus with apothecia.

densely arranged, giving the thallus a felty appearance, whereas in *C. interpositum* they are loosely interwoven. Both species also agree in the non-septate ascospores, but in *C. itabaianense* they are comparatively broader and uniseriately arranged (Rivas-Plata et al. 2006).

Additional material. BRAZIL. Sergipe: Same as the type, 55060; 55061; 55062; 55064 (ISE, ABL).

Coenogonium pilosum D.O. Lima, Aptroot, Lücking & M. Cáceres, sp. nov. (Fig. 3E–F)

MycoBank MB 851538

Diagnosis: Corticolous, filamentous, flabelliform *Coenogonium* differing from the otherwise similar *C. congense* and *C. linkii* in the apothecia having a finely pilose margin.

Type: Brazil, Bahia: Porto Seguro, Parque Nacional do Monte Pascoal, alt. 500 m, 16°51′51″S, 39°16′15″W, on tree in Atlantic rain forest, 19 May 2022, I. Oliveira Junior 55065 (ISE – holotype; ABL – isotype).

Description. Thallus filamentous, flabelliform, projecting horizontally from the substrate, composed of tufts of filaments connected at the base, with a single point of attachment, yellowish green, up to 20 mm long and broad; prothallus absent. Photobiont *Trentepohlia*, cells in distinct filaments, cylindrical, 35–40 × 10–12 µm. Apothecia formed on the underside, sessile, rounded, 0.4–1.0 mm diam. and 100–150 µm high; disc plane, pale orange-yellow; margin cream-colored, finely pilose; hairs septate, up to 70 × 6 µm. Excipulum paraplectenchymatous, with radiating cell rows, 85–125 µm broad, colorless, I+ sordid yellow-green; cells isodiametric and thin-walled, 3–7 µm diam. Hypothecium 25–40 µm high, colorless. Hymenium 65–90 µm high, colorless, I+ blue then quickly sordid green then reddish brown. Asci 50–55 × 3–4 µm. Ascospores uniseriate, ellipsoid, 1-septate, 7.5–9 × 2.5–3 µm, 2.7–3.3 times as long as broad. Pycnidia not observed.

Etymology. The epithet refers to the pilose apothecia.

Ecology and distribution. On tree bark in primary Atlantic rain forest; so far only known from the type locality.

Discussion. While the overall morphology and anatomy of this new species is similar to *Coenogonium congense* and *C. linkii*, both also sharing the 1-septate ascospores, it differs from the latter, and all other filamentous species known to date, by the pilose apothecial margins. Rivas Plata et al. (2006) mentioned material of *C. congense* from Costa Rica with thinly pilose apothecial margins, but this likely represents the new species. Pilose apothecial margins are otherwise only known from the crustose species *C. ciliatum*, which is morphologically intermediate between crustose and filamentous species of the genus, as the crustose thallus furnishes short hairs formed by algal filaments.

Coenogonium subimplexum D.O. Lima, Aptroot, Lücking & M. Cáceres, sp. nov. (Fig. 3G–H)

MycoBank MB 851539

Diagnosis: Corticolous, filamentous, cushion-like *Coenogonium* differing from *C. implexum* by the smaller ascospores.

Type: Brazil, Minas Gerais: Catas Altas, Parque Nacional do Caraça, alt. 1200–1400 m, 20°06′S, 43°29′W, on tree in Atlantic rain forest, 21 May 2021, D.O. Lima & A. Aptroot 52253 (ISE – holotype; ABL – isotype).

Description. Thallus filamentous, prostrate, forming flat cushions of very densely woven filaments, yellowish green, up to 5 cm diam.; prothallus absent. Photobiont *Trentepohlia*, cells in distinct filaments, cylindrical, 15–25 × 5–12 µm diam. Apothecia formed on the upper surface, sessile, rounded, 0.3–0.6 mm diam; disc flat to slightly convex, pale yellow; margin paler, not prominent (slightly so in young apothecia), smooth to somewhat irregular, creme-colored. Excipulum paraplectenchymatous, with radiating cell rows, 60–75 µm broad, colorless, I+ sordid yellow green; cells isodiametric and thin-walled, 3–7 µm diam. Hypothecium 15–20 µm high, colorless. Hymenium 75–85 µm high, colorless, I+ blue then quickly sordid green then reddish brown. Asci 55–75 × 5–7 µm. Ascospores uniseriate, ellipsoid, 1-septate, 7–9 × 2.5–3 µm, 2.5–3 times as long as broad. Pycnidia not observed.

Etymology. The epithet refers to the smaller ascospores in comparison with *Coenogonium implexum*.

Ecology and distribution. On tree bark in primary Atlantic rain forest; so far only known from the type locality.

Discussion. This species agrees with *Coenogonium implexum* in the rather flat, cushion-shaped thallus formed by very densely woven filaments. It differs in the smaller ascospores, which in genuine *C. implexum* from Australasia are 8–12 × 3–4.5 µm. While *C. implexum* is supposed to also occur in the Americas, Rivas Plata et al. (2006) already suggested that the material from that region may be a different species. Their argument focused on thallus morphology, but it appears the diagnostic difference is ascospore size, which requires checking ascospores in reported occurrences of *C. implexum*.

Additional material. BRAZIL. Minas Gerais: Same as the type, 52001; 52112; 52017; 52290 (ISE, ABL).

