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Standard Paper

High diversity of *Bacidia* (*Ramalinaceae*, *Lecanorales*) species in the Caucasus as revealed by molecular and morphological analyses

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Abstract

During a study of the incompletely known lichen flora of the Caucasus, we analyzed 237 specimens of corticolous *Bacidia* s. str. collected in the Northern and Southern Caucasus, including Armenia, Azerbaijan, Georgia, and Russia. Of these, 54 specimens belonging to 11 species of *Bacidia* s. str. were selected for molecular studies, representing the observed morphological variability of the genus. We obtained 142 sequences from three RNA-coding genes (nrITS, nrLSU, and mtSSU) and two protein-coding genes (*RPB*1 and *RPB*2). The single and concatenated datasets were complemented with *Bacidia* s. str. sequences from GenBank and subjected to Bayesian inference and two maximum likelihood analyses (RAxML and IQ-TREE). The resulting trees yielded highly concordant topologies of the groups and corresponded with previous results, supporting two main clades correlating with apothecia pigmentation. Our analyses are the first to reveal the presence of *Bacidia heterochroa* in the Caucasus. An exceptionally high degree of morphological plasticity was found in the Rubella and Suffusa groups. As a result of morphological examination and phylogenetic results, *B. caucasica* (Suffusa group) was described as new to science. Furthermore, two putative taxa in the Rubella group, *Bacidia inconspicua* ined. and *B. maritima* ined., were introduced. This study furthers our understanding and documentation of the understudied lichen flora of the Caucasus, bringing the total number of *Bacidia* species for the region to 13.

Keywords: *Bacidia* s. str.; crustose lichens; new species; phylogeny; taxonomy

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Introduction

The crustose lichen genus *Bacidia* De Not. s. lat. is distributed worldwide and includes up to 230 species (Lücking *et al.* 2017; Wijayawardene *et al.* 2022). *Bacidia* diversity is most comprehensively documented in Europe due mainly to the accessibility and long tradition of lichenology in the region. Species have been recorded in many European lichen floras, for example, in areas of Germany, the British Isles, and the Iberian Peninsula (e.g. Llop 2007; Wirth *et al.* 2013; Cannon *et al.* 2021), and *Bacidia* diversity is also widely studied in North America (Ekman 1996). However, the diversity of *Bacidia* in Asia and the Caucasus remains largely unknown.

The Caucasus region harbours a rich, relict tertiary flora due to its unique environmental conditions that have remained stable for a long time. One of the first lichen checklists for the Caucasus region was made by Vainio (1899) based on the Caucasian collection of Déchy and Lojka, which included several specimens of *Bacidia* s. lat. In the 20th century, extensive research on the Caucasus flora was carried out by Barkhalov (1975, 1983), and by Vězda who worked particularly in the Caucasian reserve on the Black Sea coast and Abkhazia (Vězda 1983); these accounts also documented several species of *Bacidia* s. lat. More recently, *Bacidia* species have been reported in many lichenofloristic papers and checklists of the Caucasus covering northern (Urbanavichus & Urbanavichene 2002, 2017*b*, 2018; Urbanavichene & Urbanavichus 2019; Urbanavichus *et al.* 2021), north-western (Otte 2001, 2004, 2007*a*, *b*; Blinkova & Urbanavichus 2005; Urbanavichus & Urbanavichene 2014, 2017*a*), western (Urbanavichene & Urbanavichus 2016; Urbanavichus *et al.* 2020), south-western (Urbanavichene & Urbanavichus 2014), north-eastern (Urbanavichus & Ismailov 2013), central (Urbanavichene & Urbanavichus 2018), eastern (Ismailov *et al.* 2017), and southern (Harutyunyan *et al.* 2011; Alverdiyeva & Novruzov 2014; Gasparyan & Sipman 2016; Inashvili *et al.* 2022) parts of the region.

