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Alloarthopyrenia aptrootiana sp. nov. (*Trypetheliaceae*), the second recognized species in the genus and the first tropical member of *Alloarthopyrenia*, with a revised taxonomic concept for *Arthopyrenia cinereopruinosa*

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Abstract. We describe the new species *Alloarthopyrenia aptrootiana* from western Mexico, representing the second known species in the genus and its first tropical member. The new species is characterized by its narrow, 1-septate ascospores of 17–21 × 6–7.5 µm, with additional strong constrictions in the middle of each cell. We present a phylogeny of *Trypetheliaceae* that confirms the position of the new species in the genus. We propose the new combination *Naetrocymbe cinereopruinosa* to accommodate the historically misapplied *Arthopyrenia cinereopruinosa* based on its type collection and confirm *Alloarthopyrenia italica* as a different and valid species. Based on our phylogenetic analysis, we also propose the new combination *Pseudobogoriella confusa* to accommodate a species previously known in the genus *Mycomicrothelia*.

Key words: *Arthopyrenia*, Chamela-Cuixmala Biosphere Reserve, lichens, Mexico, *Naetrocymbe cinereopruinosa*, phylogeny, *Pseudobogoriella confusa*, tropical dry forest

Introduction

Over the last decades, the once large genus *Arthopyrenia* A. Massal. has been split into several genera representing different families (Harris 1975; Coppins 1988; Nelsen et al. 2009, 2011; Vondrák et al. 2023). Many tropical and some temperate members of *Arthopyrenia* s.lat. were found to represent basal lineages in *Trypetheliaceae*, with several new genera segregated in recent years (Nelsen et al. 2014; Hyde et al. 2016; Lücking et al. 2016; Hongsanan et al. 2020). The type species of *Arthopyrenia*, *A. cerasi* (Schrad.) A. Massal., was also shown to belong in *Trypetheliaceae*, along with a tropical species of *Julella* Fabre s.lat. (Thiyagaraja et al. 2021). One of these new genera, *Alloarthopyrenia* Phukhams., Lücking & K.D. Hyde, was introduced as a monospecific genus to accommodate a new species resembling a non-lichenized *Arthopyrenia*, but representing an isolated clade in the *Trypetheliaceae* phylogeny (Hyde et al. 2016).

Alloarthopyrenia italica Phukhams., Camporesi, Ariy. & K.D. Hyde, a European species (Hyde et al. 2016; Vondrák et al. 2023; Roux et al. 2024), is characterized by carbonaceous involucrellum, branched and anastomosing pseudoparaphyses, and hyaline ascospores with one septum and additional strong median constrictions in the lumina. The species was initially characterized as non-lichenized, but was recently reassessed as a borderline lichen or "semilichen" (Vondrák et al. 2026), i.e., being weakly or facultatively lichenized. Thiyagaraja et al. (2021) emphasized the similarities of the new species with the concept of *Arthopyrenia cinereopruinosa* (Schaer.) A. Massal. proposed by Harris (1975), arguing that *A. cinereopruinosa* s.str. represented an unrelated taxon, thus suggesting the possibility of the presence of *A. italica* in North America.

In this study, we describe a second species in the genus *Alloarthopyrenia*, discovered in material from Mexico. We also reassessed the status of *A. italica*, finding that the type of *Verrucaria cinereopruinosa* Schaer. indeed represents a different species, for which we propose the new combination *Naetrocymbe cinereopruinosa*.

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Materials and methods

Anatomical studies

Lichen samples were studied at the Instituto de Biología, UNAM, using standard techniques in an Olympus SZ61 dissecting microscope and an Euromex iscope compound microscope connected to an AmScop MU1803 digital camera. Sections were mounted in tap water. KOH and IKI reagents were used at 10% and 0.3%, respectively (Bungartz 2002). All anatomical measurements were made in tap water. Thallus images were taken with a Nikon Zf attached to a series of macro-objectives and stacked in Helicon Focus.

Taxon sampling for molecular analysis

We followed recent broad phylogenetic analyses of *Trypetheliaceae* (Hyde et al. 2016; Lücking et al. 2016; Hongsanan et al. 2020; Miranda-González et al. 2020; Thiyagaraja et al. 2021) and included all available sequences (up to March 2026) in GenBank of the basal lineages of the family, together with representative sequences of the more derived genera, and new sequences generated in this study (Table 1). Two nuITS sequences (OQ717306 and OQ717706) correctly representing *Arthopyrenia* s.str. were excluded due to lack of complementary molecular markers, which produced the false impression of polyphyletic species. The family *Polycoccaceae* was selected as the outgroup following Ertz et al. (2015).

DNA extraction, PCR amplification, and sequencing

Molecular work followed Miranda-González et al. (2020) which consists of extracting total DNA using the Sigma-Aldrich REDExtract-N-Amp Plant PCR Kit (St. Louis, MO, USA). The whole nuITS and portions of mtSSU and nuLSU were amplified and sequenced using the following primers: ITS1F/ITS4 (White et al. 1990; Gardes & Bruns 1993), mrSSU1/mrSSU3R (Zoller et al. 1999), and AL2R/LR6 (Vilgalys & Hester 1990; Mangold et al. 2008), respectively.

Each 10 µL PCR reaction consisted of 5 µL R4775 Sigma-Aldrich REDExtract-n-Amp PCR Ready Mix, 0.5 µL of each primer (10 µM), 3 µL water, and 1 µL diluted DNA. The PCR cycling conditions for nuITS were: 95°C for 5 min, followed by 35 cycles of 95°C for 30 s, 52°C for 45 s, and 72°C for 105 s, followed by 72°C for 5 min. The PCR cycling conditions for the rest of the markers were: 95°C for 5 min, followed by 35 cycles of 95°C for 1 min, 53°C (for mtSSU) or 57°C (for nuLSU) for 1 min, and 72°C for 105 s, followed by 72°C for 10 min. Each PCR product (2 µL) was visualized on 1.5% TAE agarose gel stained with GelRed (Biotium). PCR products were cleaned with ExoSAP-IT (ThermoFisher). All Molecular work, including sequencing, was done at the Laboratorio de Biología Molecular, as part of the Laboratorio Nacional de Biodiversidad, in the Instituto de Biología of the Universidad Nacional Autónoma de México.

Phylogenetic analysis

New sequences were edited in Geneious Prime 2026.0.2 (Kearse et al. 2012). All sequences from each molecular marker were aligned independently with MAFFT 7.490 (Katoh & Standley 2013) and manually corrected. The final concatenated alignment is available as Appendix A. The maximum likelihood (ML) analysis of all markers, partitioned by marker, was performed using RAxML v. 8.2.11 (Stamatakis 2014), with 550 bootstrapping replicates. The Bayesian analysis was performed using MrBayes v. 3.2.6 (Ronquist et al. 2012), with one million generations and default settings. All analyses were performed with the GTR GAMMA model and run on Geneious Prime. The final ML trees were plotted in Geneious Prime and edited in Photoshop.