Annotated checklist of *Coenogonium* from Brazil

Abbreviations refer to the acronyms of Brazilian states: Acre (AC); Alagoas (AL); Amapá (AP); Amazonas (AM); Bahia (BA); Ceará (CE); Distrito Federal (DF); Espírito Santo (ES); Goiás (GO); Maranhão (MA); Mato Grosso (MT); Mato Grosso do Sul (MS); Minas Gerais (MG); Pará (PA); Paraíba (PB); Paraná (PR); Pernambuco (PE); Piauí (PI); Rio de Janeiro (RJ); Rio Grande do Norte (RN); Rio Grande do Sul (RS); Rondônia (RO); Roraima (RR); Santa Catarina (SC); São Paulo (SP); Sergipe (SE);Tocantins (TO)

Coenogonium acrocephalum Müll. Arg., Flora, Regensburg 64: 525. 1881.

Distribution in Brazil. SP (Rivas Plata et al. 2006).

Coenogonium atroluteum (Vain.) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Gyalecta atrolutea* Vain.

Distribution in Brazil. RJ, RS (Malme 1934); SP (Kalb 1982b).

Coenogonium bacilliferum (Malme) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella bacillifera* Malme 1935.

Distribution in Brazil. RS (Spielmann 2006).

Coenogonium barbatellum Kalb, Biblthca Lichenol. 95: 303. 2007.

Distribution in Brazil. AM (Cáceres & Aptroot 2017); SE (Cáceres 2007).

Coenogonium barbatum Lücking, Aptroot & L. Umaña, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 273. 2006.

Distribution in Brazil. AC (Aptroot et al. 2021b); AL (Oliveira Junior et al. 2020); AM (Aptroot et al. 2021c); BA (Oliveira Junior et al. 2021); CE (Alves 2014); MS (Aptroot & Spielmann 2020b); MT (Aptroot et al. 2022b); PR (Aptroot & Souza 2021b); RO (Cáceres et al. 2014).

Coenogonium chloroticum Xavier-Leite, M. Cáceres & Aptroot, Nova Hedwigia 98(1–2): 198. 2013. [2014]

Distribution in Brazil. AL (Oliveira Junior et al. 2020); AM (Cáceres & Aptroot 2017); AP (Cáceres & Aptroot 2016); CE (Alves 2014); MA (Aptroot et al. 2017); MS (Aptroot & Spielmann 2020a); PB (Xavier-Leite et al. 2014); SE (Aptroot et al. 2022a).

Coenogonium ciliatum Kalb & Lücking, in Lücking & Kalb, Bot. Jb. 122(1): 29. 2000.

Distribution in Brazil. AM (Cáceres 2007); MT (Lücking & Kalb 2000); PA (Lücking & Cáceres 2002); RO (Cáceres et al. 2014).

Coenogonium confervoides Nyl., Flora, Regensburg 41: 380. 1858.

Distribution in Brazil. AC (Aptroot et al. 2021b); AL (Lücking 2008); AM (Leighton 1866); AP (Cáceres & Aptroot 2016); BA (Aptroot et al. 2022a); MT (Aptroot et al. 2022b); PA (Aptroot et al. 2017); PE (Aptroot et al. 2022a).

Coenogonium congense C.W. Dodge [as 'congensis'], Ann. Mo. bot. Gdn 40: 350. 1953.

Distribution in Brazil. PR (Aptroot et al. 2022a).

Coenogonium coppinsii Aptroot & M. Cáceres, The Lichenologist 46(3): 369. 2014.

Distribution in Brazil. AM (Aptroot et al. 2021c); AP (Cáceres & Aptroot 2016); BA (Oliveira Junior et al. 2021); MS (Aptroot & Spielmann 2020b); RO (Aptroot & Cáceres 2014); SE (Cáceres et al. 2014).

Coenogonium curvulum Zahlbr., Annals Cryptog. Exot. 1(2): 164. 1928.

Distribution in Brazil. PE (Lücking & Kalb 2000).

Coenogonium deplanatum Kremp., Flora, Regensburg 59: 250. 1876.

Distribution in Brazil. RJ (Krempelhuber 1876, in Rivas Plata et al. 2006).

Coenogonium dilucidum (Kremp.) Kalb & Lücking, Bot. Jb. 122(1): 32. 2000.

≡ *Lecidea dilucida* Kremp. 1874.

Distribution in Brazil. AL (Oliveira Junior et al. 2020); BA (Oliveira Junior et al. 2021); MS (Aptroot & Spielmann 2020a); MT (Aptroot et al. 2022b); PE (Lücking 2008); RJ, SP (Lücking 2008); RO (Cáceres et al. 2014); RS (Spielmann 2006); SC (Aptroot et al. 2021a).

Coenogonium disjunctum Nyl., Annls Sci. Nat., Bot., sér. 4 16: 91. 1862.

Distribution in Brazil. PE (Cáceres 2007); SC (Aptroot et al. 2021a); RS (Spielmann 2006); SE (Aptroot et al. 2022a).

Coenogonium fallaciosum (Müll. Arg.) Kalb & Lücking, Bot. Jb. 122(1): 32. 2000.

≡ *Patellaria fallaciosa* Müll. Arg. 1890.

Distribution in Brazil. AM (Lücking & Kalb 2000); MS (Aptroot & Spielmann 2020a); MT (Aptroot et al. 2022b); PA (Lücking & Cáceres 2002); SP (Lücking 2008).

Coenogonium flavoviride M. Cáceres & Lücking, Nova Hedwigia 70(1–2): 219. 2000.

Distribution in Brazil. BA (Aptroot & Cáceres 2018b); PE (Lücking 2008); RO (Cáceres et al. 2014).