Urbanavichus (2010) was the first to compile data on lichens known for the Russian territory (incorporating the Caucasus), including 18 species of *Bacidia* s. lat. in the checklist currently known from the Caucasus. In subsequent studies, nearly half of these species were transferred to other genera, such as *Aquacidia*, *Bacidina*, *Bellicidia*, *Biatora*, *Bibbya*, *Catillaria*,

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Scutula and *Toniniopsis*, and several new species were later described or recorded for the region (Urbanavichus & Urbanavichene 2014; Urbanavichene & Urbanavichus 2016; Kistenich *et al.* 2018; Malíček *et al.* 2018; Cannon *et al.* 2021; Gerasimova *et al.* 2021*a*). In addition, several species have been synonymized and/or recognized as belonging to other genera, such as *Arthrorhaphis*, *Haematomma*, *Lecania* and *Scoliciosporum* (Davydov & Printzen 2012; Gerasimova & Ekman 2017). Yet, the taxonomic position of some species is still unknown, such as *Bacidia freshfieldii* (Vain.) Zahlbr., which appears to be closely related to *Catillaria* (Gerasimova & Ekman 2017). As such, at the beginning of our investigation 11 species of *Bacidia* s. str. were known from the Caucasus: *Bacidia absistens* (Nyl.) Arnold, *B. albogranulosa* Malíček *et al.*, *B. arceutina* (Ach.) Th. Fr., *B. biatorina* (Körb.) Vain., *B. fraxinea* Lönnr., *B. herbarum* (Stizenb.) Arnold, *B. laurocerasi* (Delise ex Dube) Zahlbr., *B. polychroa* (Th. Fr.) Körb., *B. rosella* (Pers.) De Not., *B. rubella* (Hoffm.) A. Massal. and *B. suffusa* (Fr.) A. Schneid. However, a revision of the genus integrating molecular and morphological analysis was needed to comprehensively document the diversity of *Bacidia* in the region. Therefore, our research aimed to investigate the diversity of *Bacidia* s. str. in the Caucasus by applying an integrative approach, including morphological, anatomical, and molecular analyses.

Material and Methods

Study area and sampling

The Caucasus is located between the Caspian and the Black Seas and is bounded on the north by Russia (Kumo-Manych Depression) and on the south by Georgia, Armenia and Azerbaijan (Brummitt *et al.* 2001). The climatic conditions of the Caucasus range from warm and moist in the western Colchic region to hot and dry (Kura valley) in the east, spanning eight of the ten oceanity levels of the Northern Hemisphere, compared to only four observed in the Alps, according to the system of Jäger (1968).

The specimens of *Bacidia* were mainly collected in the National Parks and Nature Reserves of the Northern Caucasus (Russia), namely in and around the Nature Reserve Bol'shoy Tkhach and the Caucasian Biosphere Reserve (1999–2019), Utrish (2001–2020), Erzi (2018) and Samursky National Park (2017), but also in Georgia (2012, 2015), Azerbaijan (2013) and Armenia (2015).

We studied the morphology of 237 specimens of *Bacidia* s. str. collected in the Caucasus (Supplementary Material File S1, available online). Of these, we obtained molecular sequences from 54 specimens belonging to 10 species and two putatively introduced, provisional taxa (*B. inconspicua* ined. and *B. maritima* ined.) of *Bacidia* s. str. that were representative of the known species diversity and inter- and infra-specific morphological variability. The only exception to this was *B. herbarum*, which we were not able to include in the molecular analysis as it is known only from one herbarium specimen (GLM-L-0054141, collected in Krasnodarskiy Krai at 2115 m a.s.l.). The specimens sampled for molecular analysis were collected in the northern part of the Caucasus (64.2%), Azerbaijan (20.7%), Georgia (9.4%), and Armenia (5.7%) from the bark of various phorophytes (Table 1).

Morphology

Microscopic observations were made using a Zeiss Axioplan (Oberkochen, GmbH) light microscope equipped with differential interference contrast (DIC). Cross sections of apothecia were made on a Leica Jung Histoslide 2000 Mikrotom (Heidelberg, GmbH), with a thickness of 8–10 µm. Micrographs of cross-sections were taken on a Zeiss Axioplan with an attached AxioCam 512 Color camera, and images were processed with Zeiss ZEN v. 2.3 (blue edition). Macrographs of external characters were taken on a Leica Z6 Apo microscope (with a 2.0× Planapo lens; Leica, Germany) with a Sony Alpha 6400 camera (Sony, Japan) attached and equipped with a Stack Shot Rail macro rail (Cognisys, USA). A single image was mounted from 30–40 serial images using Helicon Focus v. 7 (Helicon, USA).