Results and discussion

A total of four new sequences were generated in this study (Table 1). Our phylogenetic analysis dataset included 99 taxa (Table 1) and consisted of 1,900 unambiguously aligned characters, 526 for nuITS, 516 for nuLSU, and 858 for mtSSU, of which 378, 302, and 466, respectively, were phylogenetically informative. Our phylogenetic analysis agrees with previous work in the *Trypetheliaceae* (Hyde et al. 2016; Lücking et al. 2016; Hongsanan et al. 2020; Miranda-González et al. 2020; Thiyagaraja et al. 2021), showing several monophyletic genera with good support at the base of the phylogeny, but with poor support in their relation to each other. Similar to previous reports (Miranda-González et al. 2020; Thiyagaraja et al. 2021), *Alloarthopyrenia* was resolved as one of the basal lineages in the family, but its sister clade was not defined with support. We describe below a second known species of *Alloarthopyrenia* from Mexico that fell in this clade. Our results also resolved *Arthopyrenia* s.str., so far including *A. analepta* (Ach.) A. Massal., *A. cerasi*, and *A. fallaciosa* (Stizenb. ex Arnold) V. Thiyag., Ertz, Lücking, Coppins and K.D. Hyde, as a clade separate from *Alloarthopyrenia*. Sequences of *Mycomicrothelia confusa* D. Hawksw. were resolved in the *Pseudobogoriella* Lücking, R. Miranda & Aptroot clade. Based on the obtained topology, we propose below a new combination of *M. confusa* into *Pseudobogoriella*.

Taxonomy

Alloarthopyrenia aptrootiana R. Miranda, Lücking, Herrera-Camp. & Campos-Cerda, sp. nov. (Figs 2, 3)

MycoBank MB 864419

Diagnosis: Similar to *Alloarthopyrenia italica*, but differing by having narrower ascospores, a tropical distribution, and by phylogenetic analyses.

Type: Mexico, Jalisco, Tomatlán Mun., San Carlos Coacoyul. 20°07′48.3″N, 105°32′11.1″W, 78 m, 14 Mar. 2013., M.A. Herrera-Campos et al. 2013 #1608. (MEXU – holotype!). GenBank Accession nos.: PZ602877 (nuITS), PZ602880 (nuLSU), PZ602879 (mtSSU).

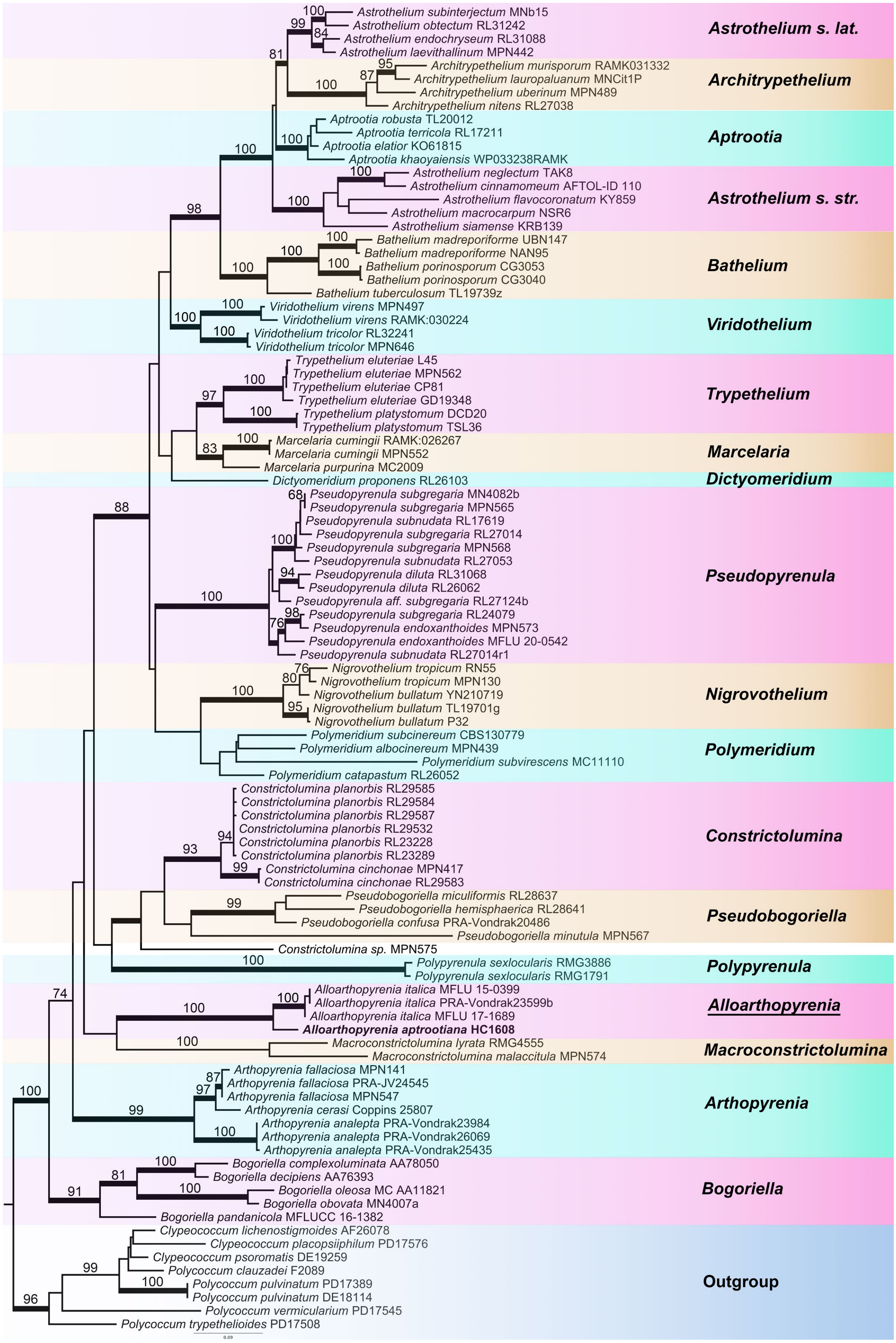

Figure 1. Phylogeny of the *Trypetheliaceae* family based on a maximum likelihood (ML) analysis of the molecular markers nuITS, nuLSU, and mtSSU. Support values are shown as numbers if ML bootstrap values are >60 and as bold branches if Bayesian posterior probabilities are ≥ 0.95. Bold names show new sequences from this study.