Coenogonium flavum (Malcolm & Vězda) Malcolm, Australas. Lichenol. 54: 19. 2004.

≡ *Dimerella flava* Malcolm & Vězda 1995.

Distribution in Brazil. MT (Aptroot et al. 2022b); PE (Lücking 2008).

Coenogonium geralense (Henn.) Lücking, Fl. Neotrop., Monogr. 103: 579. 2008.

≡ *Ombrophila geralensis* Henn. 1899.

= *Coenogonium flavicans* (Vězda & Farkas) Kalb & Lücking.

≡ *Dimerella flavicans* Vězda & Farkas.

Distribution in Brazil. AL (Cáceres 2007); AM (Lücking 2008), CE (Menezes 2013); BA, PB (Santos et al. 2016); MS (Aptroot et al. 2022a); PA (Lücking & Cáceres 2002); PE, SC, SP (Lücking 2008); RS (Martins & Marcelli 2011); SE (Dantas 2016).

Coenogonium hypophyllum (Vězda) Kalb & Lücking, Bot. Jb. 122(1): 32. 2000.

≡ *Dimerella hypophylla* Vězda 1975.

Distribution in Brazil. AL (Oliveira Junior et al. 2020); AM (Lücking 2008); BA (Santos et al. 2016); PA (Lücking & Cáceres 2002); MT (Aptroot et al. 2022b); PE (Lücking 2008); RO (Cáceres et al. 2014); SP (Kalb 1984).

Coenogonium implexum Nyl., Annls Sci. Nat., Bot., sér. 4, 16: 92. 1862.

Distribution in Brazil. RS (Spielmann 2006); SC (Müller 1891b).

Coenogonium interplexum Nyl., Annls Sci. Nat., Bot., sér. 4, 16: 92. 1862.

Distribution in Brazil. AC (Aptroot et al. 2021b); AL (Cáceres 2007); AM (Lücking & Kalb 2000); PA (Lücking & Cáceres 2002); PB (Santos et al. (2016); PE (Lücking 2008); RS (Spielmann 2006); SE (Cáceres et al. 2014).

Coenogonium interpositum Nyl.

Distribution in Brazil. AM (Kalb 1986); MT (Aptroot et al. 2022b); PA (Lücking & Cáceres 2002); PR (Osorio 1977a, b); RO (Cáceres et al. 2014); RS (Spielmann 2006).

Coenogonium isidiatum (G. Thor & Vězda) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella isidiata* G. Thor & Vězda 1984.

Distribution in Brazil. SE (Cáceres et al. 2014).

Coenogonium isidiigerum (Vězda & Osorio) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella isidiigera* Vězda & Osorio, in Vězda 1989.

Distribution in Brazil. RS (Spielmann 2006).

Coenogonium isidiosum (Breuss) Rivas Plata, Lücking, L. Umaña & Chaves, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella insidiosa* Breuss. 2002.

Distribution in Brazil. AC (Aptroot et al. 2021b); AL (Cavalcante 2012); MS (Aptroot & Spielmann 2020b); PB, PE (Andrade 2020); SE (Cáceres 2007).

Coenogonium leprieurii (Mont.) Nyl., Annls Sci. Nat., Bot., sér. 4 16: 89. 1862.

≡ *Coenogonium linkii* var. *leprieurii* Mont. 1851.

Distribution in Brazil. AM (Leighton 1866); AC (Aptroot et al. 2021b); AL, SE (Cáceres 2007); AP (Cáceres & Aptroot 2016); BA (Oliveira Junior et al. 2021); CE (Alves 2014); MG (Vainio 1890); MT (Kalb 2001); PA (Zahlbruckner 1909); PE (Lücking 2008); PR (Xavier Filho et al. 1983); RJ (Malme 1937); RO (Cáceres et al. 2014); RS (Spielmann 2006); SC (Müller 1891a).

Coenogonium linkii Ehrenb., in Nees von Esenbeck (Ed.), Horae Phys. Berol.: 120, (1820)

Distribution in Brazil. AC (Aptroot et al. 2021b); AL, SE (Cáceres 2007); AM (Lücking 2008); AP (Cáceres & Aptroot 2016); BA (Santos et al. 2016); MA (Aptroot et al. 2017b); PA (Cengia Sambo 1940); MG (Aptroot 2002); MT (Aptroot et al. 2022b); PB (Andrade 2020); PE (Lücking 2008); PR (Eliasaro et al. 2012); RJ, SC (Cengia Sambo 1940); RO (Cáceres et al. 2014); RS (Spielmann 2006); SP (Kalb 1982c).

Coenogonium luteocitrinum Rivas Plata, Lücking & L. Umaña, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 283. 2006.

Distribution in Brazil. AL, SE (Cáceres 2007); CE (Alves 2014); PB (Xavier-Leite et al. 2015); PE (Sobreira 2015).

Coenogonium luteum (Dicks.) Kalb & Lücking, Bot. Jb. 122(1): 32. 2000.

≡ *Lichen luteus* Dicks. 1785.

Distribution in Brazil. BA, SE (Santos et al. 2016); MG, RJ (Vainio 1890); MS (Aptroot & Spielmann 2020a); MT (Kalb 1983b); PE (Cáceres et al. 2000); RS (Spielmann 2006); SC (Müller 1891b).

Coenogonium minidenticulatum Aptroot & M. Cáceres, The Bryologist 119(3): 257. 2016.

Distribution in Brazil. AP (Cáceres & Aptroot 2016).