Measurements are given as (min–) $\bar{x}$ ± SD (–max) (SD = standard deviation, n_1 = number of all observations, n_2 = number of specimens observed). We provide a detailed description of specimens using traditional microscopic techniques following Smith *et al.* (2009) and the subdivision scheme of the proper exciple according to Ekman (1996), differentiating the following structures: rim, lateral part, and medullary part. We used the following diagnostic characters to delimit the species lineages: 1) thallus structure; 2) colour of disc and margin of apothecium; 3) hypothecium colour; 4) colour and structure of exciple; 5) shape and size of ascospores. The standard reagents were used to study the colour reaction of the apothecia cross-sections and crystals solubility: a solution of 10% potassium hydroxide (KOH) in water, abbreviated K, and 50% solution of nitric acid (HNO_3), abbreviated N. Pigment characterizations follow Meyer & Printzen (2000).

DNA extraction, PCR amplification and DNA sequencing

DNA extraction was carried out using the Stratec Invisorb Spin Plant Mini Kit (Stratec Molecular GmbH, Berlin) following the manufacturer's instructions. Five to eight apothecia were used from fresh material not older than five years, and thallus fragments were removed to minimize the risk of contamination by, for example, lichenicolous fungi. The same five target loci (three RNA-coding genes (nrITS, nrLSU, and mtSSU) and two protein-coding genes (*RPB*1 and *RPB*2)) as in Gerasimova *et al.* (2021*a*) have been selected for PCR; amplification, purification and sequencing were performed as described in Gerasimova *et al.* (2018). Cycling conditions included initial denaturation at 95 °C for 2 min, 5 cycles of 95 °C for 40 s, 54 °C for 60 s, 72 °C for 90 s, 33 cycles of 95 °C for 40 s, 54 °C for 60 s, 72 °C for 90 s, and a final extension step at 72 °C for 7 min. In cases where the concentration of PCR product was not sufficient, a second PCR with a reduced number of cycles was conducted: denaturation at 95 °C for 2 min, 5 cycles of 95 °C for 40 s, 54 °C for 60 s and 72 °C for 90 s, 22 cycles of 95 °C for 40 s, 54 °C for 60 s and 72 °C for 90 s, with a final extension step at 72 °C for 7 min. We used five pairs of primers: ITS1F (Gardes & Bruns 1993) and ITS4m (Beck & Mayr 2012), LR0R (Rehner & Samuels 1994) and LR5 (Vilgalys & Hester 1990), mtSSU1 and mtSSU3R (Zoller *et al.* 1999), fRPB2-5F and fRPB2-7cR (Liu *et al.* 1999) and newly designed primers gRPB1AFba (GAGTG YCCGGGACATTTTGG) and fRPB1cRba2 (GSCCRGCAATRT CGTTATCCA) for *Bacidia*.

Alignment and phylogenetic analyses

We obtained 142 sequences of *Bacidia* s. str. from the Caucasus, augmented the dataset with sequences of *Bacidia* s. str. from GenBank (Table 1) and included *Sporacestra borbonica* comb.

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Table 1. DNA numbers and specimen information for *Bacidia* species used in this study, with their respective GenBank Accession numbers. New sequences are in bold.