Table 1. GenBank Accession numbers of sequences used in this study. Bold letters indicate new sequences generated in this study. – Indicates missing data. * Indicates holotype.

Taxa	Voucher	Isolate	Country	Reference	nuITS	nuLSU	mtSSU
Alloarthopyrenia aptrootiana	HC1608*	RMG093	Mexico	This study	**PZ602877**	**PZ602880**	**PZ602879**
Alloarthopyrenia italica	MFLU 15-0399*	IT-122	Italy	Hyde et al. 2016	KX655560	KX655550	KX655555
Alloarthopyrenia italica	MFLU 17-1689		Italy	Thiyagaraja et al. 2021	–	–	MZ221609
Alloarthopyrenia italica	PRA-Vondrak23599b		Czech Republic	Vondrák et al. 2023	–	–	OQ646102
Aptrootia elatior	KO61815	MPN560B	New Zealand	Nelsen et al. 2014	–	KM453754	KM453821
Aptrootia khaoyaiensis	WP033238RAMK*		Thailand	Polyiam et al. 2024	–	–	OR392814
Aptrootia robusta	TL20012	MPN235B	Australia	Nelsen et al. 2014	–	KM453755	KM453822
Aptrootia terricola	RL17211	HTL1501	Costa Rica	Nelsen et al. 2014	–	KM453756	DQ328995
Architrypethelium lauropaluanum	MNCit1P	MPN48	Peru	Lücking et al. 2016	–	KX215605	KX215566
Architrypethelium murisporum	RAMK031332*		Thailand	Luangsuphabool et al. 2018	–	LC361340	LC361339
Architrypethelium nitens	RL27038	MPN257	Panama	Nelsen et al. 2014	–	KM453757	KM453823
Architrypethelium uberinum	MPN489	MPN489	Brazil	Nelsen et al. 2014	–	KM453758	–
Arthopyrenia analepta	PRA-Vondrak23984		Czech Republic	Vondrák et al. 2023	–	–	OQ646100
Arthopyrenia analepta	PRA-Vondrak25435		Czech Republic	Vondrák et al. 2023	–	–	OQ646101
Arthopyrenia analepta	PRA-Vondrak26069		Australia	Vondrák et al. 2023	OQ717305	–	OQ682863
Arthopyrenia cerasi	Coppins 25807		UK	Thiyagaraja et al. 2021	–	–	MZ221617
Arthopyrenia fallaciosa	MPN141	MPN141	USA	Nelsen et al. 2011	–	JN887399	JN887411
Arthopyrenia fallaciosa	MPN547	MPN547	USA	Nelsen et al. 2011	–	JN887400	JN887412
Arthopyrenia fallaciosa	PRA-JV24545		Czech Republic	Vondrák et al. 2022	–	–	OK465529
Astrothelium cinnamomeum	AFTOL-ID 110	AFTOL-ID 110	Costa Rica	Lutzoni et al. 2004	DQ782839	AY584652	AY584632
Astrothelium endochryseum	RL31088	MPN436	Brazil	Nelsen et al. 2014	–	KM453772	KM453837
Astrothelium flavocoronatum	KY859	KY859	Thailand	Luangsuphabool et al. 2016a	LC127381	LC127398	LC128014
Astrothelium laevithallinum	MPN442	MPN442	Brazil	Nelsen et al. 2014	–	KM453771	KM453836
Astrothelium macrocarpum	NSR6	NSR6	Thailand	Luangsuphabool et al. 2016a	AB759880	LC127402	AB759879
Astrothelium neglectum	TAK8	TAK8	Thailand	Luangsuphabool et al. 2016a	LC127392	LC127410	LC128025
Astrothelium obtectum	RL31242	MPN422	Brazil	Nelsen et al. 2014	–	KM453767	KM453832
Astrothelium siamense	KRB139	KRB139	Thailand	Luangsuphabool et al. 2016a	LC127388	LC127406	LC128021
Astrothelium subinterjectum	MNb15	MPN157	Brazil	Lücking et al. 2016	–	KX215660	KX215583
Bathelium madreporiforme	NAN95	NAN95	Thailand	Luangsuphabool et al. 2016a	LC127396	LC127414	LC128029
Bathelium madreporiforme	UBN147	UBN147	Thailand	Luangsuphabool et al. 2016a	LC127395	LC127413	LC128028
Bathelium porinosporum	CG3040*	MPN743	Vietnam	Nelsen et al. 2014	KU504486	KM453776	KM453841
Bathelium porinosporum	CG3053	MPN747	Vietnam	Lücking et al. 2016	KU504488	KX215667	KX215587
Bathelium tuberculosum	TL19739z	MPN81	India	Nelsen et al. 2014	–	KM453777	KM453842
Bogoriella complexoluminata	AA78050*	Aptroot-18829	Brazil	Hongsanan et al. 2020	–	–	MT968880
Bogoriella decipiens	AA76393	Aptroot-19369	Puerto Rico	Hongsanan et al. 2020	–	–	MT968881
Bogoriella obovata	MN4007a	MPN95	Peru	Nelsen et al. 2009	–	GU327721	GU327697
Bogoriella oleosa	MC AA11821	MPN700	Brazil	Nelsen et al. 2014	–	KM453794	KM453857
Bogoriella pandanicola	MFLUCC 16-1382*	MFLUCC 16-1382	Thailand	Zhang et al. 2017	–	KY968641	MT967501
Clypeococcum lichenostigmoides	AF26078		Bolivia	Senanayake et al. 2023	–	OR133231	–

Table 1. Continued.