Coenogonium moniliforme Tuck., Proc. Amer. Acad. Arts & Sci. 5: 416. 1862. [1860]

Distribution in Brazil. AL (Menezes et al. 2011); BA (Andrade 2020); CE (Alves 2014); MS (Aptroot & Spielmann 2020b); MT (Malme 1937); PE (Lücking & Kalb 2000); SE (Cáceres 2007).

Coenogonium nepalense (G. Thor & Vězda) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella nepalensis* G. Thor & Vězda 1984.

Distribution in Brazil. AL (Cáceres 2007); BA (Aptroot et al. 2022a); CE (Alves 2014); MA (Aptroot et al. 2017); PB (Xavier-Leite et al. 2015); PE (Sobreira 2015); RO (Cáceres et al. 2014); RS (Käffer et al. 2015).

Coenogonium pannosum Müll. Arg., Flora, Regensburg 64(15): 234. 1881.

Distribution in Brazil. SP (Rivas Plata et al. 2006).

Coenogonium persistens (Malme) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 297. 2006.

≡ *Dimerella lutea* f. *persistens* Malme 1935.

Distribution in Brazil. MT (Rivas Plata et al. 2006).

Coenogonium pineti (Ach.) Lücking & Lumbsch, in Lücking, Stuart & Lumbsch, Mycologia 96(2): 290. 2004.

≡ *Lecidea pineti* Ach. 1810.

Distribution in Brazil. AL (Oliveira Junior et al. 2020); PE (Lima 2013); RJ (Krempelhuber 1876); RS (Spielmann 2006).

Coenogonium pulchrum (Müll. Arg.) Kalb, Lichenes Neotropici, Fascicle 13(nos 525–575): 3 (sched.) (2001)

≡ *Biatorinopsis pulchra* Müll. Arg. 1881.

Distribution in Brazil. SP (Rivas Plata et al. 2006).

Coenogonium pusillum (Mont.) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 298. 2006.

≡ *Biatora pusilla* Mont., in Sagra 1845.

Distribution in Brazil. MS (Malme 1934); SP (Kalb 1982c).

Coenogonium pyrophthalmum (Mont.) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 298. 2006.

≡ *Biatora pyrophthalma* Mont. 1843.

Distribution in Brazil. BA (Aptroot & Cáceres 2018a); MS (Aptroot & Spielmann 2020a); MT (Aptroot et al. 2022b); PE (Lima 2013); RS (Spielmann 2006); SE (Cáceres 2007); SP (Kalb 1982c).

Coenogonium riparium (Vain.) Kalb, Biblthca Lichenol. 95: 306. 2007.

≡ *Gyalecta riparia* Vain. 1890.

Distribution in Brazil. MG, RJ (Vainio 1890).

Coenogonium roumeguerianum (Müll. Arg.) Kalb, Lichenes Neotropici, Fascicle 13: 3 (sched.) (2001)

≡ *Biatorinopsis roumegueriana* Müll. Arg. 1887.

Distribution in Brazil. MS (Kalb 1982a); MT (Malme 1934).

Coenogonium saepincola Aptroot, Sipman & Lücking, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 288. 2006.

Distribution in Brazil. PB (Xavier-Leite et al. 2015).

Coenogonium siquirrense f. denticulatum Rivas Plata & Lücking, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 289. 2006.

Distribution in Brazil. PB (Xavier-Leite et al. 2015); RO (Cáceres et al. 2014); RS (Käffer et al. 2015).

Coenogonium stenosporum (Malme) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 298. 2006.

≡ *Dimerella stenospora* Malme 1935.

Distribution in Brazil. RS (Malme 1934).

Coenogonium strigosum Rivas Plata, Lücking & Chaves, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 290. 2006.

Distribution in Brazil. AL, PE, SE (Cáceres 2007); AM (Cáceres & Aptroot 2017); AP (Cáceres & Aptroot 2016); BA (Aptroot et al. 2022a); MS (Aptroot & Spielmann 2020a); MT (Aptroot & Souza 2021a); PA (Aptroot et al. 2017); PR (Aptroot & Souza 2021b), RS (Aptroot et al. 2021a).

Coenogonium subdentatum (Vězda & G. Thor) Rivas Plata, Lücking, L. Umaña & Chaves, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 298. 2006.

≡ *Dimerella subdentata* Vězda & G. Thor, in Vězda 1989.

Distribution in Brazil. AL, PE (Cáceres 2007); BA (Aptroot & Cáceres 2018a); CE (Menezes 2013); MS (Aptroot & Spielmann 2020a); MT (Aptroot & Souza 2021a); PA (Aptroot et al. 2017); PB (Andrade 2020); PR (Aptroot & Souza 2021b); SC (Aptroot et al. 2022a); SE (Cáceres et al. 2014).

Coenogonium subdilutum (Malme) Kalb, Lichenes Neotropici, Fascicle 13: no. 545. 2001.

≡ *Dimerella subdiluta* Malme 1935.

Distribution in Brazil. AL (Cáceres 2007); AP (Cáceres & Aptroot 2016); BA (Oliveira Junior et al. 2021); CE (Alves 2014); MS, MT (Malme 1934); PE (Sobreira 2015); RO, SE (Cáceres et al. 2014); RS (Spielmann 2006); SP (Kalb 1983a); TO (Aptroot et al. 2017).

Coenogonium subfallaciosum (Vězda & Farkas) Lücking, Aptroot & Sipman, in Rivas Plata, Lücking, Aptroot, Sipman, Chaves, Umaña & Lizano, Fungal Diversity 23: 298. 2006.