DNA no. (JG)	Name	Country	Specimen voucher/isolate	GenBank Accession Number				
				nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2
JG123	*Bacidia absistens*	Russia	*Urbanavichus* & *Urbanavichene* M-0311923 (M)	**MW523506**	**MW489423**			**MW522879**
	B. absistens	Norway	*Ekman* 3223 (BG)	AF282085		MG925845	MG926139	MG926229
	B. albogranulosa	Czech Republic	*Vondrák* 17113 (PRA)	MK158339		MK158334		
	B. albogranulosa	Russia	*Malíček* 9622 (hb. Malíček)	MK158340		MK158335		
	B. albogranulosa	Czech Republic	*Vondrák* 11888 (PRA)	MK158342		MK158332		
	B. albogranulosa	Czech Republic	*Vondrák* 11889 (PRA)	MK158341		MK158333		
	B. albogranulosa	Czech Republic	*Malíček* 8013 (hb. Malíček)			MK158336		
	B. albogranulosa	Ukraine	*Vondrák* 12235 (PRA)			MK158337		
	B. albogranulosa	Czech Republic	*Vondrák* 12865 (PRA)			MK158338		
JG126	*B. arceutina*	Georgia	*Gagarina* M-0182569 (M)	**MW523507**				
JG163	*B. arceutina*	Russia	*Otte* GLM-0048917 (GLM)	**MW523508**	**MW489424**	**MW506364**	**MW540436**	**MW522880**
	B. arceutina	Sweden	*Ekman* 3110 (BG)	AF282083	MG926041	MG925846	MG926140	MG926230
	B. arceutina	Switzerland	*van den Boom* (LG DNA 579)	JQ796851	JQ796842	JQ796829		
	B. arceutina	United Kingdom	EDNA09-01505	FR799125				
	B. arceutina	United Kingdom	EDNA09-01507	FR799126				
	B. arceutina	United Kingdom	EDNA09-01587	FR799127				
JG037	*B. areolata*	Russia	*Gerasimova* M-0182592 (M)	MH048614		MW506357	MW540434	MW522875
JG114	*B. areolata*	Russia	Davydov 17428 & Yakovchenko (ALTB)	MW491455		MW506358		
JG006	*B. biatorina*	Georgia	*Gerasimova* M-0182570 (M)	**MW523509**				
JG122	*B. biatorina*	Russia	*Urbanavichene* & *Urbanavichus* M-0311922 (M)	**MW523510**	**MW489425**	**MW506365**	**MW540437**	**MW522881**
JG164	*B. biatorina*	Russia	*Otte* GLM-0053198 (GLM)	**MW523511**	**MW489426**	**MW506366**	**MW540438**	**MW522882**
	B. biatorina	Sweden	*Knutsson* 94-148 (hb. Knutsson)	AF282079				
JG182	*B. caucasica*	Russia	*Otte* GLM-0048447 (GLM)	**MW523553**	**MW489444**	**MW506388**		
JG083	*B. diffracta*	USA	*Wetmore* 46555-A (M)	MH048620				
	B. diffracta	USA	*Wetmore* 26401 (MIN)	AF282090				
	B. ekmaniana	USA	*Lendemer* 33836 (NY)			KX151741		
	B. ekmaniana	USA	*Lendemer* 33920 (NY)			KX151743		
	B. ekmaniana	USA	*Lendemer* 30488A (NY)			KX151746		
	B. ekmaniana	USA	*Lendemer* 31362 (NY)			KX151744		
	B. ekmaniana	USA	*Lendemer* 33783 (NY)			KX151745		
	B. ekmaniana	USA	*Lendemer* 34000 (NY)			KX151742		

(*Continued*)

Table 1. (*Continued*)