Taxa	Voucher	Isolate	Country	Reference	nuITS	nuLSU	mtSSU
Clypeococcum placopsiiphilum	PD17576		Iceland	Ertz et al. 2015	–	KT383789	–
Clypeococcum psoromatis	DE19259		France	Ertz et al. 2015	–	KT383790	–
Constrictolumina cinchonae	MPN417	MPN417	Brazil	Nelsen et al. 2014	–	KM453759	KM453825
Constrictolumina cinchonae	RL29583		Brazil	Nelsen et al. 2011	–	JN872351	JN872349
Constrictolumina planorbis	RL23228	AAS-2011	Brazil	Nelsen et al. 2011	–	JN872354	–
Constrictolumina planorbis	RL23289	AAS-2011	Brazil	Nelsen et al. 2011	–	JN872353	–
Constrictolumina planorbis	RL29532	MPN330	Brazil	Lücking et al. 2016	–	KX215670	–
Constrictolumina planorbis	RL29584	AAS-2011	Brazil	Nelsen et al. 2011	–	JN872352	JN872350
Constrictolumina planorbis	RL29585	MPN332	Brazil	Lücking et al. 2016	–	KX215672	–
Constrictolumina planorbis	RL29587	MPN331	Brazil	Lücking et al. 2016	–	KX215671	–
Constrictolumina sp.	MPN575	MPN575	Thailand	Lücking et al. 2016	–	–	KX215588
Dictyomeridium proponens	RL26103	MPN359	Venezuela	Nelsen et al. 2011	–	JN887403	KM453860
Macroconstrictolumina lyrata	RMG4555	RMG014	Mexico	Hongsanan et al. 2020; this study	**PZ602878**	–	MT948052
Macroconstrictolumina malaccitula	MPN574	MPN574	Thailand	Nelsen et al. 2014	–	–	KM453824
Marcelaria cumingii	MPN552	MPN552	Thailand	Nelsen et al. 2014	–	KM453789	KM453854
Marcelaria cumingii	RAMK:026267	SNK1	Thailand	Luangsuphabool et al. 2016b	LC034179	–	LC034283
Marcelaria purpurina	MC2009	MPN323A	Brazil	Nelsen et al. 2014	–	KM453790	KM453855
Nigrovothelium bullatum	P32	MPN579	Thailand	Lücking et al. 2016	–	KX215674	KX215590
Nigrovothelium bullatum	TL19701g	MPN114/ 82	India	Lücking et al. 2016	–	KX215673	KX215589
Nigrovothelium bullatum	YN210719	YN210719		Direct submission	OP360946	OP359019	OP359421
Nigrovothelium tropicum	MPN130	MPN130	USA	Nelsen et al. 2014	–	KM453819	KM453883
Nigrovothelium tropicum	RN55	RN55	Thailand	Luangsuphabool 2015	AB758903	–	AB759877
Polycoccum clauzadei	F2089	F2089	Canada	Ertz et al. 2015	–	KT383804	–
Polycoccum pulvinatum	DE18114	DE18114	Belgium	Ertz et al. 2015	–	KT383806	–
Polycoccum pulvinatum	PD17389	PD17389	Luxembourg	Ertz et al. 2015	–	KT383805	–
Polycoccum trypethelioides	PD17508	PD17508	Iceland	Ertz et al. 2015	–	KT383807	–
Polycoccum vermicularium	PD17545	PD17545	Iceland	Ertz et al. 2015	–	KT383808	–
Polymeridium albocinereum	MPN439	MPN439	Brazil	Nelsen et al. 2014	–	KM453795	KM453858
Polymeridium catapastum	RL26052	MPN358	Venezuela	Nelsen et al. 2011	–	JN887402	KM453859
Polymeridium subcinereum	CBS130779	CBS 130779	USA	McDonald et al. 2013	KC592279	–	KC592287
Polymeridium subvirescens	MC11110	MPN702	Brazil	Lücking et al. 2016	–	KX215681	–
Polypyrenula sexlocularis	RMG1791	RMG057	Mexico	Miranda-González et al. 2020	MK503259	MK503258	MK503257
Polypyrenula sexlocularis	RMG3886	RMG058	Mexico	Miranda-González et al. 2020	MK503262	MK503261	MK503260
Pseudobogoriella confusa	PRA-Vondrak20486		UK	Vondrák et al. 2023	OQ717968	–	OQ646344
Pseudobogoriella hemisphaerica	RL28641	MPN102	Nicaragua	Nelsen et al. 2009	–	GU327719	GU327695
Pseudobogoriella miculiformis	RL28637	MPN101B	Nicaragua	Nelsen et al. 2009	–	GU327720	GU327696
Pseudobogoriella minutula	MPN567	MPN567	Thailand	Nelsen et al. 2014	–	–	KM453856
Pseudopyrenula aff. *subgregaria*	RL27124b	MPN288	Panama	Lücking et al. 2016	–	KX215682	–
Pseudopyrenula diluta	RL26062	MPN362	Venezuela	Nelsen et al. 2014	–	KM453797	KM453861

Pseudopyrenula diluta	RL31068	MPN697	Brazil	Nelsen et al. 2014	–	KM453798	KM453862
Pseudopyrenula endoxanthoides	MFLU 20-0542		Thailand	Thiyagaraja et al. 2021	–	MZ206304	MZ221618
Pseudopyrenula endoxanthoides	MPN573	MPN573	Thailand	Lücking et al. 2016	–	–	KX215595
Pseudopyrenula subgregaria	MN4082b	MPN391	USA	Nelsen et al. 2014	–	KM453799	KM453863
Pseudopyrenula subgregaria	MPN565	MPN565	Thailand	Lücking et al. 2016	–	–	KX215596
Pseudopyrenula subgregaria	MPN568	PMN568	Thailand	Lücking et al. 2016	–	KX215684	KX215597
Pseudopyrenula subgregaria	RL24079	MPN106	Thailand	Nelsen et al. 2009	–	GU327724	GU327699
Pseudopyrenula subgregaria	RL27014	MPN297	Panama	Lücking et al. 2016	–	KX215683	–
Pseudopyrenula subnudata	RL17619		Costa Rica	del Prado et al. 2006	–	–	DQ328997
Pseudopyrenula subnudata	RL27014r1	MPN293	Panama	Nelsen et al. 2014	–	KM453801	KM453865
Pseudopyrenula subnudata	RL27053	MPN292	Panama	Nelsen et al. 2014	–	KM453800	KM453864
Trypethelium eluteriae	CP81	CP81	Thailand	Luangsuphabool et al. 2016b	AB753017	–	AB755065
Trypethelium eluteriae	GD19348		China	Yao et al. 2020	MT420847	MT420792	–
Trypethelium eluteriae	L45	L45	Thailand	Luangsuphabool et al. 2016b	AB753051	–	AB755075
Trypethelium eluteriae	MPN562	MPN562	Thailand	Lücking et al. 2016	–	KX215685	KX215598
Trypethelium platystomum	DCD20	DCD20	Thailand	Luangsuphabool et al. 2016b	AB753020	–	AB755068
Trypethelium platystomum	TSL36	TSL36	Thailand	Luangsuphabool et al. 2016b	AB758895	–	AB759869
Viridothelium tricolor	MPN646	MPN646	Panama	Nelsen et al. 2014	–	KM453780	KM453845
Viridothelium tricolor	RL32241	MPN399	Venezuela	Nelsen et al. 2014	–	KM453779	KM453844
Viridothelium virens	MPN497	MPN497	USA	Nelsen et al. 2014	–	KM453820	KM453884
Viridothelium virens	RAMK:030224	CM161	Thailand	Luangsuphabool et al. 2017	–	LC223102	LC223103

Etymology. We dedicate this species to André Aptroot on his 65th birthday for his extensive and groundbreaking contributions to the systematics of *Trypetheliaceae*.