≡ *Dimerella subfallaciosa* Vězda & Farkas, in Vězda 1990.

Distribution in Brazil. PB (Xavier-Leite et al. 2015); PE (Cáceres 2007).

Coenogonium subluteum (Rehm) Kalb & Lücking

≡ *Biatorina sublutea* Rehm 1913.

Distribution in Brazil. RJ (Krempelhuber 1876, in Rivas Plata et al. 2006).

Coenogonium subzonatum (Lücking) Lücking & Kalb, Biblthca Lichenol. 78: 254. 2001.

≡ *Dimerella subzonata* Lücking 1999.

Distribution in Brazil. AC (Aptroot et al. 2021b); AL, PE (Cáceres 2007); BA (Oliveira Junior et al. 2021); CE (Menezes 2013); MS (Aptroot & Spielmann 2020a); MT (Lücking 2008); PB (Santos et al. 2016).

Coenogonium upretianum M. Cáceres & Aptroot, in Aptroot & Cáceres, Cryptogam Biodiversity and Assessment, Special volume: 11. 2018.

Distribution in Brazil. MS (Aptroot et al. 2022a); MT (Aptroot & Souza 2021a); RS (Aptroot & Cáceres 2018b).

Coenogonium vezdanum (Lücking) Lücking, Fl. Neotrop., Monogr. 103: 582. 2008.

≡ *Dimerella vezdana* Lücking 1999.

Distribution in Brazil. PE (Lücking 2008).

Coenogonium zonatum (Müll. Arg.) Kalb & Lücking, in Lücking & Kalb, Bot. Jb. 122(1): 34. 2000.

≡ *Biatorinopsis zonata* Müll. Arg. 1890.

Distribution in Brazil. AL (Oliveira Junior et al. 2020); AP (Cáceres & Aptroot 2016); BA (Santos et al. 2016); MS (Aptroot & Spielmann 2020b); PE (Lücking 2008); RO (Cáceres et al. 2014); RS (Spielmann 2006).

Conclusions

The present study contributes to the knowledge of the genus *Coenogonium* in Brazil and is also the first study with a larger molecular sample of species of this genus. However, as our findings show, the genus is still insufficiently known and it is unknown to what extent the current phenotype-based species concept holds, even if much refined. Largely unresolved questions that require molecular data include the evolution of crustose vs. filamentous growth forms, the amount of phenotypical homoplasy, and instances of cryptic speciation. If the limited data currently available are any clue, this genus is much more diverse than indicated by the approximately one hundred species known to date. More than half of these

are known from Brazil, making this country a diversity hotspot for the genus and an excellent study area to tackle the above questions.

Acknowledgments

All materials cited were collected under corresponding permits and holotypes are kept in the Brazilian herbaria CGMS or ISE. DOL thanks the Fundação de Amparo a Ciência e Tecnologia do Estado de Pernambuco (FACEPE) for a Master's scholarship. The costs of the collecting expeditions were partly financed by the Conselho Nacional de Pesquisa e Desenvolvimento – CNPQ (e.g., CNPq-Sisbiota Processo 563342/201-2 and Processo 401186/2014-8) and research grants to MESC (Processos 309058/2015-5 and 307569/2019-5). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – (CAPES Brasil) – Finance Code 001 who provided a visiting professorship to the first author. The first author warmly thanks the Stichting Hugo de Vries-fonds for various travel funds.

Supplementary electronic materials

Table S1. Alignment of ITS sequence used in the study. Download file

References

Alves, M. M. E. 2014. Levantamento das espécies de liquens em áreas de Cerrado na Chapada do Araripe – CE. Master's thesis – Universidade Regional do Cariri, Crato, Brazil.

Andrade, D. S. 2020. Liquens corticícolas da restinga no Nordeste do Brasil: aspectos taxonômicos, ecológicos e filogenéticos. PhD Dissertation – Universidade Federal de Pernambuco, Brazil.

Aptroot, A. 2002. New and interesting lichens and lichenicolous fungi in Brazil. *Fungal Diversity* 9(1): 15–45.

Aptroot, A. & Cáceres, M. E. S. 2014. New lichen species from termite nests in rainforest in Brazilian Rondônia and adjacent Amazonas. *The Lichenologist* 46(3), 365–372. https://doi.org/10.1017/S0024282913000340

Aptroot, A. & Cáceres, M. E. S. 2018a. *Coenogonium upretianum* (*Ascomycota*: *Coenogoniaceae*), a new corticolous lichen species from Brazil. *Cryptogam Biodiversity and Assessment Special* 11–13.

Aptroot, A. & Cáceres, M. E. S. 2018b. New species and new records of lichens from inselbergs and surrounding Atlantic rain forest in the Chapada Diamantina (Bahia, Brazil). *Herzogia* 31(1): 359–373. https://doi.org/10.13158/heia.31.1.2018.359

Aptroot, A. & Spielmann, A.A 2020a. New lichen species and records from the Serra da Bodoquena, Mato Grosso do Sul, Brazil, the westernmost Atlantic rain forest. *Archive for Lichenology* 17: 1–26.

Aptroot, A. & Spielmann, A. A. 2020b. Four new Astrothelium species and a Mazaediothecium from Várzea areas in Mato Grosso do Sul, Brazil. *Archive for Lichenology* 21: 1–17.