Description. Non-lichenized on the bark of a living tree. Thallus inconspicuous, not changing the bark color, but clearly occupying a space and inducing a prothallus at contact areas with neighboring lichens. Photobiont not detected. Ascomata perithecial, solitary to frequently aggregate, but then not forming a pseudostroma and each perithecium clearly differentiated and apparently originating as a chronosequence, scattered, semi-immersed, ellipsoid to pyriform, black, 0.3–0.6 mm wide. Ostiole apical, brownish black, up to 40 µm wide. Wall without crystals, proper exciple apically and laterally carbonized, but basally yellowish. Involucrellum well defined, extending laterally, carbonized. Hamathecium not inspersed, IKI−, pseudoparaphyses persistent, branched and anastomosing, 0.8–1.5 µm diam., embedded in a gelatinous matrix. Asci bitunicate, cylindrical, tholus not amyloid, ocular chamber thickened, apically rounded, 8-spored, 65–95 × 10–15 µm. Ascospores biseriate to irregularly uniseriate in the asci, narrowly ellipsoid, with rounded ends, hyaline, 17–21 × 6–7.5 µm (n = 21), 1-septate, endospore thin, strongly constricted in the middle of each cell, cells of similar size, but sometimes the upper cell is larger, spore wall smooth, I−. Pycnidia not observed.

Ecology and distribution. The species is so far only known from the type locality in a tropical dry forest surrounding the Chamela-Cuixmala Biosphere Reserve. The area contains abundant crustose lichen communities in the families *Arthoniaceae*, *Graphidaceae*, and *Pyrenulaceae* (Herrera-Campos et al. 2019; Miranda-González & McCune 2020). All samples were associated with smooth bark on living trees. No photobiont was conspicuously associated with the species, but the genus was previously described as a semilichen (Vondrák et al. 2026).

Notes. *Alloarthopyrenia aptrootiana* resembles diverse species with constricted cells in the ascospores that represent various early diverging lineages in the *Trypetheliaceae*. The sister species, *A. italica* (see below), has larger ascospores of 18–22(24) × 8–12 µm (Thiyagaraja et al. 2021), the upper cell of the ascospores is typically larger, and it occurs in temperate ecosystems. There are few available DNA sequences for these two species, but the *mtSSU* alignment shows several identical positions in all sequences of *A. italica* that change in the only available sequence of *A. aptrootiana* (Appendix B: alignment positions 71–72, 116, 246–248, 250, 464, 472, etc.). *Arthopyrenia plumbaria* (Stizenb.) R.C. Harris probably belongs in *Alloarthopyrenia* as well, but it has slender ascospores of 4.5–6.5 µm with mostly pointed ends. The lichenized genera *Constrictolumina* Lücking, M.P. Nelsen & Aptroot and *Macroconstrictolumina* Lücking, R. Miranda & Aptroot share the ascospores with constricted cells, but their ascospores tend to become 3-celled at old age, are typically larger, and in the case of *Macroconstrictolumina* are granularly ornamented (Aptroot & Lücking 2016; Hongsanan et al. 2020).

Additional specimen examined (paratype). MEXICO. Jalisco, Tomatlán Mun., San Carlos Coacoyul. 20°07′48.3″N, 105°32′11.1″W, 78 m, 14 Mar. 2013., M.A. Herrera-Campos et al. 2013 #1609 (MEXU).

Resolving the taxonomic concepts of *Alloarthopyrenia italica* and *Arthopyrenia cinereopruinosa*

Alloarthopyrenia aptrootiana is only the second species confirmed to belong in this early diverging genus of *Trypetheliaceae*. The genus was originally established for a single new species, *A. italica* (Hyde et al. 2016). Apart from a comparison with *Arthopyrenia cerasi*, the type of *Arthopyrenia*, these authors distinguished the new species from the morphologically similar *Arthopyrenia cinereopruinosa* based on presumably 3-septate ascospores in the latter, referring to Coppins (1988) and Aptroot et al. (2008). However, Coppins (1988) described *A. cinereopruinosa* as 1-septate (though with distinct secondary invaginations), following Harris (1975), and Aptroot et al. (2008) do not mention the species. The concept

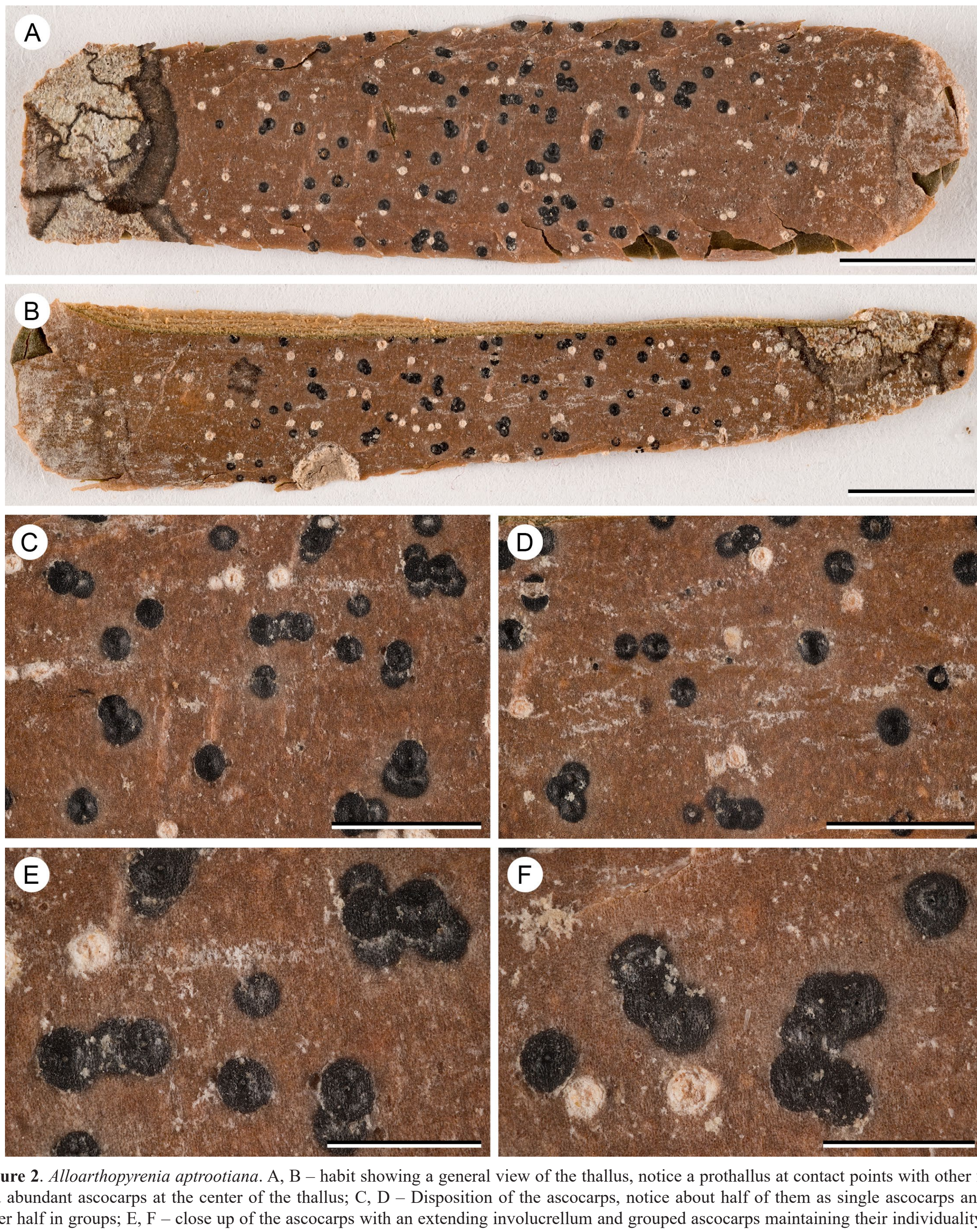

Figure 2. *Alloarthopyrenia aptrootiana*. A, B – habit showing a general view of the thallus, notice a prothallus at contact points with other fungi and abundant ascocarps at the center of the thallus; C, D – Disposition of the ascocarps, notice about half of them as single ascocarps and the other half in groups; E, F – close up of the ascocarps with an extending involucrellum and grouped ascocarps maintaining their individuality and develop in the vicinity at different points in time. Scales: A, B = 5 mm; C, D = 2 mm; E, F = 1 mm. Specimens: A, C, E, F – M.A. Herrera-Campos et al. 2013 # 1608 (holotype, MEXU); B, D – M.A. Herrera-Campos et al. 2013 # 1609 (MEXU).

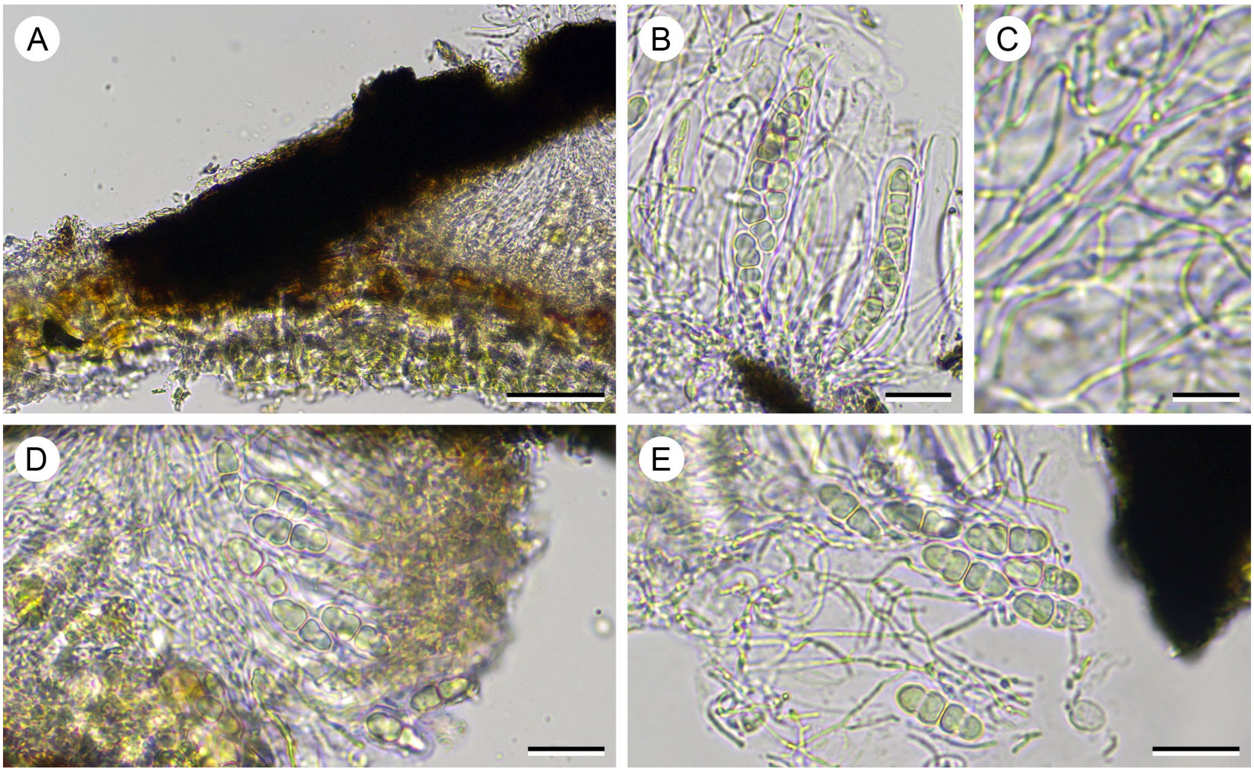

Figure 3. *Alloarthopyrenia aptrootiana*. A – section of ascocarp showing an extended involucrellum and a lack of basal carbonization; B – bitunicate asci with a thickened ocular chamber, cylindrical; C – branching pseudoparaphyses showing anastomose; D, E – hyaline ascospores with strong constrictions in the middle of each. Scales: A = 50 µm; B, D, E = 20 µm; C = 10 µm. Specimens: A, D – M.A. Herrera-Campos et al. 2013 # 1609 (MEXU); B, C, E – M.A. Herrera-Campos et al. 2013 # 1608 (holotype, MEXU).

of a 3-septate *A. cinereopruinosa* was likely based on presumed type material of *V. caesiopruinosa*, which contained drawings of 3-septate ascospores, as outlined in Thiyagaraja et al. (2021). However, the latter authors concluded that the presumed 3-septate type in H (Switzerland, Schaerer s.n., H-NYL 6684) could not be original, giving its collection date of 1850 vs. the original description of *Verrucaria cinereopruinosa* much earlier by Schaerer (1836). Indeed, the 3-septate type from 1850 in H belongs to the unrelated species *Arthonia cinereopruinosa* Schaer. (now *Leprantha cinereopruinosa* (Schaer.) Körb.), but was mistakenly annotated as "≡ *Arthopyrenia cinereopruinosa*".