Aptroot, A. & Souza, M. F. 2021a. New lichen species and records from the Chapada dos Guimarães, Mato Grosso, Brazil. *Cryptogamie Mycologie* 42(10): 171–180. https://doi.org/10.5252/cryptogamie-mycologie2021v42a10

Aptroot, A. & Souza, M. F. 2021b. New crustose lichens from a tropical coastal area in Paraná (Brazil). *Cryptogamie Mycologie* 42(12): 191–197. https://doi.org/10.5252/cryptogamie-mycologie2021v42a12

Aptroot, A., Feuerstein, S. C., Cunha-Dias, I. P. R., Lucena Nunes, Á. R., Honorato, M. E. & Cáceres, M. E. S. 2017. New lichen species and lichen reports from Amazon forest remnants and Cerrado vegetation in the Tocantina Region, northern Brazil. *The Bryologist* 120(3): 320–328. https://doi.org/10.1639/0007-2745-120.3.320

Aptroot, A., Spielmann, A. A. & Gumboski, E. L. 2021a. New lichen species and records from Santa Catarina and Rio Grande do Sul, Brazil. *Archive for Lichenology* 23: 1–18.

Aptroot, A., Santos, L. A. D., Oliveira Junior, I., Cavalcante, J. G. & Cáceres, M. E. S. 2021b. Lichens from Brazil: a checklist of lichenized fungi from Acre, in the Amazon. *Mycotaxon* 136(2): 541–541. https://doi.org/10.5248/136.541

Aptroot, A., Cavalcante, J. G., Santos, L. A. D., Oliveira Junior, I., Lima, D. D. O. & Cáceres, M. E. S. 2021c. Checklist of the lichens of The Reserva Florestal Adolphe Ducke in Manaus (Amazonas, Brazil). *Mycotaxon* 136(3): 685–685. https://doi.org/10.5248/136.685

Aptroot, A., Souza, M. F., Cáceres, M. E. S., Santos, L. A. & Spielmann, A. A. 2022a. New lichen records from Brazil. *Archive for Lichenology* 31: 1–51.

Aptroot, A., Souza, M. F., Santos, L. A., Oliveira Junior, I., Barbosa, B. M. C. & da Cáceres, M. E. S. 2022b. New species of lichenized fungi from Brazil, with a record report of 492 species in a small area of the Amazon Forest. *The Bryologist* 125(3): 433–465. https://doi.org/10.1639/0007-2745-125.3.433

Cáceres, M. E. S. 2007. Corticolous crustose and microfoliose lichens of northeastern Brazil. *Libri Botanici* 22: 1–168.

Cáceres, M. E. S. & Lücking, R. 2000. Three new species and one new combination of foliicolous lichens and lichenicolous fungi from the Atlantic Rainforest in Pernambuco state, Brazil. *Nova Hedwigia* 70(1–2): 217–226.

Cáceres, M. E.S & Aptroot, A. 2016. First inventory of lichens from the Brazilian Amazon in Amapá State. *The Bryologist* 119(3): 250–265. https://doi.org/10.1639/0007-2745-119.3.250

Cáceres, M. E. S. & Aptroot, A. 2017. Lichens from the Brazilian Amazon, with special reference to the genus Astrothelium. *The Bryologist* 120(2): 166–182.

Cáceres, M. D. S., Maia, L. C. & Lücking, R. 2000. Foliicolous lichens and their lichenicolous fungi in the Atlantic rainforest of Brazil: diversity, ecogeography and conservation. *Bibliotheca Lichenologica* 75: 47–70.

Cáceres, M. E. S., Lima, E. L.N, Aptroot, A. & Lücking, R. 2014. Liquens brasileiros: novas descobertas evidenciam a riqueza no Norte e Nordeste do país. *Boletim do Museu de Biologia Mello Leitão* 35: 101–119.

Cavalcante, J. G. 2012. Fatores associados à estrutura da comunidade de liquens corticícolas crostosos em duas áreas de caatinga no Estado de Alagoas. Master's Thesis – Universidade Federal de Sergipe, Sergipe, Brazil.

Cengia-Sambo, M. 1940. Licheni del Brasile. *Annali di Botanica* 22: 19–41.

Dantas, J. D. O. 2016. Existe um efeito de borda na caatinga?: evidência de comunidades de liquens em Poço Verde, Sergipe. Master's Thesis – Universidade Federal de Sergipe, Sergipe, Brazil.

Ehrenberg, C. G. 1820. De Coenogonio, novo lichenum genere ex penu viri cl. Chamisso desumpto. In: Ness v. Esenbeck (ed.), *Horae Physicae Berolinenses*, pp. 117–122.

Eliasaro, S., Gerlach, A. C. L. & Gumboski, E. L. 2012. Novos registros de fungos liquenizados para o estado do Paraná, Brasil. *Revista Brasileira de Biociências* 10: 507–512.

Ferraro, L. I. & Michlig, A. 2013. New species and additional records of *Coenogonium* (*Ostropales*: *Coenogoniaceae*) from southern South America. *The Lichenologist* 45(4): 497–504. https://doi.org/10.1017/S0024282913000169

Gagarina, L. V. 2008. Gyalectoid lichens: History and the current state of study. *Novitates Systematicae Plantarum non Vascularium* 42: 153–168.

Gagarina, L. V. 2015. *Coenogonium theae* comb. et stat. nov. (Lichenized *Ascomycota*). *Herzogia* 28(2): 794–797.

Hall, T. A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Henssen, A. & Jahns, H. M. 1974. *Lichenes. Eine Einführung in die Flechtenkunde.* Stuttgart: Thieme Verlag.