When describing *Verrucaria cinereopruinosa*, Schaerer (1836) cited three collections with deviating previous identifications: *V. stigmatella* [Schleicher 1813], *V. byssacea* var. *stictica* [Schleicher 1813], and *Arthonia radiata* var. *tynnocarpa* [Schleicher 1815]. Only the first and the last are extant (in G) and are available in digital form from JSTOR Global Plants [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00290378; https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00290379]. Schaerer (1836) also included the name *V. cinereopruinosa* var. *galactina*, but that taxon is currently a synonym of the unrelated *Arthonia galactites* (DC.) Dufour, which further shows that Schaerer´s species concept of *V. cinereopruinosa* was very rough. Apparently, the name *Verrucaria cinereopruinosa* was never lectotypified and the very rudimentary description by Schaerer (1836), lacking anatomical details, neither allows for determining its exact taxonomy nor ties any of the syntypes definitely to the name. Later treatments, including Massalongo (1855) and Körber (1855), who both independently transferred *V. cinereopruinosa* to *Arthopyrenia* and described its ascospores as bilocular, did not provide descriptions based on the actual type material. Likewise, Harris (1975) stated that the type was not seen by him. It is therefore unclear what the basis was for the description and taxonomic concept first laid out by Harris (1975) and later followed by European authors (Coppins 1988), giving 1-septate ascospores with secondary constrictions in each cell as one of the diagnostic characters.

Revision of the two specimens held in G revealed that the collection previously identified as *Arthonia radiata* var. *tynnocarpa* [Schleicher 1815] is very poorly developed and does not represent a pyrenocarpous taxon; its tiny, ascomata-like structures are arthonoid rather than pyrenocarp, but contain no discernable structures. In contrast, the material previously identified as *Verrucaria stigmatella* [Schleicher 1813] is well developed and contains an arthopyrenoid taxon with the following characteristics (Figs 4, 5):

Thallus very thin, endoperidermal, greyish brown (color of the bark), not discernably lichenized. Perithecia abundant, black, usually clustered (and laterally fused) in groups of 3–5; individual perithecia hemispherical, 0.15–0.3 mm diam., basally slightly expanding and partly covered by a thin thallus cortex. Excipulum prosoplectenchymatous, inner parts colorless, outer parts brownish, covered by a (dark) brown involucrellum, the latter K– (remaining brown); upper part of the excipulum/involucrellum with short periphysoids resembling the paraphyses. Paraphyses mostly unbranched, distinctly septate, 1.5–2 μm thick, not gelatinized; asci broadly clavate to pyriform, broadest above or at the middle, 45–60 × 15–20 μm. Ascospores 1-septate, narrowly obovate, the terminal cell rounded, the distal cell somewhat acute, not different in size and lacking secondary constrictions, 14–17 × 5–8 μm, about 2–3 times as long as broad, colorless, lacking ornamentations. Pycnidia not observed.

Based on the above characters, especially the rather atypical, mostly unbranched paraphyses and the clustered perithecia, the material cannot be identified with any of the species of *Arthopyrenia* treated by Harris (1975). It is clearly not conspecific with the concept of *A. cinereopruinosa* laid out by Harris (1975). While it is possible that the second, apparently now lost collection listed in the protologue, named *V. byssacea* var. *stictica* [Schleicher 1813], corresponds to *A. cinereopruinosa* sensu Harris (1975), we consider this not likely, given that the other two collections are already quite disparate and represent unrelated taxa. If the name *A. cinereopruinosa* is lectotypified with the specimen described above, the concept of that taxon based on Harris (1975) and Coppins (1988) will be rendered incorrect. However, this does not create a substantial nomenclatural disruption, as the name *Alloarthopyrenia italica* has already been accepted for the taxon previously treated under the name *Arthopyrenia cinereopruinosa* by several authors.

An attempt to identify the material described above with another existing name in other sources failed. No taxon with such characteristics is keyed out in the *Flechten Deutschlands* (Wirth et al. 2013). The interactive keys in Italic 8.0 (Nimis & Martellos 2020) lead to *Naetrocymbe rhododendri* as the best result [https://italic.units.it/index.php?procedure=taxonpage&num=1510], but the ascospore shape (longer and slender) does not fit. The key to species of *Arthopyrenia* in the *Lichen Flora of Great Britain and Ireland* (Purvis et al. 1992; Smith et al. 2009; Orange 2013) also has no matching taxon, especially not with ascospores as short and wide as in the present material. Two possibly similar taxa with apparently clustered perithecia, both considered synonyms of *Naetrocymbe punctiformis*, are *Arthopyrenia cembrina* (Anzi) Grummann ex D. Hawksw. and *A. pyrenastrella* (Nyl.) Norman. Both have been described with longer and narrower ascospores (19–25 × 4 μm in *A. cembrina*; 17–25 × 5–6 μm in *A. pyrenastrella*). We also explored the option of this being a species of *Mycoporum*, given the laterally fused perithecia. In particular, *M. eschweileri* has somewhat similar ascospore dimensions, though a bit longer (Harris 1975, 1995). However, in *Mycoporum*, the perithecia or chambers are typically much smaller, with chambered rather than laterally fused perithecia, and the type of interascal hyphae is different.

Therefore, we consider the lectotypification of the name *Verrucaria cinereopruinosa* with the only available and suitable syntype justified and propose the following new combination for this apparently unique and little-known, taxonomically intriguing species.

Natreocymbre cinereopruinosa (Schaer.) Lücking, R. Miranda, Herrera-Camp. & Campos-Cerda, comb. nov. (Figs 4, 5)

MycoBank MB 864420

Basionym: *Verrucaria cinereopruinosa* Schaer. [as '*cinereo-pruinosa*'], Lich. Helv. Spicil. 7: 343. 1836; *Arthopyrenia cinereopruinosa* (Schaer.) A. Massal. [as '*cinereo-pruinosa*'], Symmict. Lich.: 117. 1855; non *Arthonia cinereopruinosa* Schaer. [as '*cinereo-pruinosa*'], Enum. Critic. Lich. Europ. (Bern): 243. 1850 [≡ *Leprantha cinereopruinosa* (Schaer.) Körb.]; non *Arthopyrenia cinereopruinosa* auct., non Harris (1975) nec Coppins (1988) [= *Alloarthopyrenia italica* Phukhamsakda, Camporesi, Ariyawansa & K.D. Hyde, in Hyde et al., Fungal Diversity 80: 135. 2016].

Type: Switzerland, unknown locality; 1813, Schleicher s.n. (G G00290378) [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00290378]; previously identified (on label) as *Verrucaria stigmatella*; Lectotype, here designated.

Description. See above; diagnostic characters are clustered, laterally fused perithecia; brown, K-negative involucrellum; persistent, sparsely branched, rather thick, distinctly septate, non-gelatinizing paraphyses; broadly clavate to pyriform asci up to 60 μm long; and 1-septate, narrowly obovate ascospores, with the terminal cell rounded, the distal cell somewhat acute, lacking secondary constrictions, 14–17 × 5–8 μm, about 2–3 times as long as broad.