Joshi, Y., Gagarina, L. V., Halda, J. P., Oh, S. O. & Hur, J. S. 2015. A new species and a new record of the lichen genus *Coenogonium* (*Ostropales*: *Coenogoniaceae*) from South Korea, with a world-wide key to crustose *Coenogonium* having prothalli. *Mycosphere* 6(6): 667–672. https://doi.org/10.5943/mycosphere/6/6/3

Käffer, M. I., Koch, N. M., Aptroot, A. & de Martins, S. M. A. 2015. New records of corticolous lichens for South America and Brazil. *Plant Ecology and Evolution* 148(1): 111–118. http://dx.doi.org/10.5091/plecevo.2015.961

Kalb, K. 1982a. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel II (No. 41–80). Neumarkt/Opf., 12 pp.

Kalb, K. 1982b. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel IV (No. 121–160). Neumarkt/Opf., 12 pp.

Kalb, K. 1982c. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel V (No. 161–200). Neumarkt/Opf., 12 pp.

Kalb, K. 1983a. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel VI (No. 201–250). Neumarkt/Opf., 16 pp.

Kalb, K. 1983b. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel VII (No. 251–300). Neumarkt/Opf., 16 pp.

Kalb, K. 1984. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel VIII (No. 301–350). Neumarkt/Opf., 6 pp.

Kalb, K. 1986. Lichenes Neotropic ausgegeben von Klaus Kalb. Fascikel IX (No. 351–400). Neumarkt/Opf., 16 pp.

Kalb, K. 2001. Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel XIII (No. 526–575). Schedae, Neumarkt. 16 PP.

Kalb, J., Boonpragob, K. & Kalb, K. 2016. New *Coenogonium* species (*Ostropales*: *Coenogoniaceae*) from Thailand, new reports and a revised key to the species occurring in the country. *Phytotax* 283(2): 101–122. https://doi.org/10.11646/phytotaxa.283.2.1

Kantvilas, G., Rivas-Plata, E. & Lücking, R. 2018. The lichen genus *Coenogonium* in Tasmania. *The Lichenologist* 50(5): 571–582. http://dx.doi.org/10.1017/S0024282918000385

Katoh, K., Standley, D. M. 2013. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* 30: 772–780. https://doi.org/10.1093/molbev/mst010

Katoh, K., Asimenos, G. H., Toh, H. 2009. Multiple Alignment of DNA Sequences with MAFFT. *Methods in Molecular Biology* 537: 39–64. https://doi.org/10.1007/978-1-59745-251-9_3

Kauff, F. & Lutzoni, F. 2002. Phylogeny of the *Gyalectales* and *Ostropales* (*Ascomycota*, Fungi): among and within order relationships based on nuclear ribosomal RNA small and large subunits. *Molecular Phylogenetics and Evolution* 25(1): 138–156. https://doi.org/10.1016/s1055-7903(02)00214-2

Leighton, W. A. 1866. Lichenes Amazonici et Andini lecti a Domino Spruce. *Transactions of the Linnean Society of London*. *Botany* 25: 433–460.

Lima, E. L. D. 2013. Riqueza e composição de liquens corticícolas crostosos em área de Caatinga no Estado de Pernambuco. Master's Thesis – Universidade Federal de Pernambuco, Brazil.

Lücking, R. 1999. Additions and corrections to the foliicolous lichen flora of Costa Rica. The family *Gyalectaceae*. *The Lichenologist* 31(4): 359–374. https://doi.org/10.1006/lich.1999.0205

Lücking, R. 2008. Foliicolous lichenized fungi. *Flora Neotropica Monograph* 101: 1–866.

Lücking, R. & Kalb, K. 2000. Foliikole Flechten aus Brasilien (vornehmlich Amazonien), inklusive einer Checkliste und Bemerkungen zu *Coenogonium* und *Dimerella* (*Gyalectaceae*). *Botanische Jahrbucher fur Systematik Pflanzengeschichte und Pflanzengeographie* 122(1): 1–62.

Lücking, R. & Cáceres, M. E. S. 2002. Liquens foliícolas: diversidade, taxonomia e biogeografia. In: P. L. B. Lisboa (Ed.), Caxiuanã: Populações tradicionais, Meio físico & Diversidade Biológica. Museu Paraense Emílio Goeldi: Belém, pp. 445–472.

Lücking, R., Hodkinson, B. P. & Leavitt, S. D. 2017. The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota* – Approaching one thousand genera. *The Bryologist* 119(4): 361–416. https://doi.org/10.1639/0007-2745-119.4.361

Lumbsch, H. T., Ahti, T., Altermann, S., Paz, G. A. et al. 2011. One hundred new species of lichenized fungi: a signature of undiscovered global diversity. *Phytotaxa* 18: 1–127. https://doi.org/10.11646/phytotaxa.18.1.1

Malme, G. O. A. 1934. Die Gyalectazeen der ersten Regnellschen Expedition. *Arkiv för Botanik* 26A(13): 1–10.

Malme, G. O. A. 1937. Lichenes nonnulli in expeditione Regnelliana prima collecti. *Arkiv för Botanik* 29A(7): 1–53.

Mateus, N. & Lücking, R. 2011. Contribuciones a la biota liquenica foliicola de Colombia. I. nuevos registros del genero *Coenogonium* (*Ascomycota*-ostropales: coenogoniaceae). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 35(137): 425–430.

Menezes, A. A. 2013. Resposta da comunidade de microliquens corticícolas a fatores ambientais em duas fitofisionomias. Master's Thesis – Universidade Federal de Sergipe, Sergipe, Brazil.

Menezes, A. A., Leite, A. B. X., Otsuka, A. Y., Jesus, L. S. & Cáceres, M. E. S. 2011. Novas ocorrências de liquens corticícolas crostosos e microfoliosos em vegetação de Caatinga no semi-árido de Alagoas. *Acta Botanica Brasilica* 25: 885–889.

Müller [Argoviensis] J. 1891a. Lichenes Catharinenses. *Hedwigia* 5: 235–243.

Müller [Argoviensis] J. 1891b. Lichenes Schenckiani. *Hedwigia* 5: 219–234.

Müller, J. 1881. Lichenologische Beiträge, XIII. F*lora (Regensburg)\ Flora* 64: 225–236.

Oliveira Junior, I., Aptroot, A., Santos, L. A., Cavalcante, J. G., Košuthová, A. & Cáceres, M. E. S. 2020. Two further new lichen species from the Atlantic Forest remnant Pedra Talhada (Alagoas, Brazil), with a species list. *The Bryologist* 123(4): 617–632.

Oliveira Junior, I., Aptroot, A. & Cáceres, M. E. S. 2021. Lichens from Monte Pascoal, Bahia, Brazil, with some new pyrenocarpous species and a key to the *Pyrenula* species from Brazil. *The Bryologist* 124(4): 552–568. http://dx.doi.org/10.1639/0007-2745-124.4.552

Osorio, H. S. 1977a. Contribution to the lichen flora of Brazil II. Lichens from Guarapuava, Paraná. *Dusenia* 10: 101–102.

Osorio, H. S. 1977b. Contribution to the lichen flora of Brazil III. Lichens from western Paraná. *Acta Biológica Paranaense* 6: 3–7.

Poelt, J. 1969. *Bestimmungsschlüssel europäischer Flechten*. J. Cramer, Lehre.

Rivas Plata, E., Lücking, R., Aptroot, A., Sipman, H. J. M., Chaves, J. L., Umaña, L. & Lizano, D. 2006. A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (*Ostropales*: *Coenogoniaceae*), with a world-wide key and checklist and a phenotype-based cladistic analysis. *Fungal Diversity* 23: 255–321.

Santesson, R. 1952. Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* 12(1): 1–590.

Santos, V. M., Lücking, R. & Cáceres, M. E. S. 2016. Liquens foliícolas (*Ascomycota*) em Brejos de Altitude: novos registros para o Nordeste e para o Brasil. *Iheringia, Série Botânica* 71(3): 367–376.

Santos, V. M., Cáceres, M. E. S. & Lücking, R. 2019. Diversity of foliicolous lichens in isolated montane rainforests (Brejos) of northeastern Brazil and their biogeography in a neotropical context. *Ecological Research* 35(1): 182–197. https://doi.org/10.1111/1440-1703.12071

Sobreira, P. N. B. 2015. Caracterização da micota liquenizada corticícola em brejos de altitude no Estado de Pernambuco. Master's Thesis – Universidade Federal de Pernambuco.

Spielmann, A. A. 2006. Checklist of lichens and lichenicolous fungi of Rio Grande do Sul (Brazil). *Caderno de Pesquisa Série Biologia* 18(2): 7–125.

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–26900.

Trevisan, C. V. 1880. Reale Istituto Lombardo di Scienze e Lettere, Milano, ser. 13(2): 65.

Vainio, E. A. 1890. Étude sur la classification naturelle et la morphologie des lichens du Brésil, pars prima. *Acta Societatis pro Fauna et Flora fennica* 7(1): 1–247.

Vězda, A. 1969. Neue Taxa und Kombinationen in der Familie *Gyalectaceae* (Lichenisierte Fungi). *Folia Geobotanica et Phytotaxonomica* 4: 443–446.

Watson, W. 1929a. The classification of lichens. Part I. *New Phytologist* 28: 1–36.

Watson, W. 1929b. The classification of lichens. Part II. *New Phytologist* 28: 85–116.

Xavier-Filho, L., Cavalcante, W. D. A. & Cavalcante, A. A. S. 1983. Estudio del género *Coenogonium* en Brasil. *Boletim da Sociedade Broteriana* 56(2): 115–121.

Xavier-Leite, A. B., Menezes, A. A., Aptroot, A. & Cáceres, M. E. S. 2014. *Coenogonium chloroticum* (*Ascomycota*: *Coenogoniaceae*), a new corticolous lichen species from Mata do Pau-Ferro, in Paraíba, NE Brazil. *Nova Hedwigia* 98(1–2): 197–200. http://dx.doi.org/10.1127/0029-5035/2013/0149

Xavier-Leite, A. B., Menezes, A. A., Souto, L. D. S., Aptroot, A., Lücking, R., Santos, V. M. D. & Cáceres, M. E. S. 2015. Epiphytic microlichens as indicators of phytosociological differentiation between Caatinga and Brejos de Altitude. *Acta Botanica Brasilica* 29: 457–466.

Zahlbruckner, A. 1907. Lichenes (Flechten). Specieller Teil. In: Engler, A. & Prantl, K. (eds) Die Natürlichen Pflanzenfamilien. Teil 1. Abt. 1. Engelmann, Leipzig, pp. 49–249.

Zahlbruckner, A. 1909 [‘1908’]. Lichenes amazonici. Materialien zu einer Flechtenflora Brasiliense. *Boletim do Museu Goeldi* 5: 258–261.