Resolving the phylogenetic position of *Mycomicrothelia confusa*

The genus *Mycomicrothelia* Keissl. was separated into several genera, with most of its species now placed in *Bogoriella* (Aptroot & Lücking 2016) and *Pseudobogoriella* (Hongsanan et al. 2020). Currently only eight

Figure 4. Lectotype (here selected) of *Naetrocymbe* (*Verrucaria*) *cinereopruinosa*, showing specimen mount, label, and barcode.

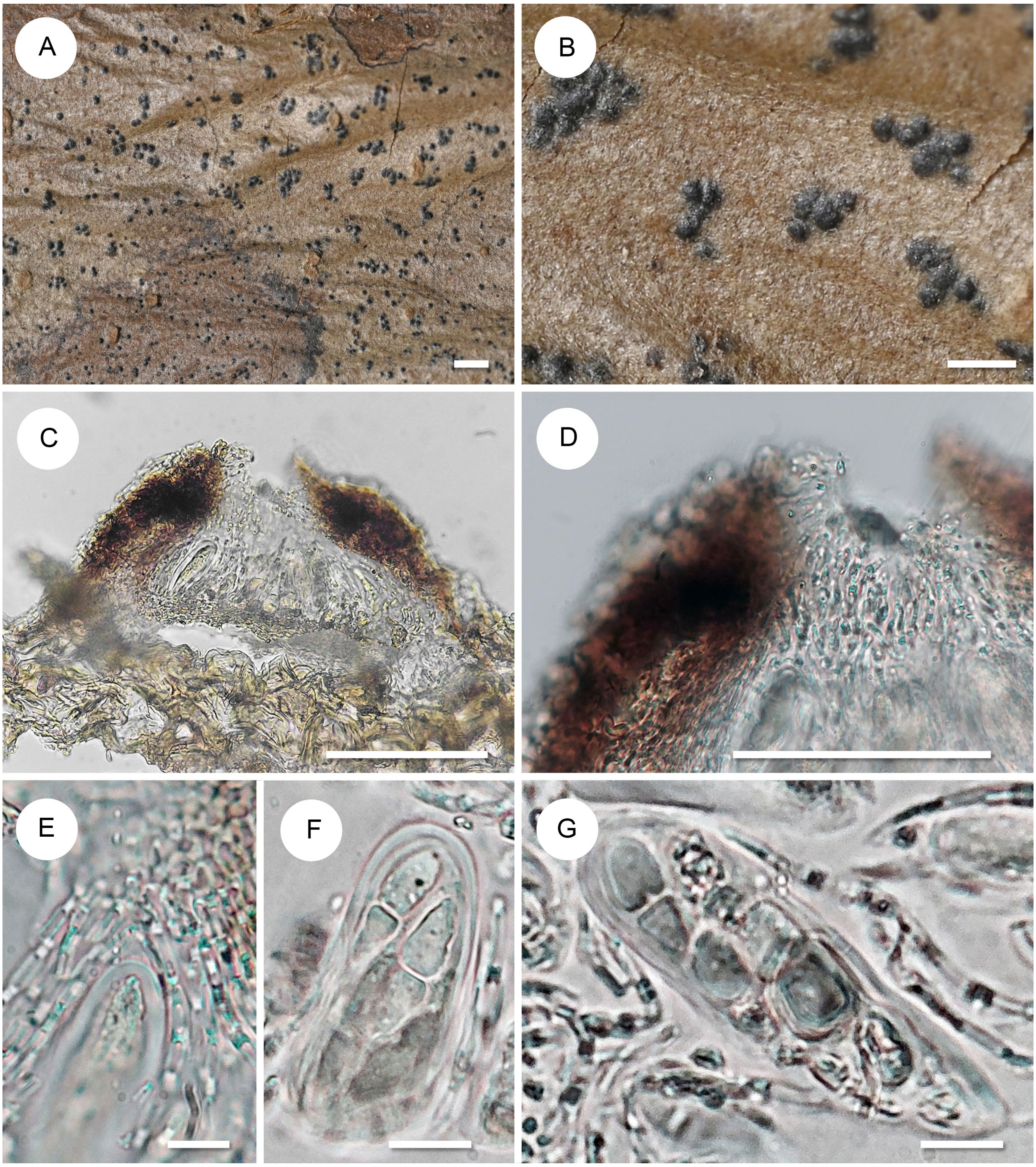

Figure 5. Lectotype (here selected) of *Naetrocymbe* (*Verrucaria*) *cinereopruinosa*. A, B – thallus with groups of fused perithecia, in B enlarged; C, D – section through perithecium showing involucrellum and hamathecium with asci, in D enlarged to show the apical periphysoids; E – immature ascus (tip) surrounded by septate, non-gelatinized, sparsely branched paraphyses; F, G – ascus with ascospores. Scales: A, B = 1 mm; C, D = 100 µm; E–G = 10 µm.

species remain in *Mycomicrothelia* and two of those, *M. confusa* and *M. wallrothii*, were recently sequenced (Vondrák et al. 2023). Unfortunately, there is no available molecular data for the type species *M. macularis* and only a nuITS sequence for *M. wallrothii*. Given that there are very few sequences of nuITS for *Trypetheliaceae* and that the topology of the phylogenetic tree is mostly resolved by the mtSSU, we decided not to include *M. wallrothii* in our concatenated phylogenetic analysis. However, a very preliminary phylogeny using only nuITS suggests that although both *M. wallrothii* and *M. confusa* are members of the *Trypetheliaceae*, they are not congeneric.

For the case of *M. confusa*, our phylogenetic results show that it belongs in the clade of *Pseudobogoriella* s.str. (Fig. 1). Most species previously in *Mycomicrothelia* are now in *Pseudobogoriella* and *M. confusa* shares their diagnostic small ascospores with fine ornamentation and without endospore thickenings (Hongsanan et al. 2020). For these reasons, we propose the following new combination.

Pseudobogoriella confusa (D. Hawksw.) R. Miranda, Lücking, Herrera-Camp. & Campos-Cerda, comb. nov.

MycoBank MB 864559

Basionym: *Mycomicrothelia confusa* D. Hawksw., Bull. Br. Mus. Nat. Hist., Bot. 14(2): 76. 1985.

Type: United Kingdom, Scotland, 1968, P.W. James 13 May 1968 (BM).

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Supplementary electronic materials

Appendix A. Concatenated alignment of the molecular markers nuITS, nuLSU and mtSSU used for the phylogenetic analyses. Download file

Appendix B. Alignment of the molecular marker mtSSU including all known sequences of *Alloarthopyrenia*. Download file

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