DNA no. (JG)	Name	Country	Specimen voucher/isolate	GenBank Accession Number				
				nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2
JG007	*B. elongata*	Russia	*Ezhkin* M-0182571 (M)	MH048626				
JG101	*B. elongata*	Russia	*Ezhkin* M-0182625 (M)	MH048627	MW493329	MW506351	MW540430	MW522870
JG102	*B. elongata*	Russia	*Ezhkin* M-0182626 (M)	MH048628	MW493330	MW506352		MW522871
JG103	*B. elongata*	Russia	*Ezhkin* M-0182627 (M)	MH048629				
JG049	*B. fraxinea*	Russia	*Urbanavichene* L-15337 (LE)	**MW523519**				
JG170	*B. fraxinea*	Russia	*Otte* GLM-0044145 (GLM)	**MW523521**	**MW489428**	**MW506373**	**MW540441**	**MW522886**
JG205	*B. fraxinea*	Russia	*Urbanavichene* & *Urbanavichus* L-15341 (LE)	**MW523522**	**MW489429**	**MW506374**		**MW522887**
	B. fraxinea	Sweden	*Johansson* 1620 (BG)	AF282088				
	B. fuscopallida	Korea	KBA-L-0001010	ON352607				
	B. fuscopallida	Korea	KBA-L-0001049	ON352608				
	B. gigantensis	Canada	Isolate MCM240			MT425199		
	B. gigantensis	Canada	Isolate MCM242	MT425200		MT425196		
	B. hostheleoides	United Kingdom	*Seaward* 1996 (priv. hb. no. 108121)	AF282081				
JG010	*B. heterochroa*	Georgia	*Gerasimova* M-0182575 (M)	**MW523515**		**MW506369**		
JG120	*B. heterochroa*	Georgia	*Gerasimova* M-0182575 (M)	**XXXXXX**				
JG128	*B. heterochroa*	Georgia	*Gagarina* L-11635 (LE)	**MW523516**		**MW506370**		
JG167	*B. heterochroa*	Russia	*Otte* GLM-0048909 (GLM)	**MW523517**		**MW506371**		**MW522884**
JG168	*B. heterochroa*	Russia	*Otte* GLM-0048864 (GLM)	**MW523518**				
	B. heterochroa	Korea	KBA-L-0000386	ON352606				
	B. heterochroa	Korea	KBA-L-0002727	ON352612				
	B. heterochroa	Korea	KBA-L-0002734	ON352613				
JG130	*B. inconspicua* ined.	Russia	*Urbanavichene* & *Urbanavichus* M-0311925 (M)	**MW523520**	**MW489427**	**MW506372**	**MW540440**	**MW522885**
	B. inconspicua ined.	Ukraine	*Vondrák* 12200 (PRA)	MK158343		MK158331		
JG092	*B. kurilensis*	Russia	*Ezhkin* M-0182620 (M)	MH048610	MW493325	MW506348	MW540427	MW522868
JG095	*B. kurilensis*	Russia	*Ezhkin* M-0182621 (M)	MH048611	MW493326			
JG096	*B. kurilensis*	Russia	*Ezhkin* M-0182622 (M)	MH048612				
JG091	*B. laurocerasi*	Russia	*Galanina* M-0311952 (M)	MH048609				
JG211	*B. laurocerasi*	Russia	*Ezhkin* M-0308500 (M)	MW491460		MW506349		
JG124	*B. laurocerasi*	Russia	*Urbanavichene* & *Urbanavichus* M-0311924 (M)	**MW523512**		**MW506367**		
JG165	*B. laurocerasi*	Russia	*Otte* GLM-0048211 (GLM)	**MW523513**	**MW489426**	**MW506366**	**MW540438**	**MW522882**
JG166	*B. laurocerasi*	Russia	*Otte* GLM-0053624 (GLM)	**MW523514**				

(*Continued*)

Table 1. (*Continued*)

DNA no. (JG)	Name	Country	Specimen voucher/isolate	GenBank Accession Number				
				nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2
	B. laurocerasi subsp. *laurocerasi*	USA	*Wetmore* 74318 (MIN)	AF282078				
	B. laurocerasi subsp. *laurocerasi*	Alaska	*Spribille* 26334 (KLGO)	MN483106	MN460211	MN508264		
	B. lutescens	USA	*Ekman* L1161 (LD)	AF282082				
JG131	*B. maritima* ined.	Georgia	*Gerasimova* M-0182578 (M)	**MW523523**				
JG172	*B. maritima* ined.	Azerbaijan	*Otte* GLM-0040829 (GLM)					**MW522890**
JG206	*B. maritima* ined.	Russia	*Urbanavichus* M-0311935 (M)	**MW523528**	**MW489432**	**MW506377**		**MW522893**
JG208	*B. maritima* ined.	Russia	*Urbanavichene* & *Urbanavichus* M-0311937 (M)	**MW523530**	**MW489434**	**MW506379**		**MW522895**
JG139	*B. obtecta*	Russia	*Ezhkin* M-0308498 (M)	MW491457	MW493335	MW506362		MW522877
JG140	*B. obtecta*	Russia	*Ezhkin* M-0308497 (M)	MW491458	MW493336	MW506363		MW522878
JG141	*B. obtecta*	Russia	*Ezhkin* M-0308496 (M)	MW491459				
JG136	*B. polychroa*	Russia	*Urbanavichus* & *Urbanavichene* M-0311928 (M)	**MW523531**	**MW489435**	**MW506380**	**MW540442**	
JG137	*B. polychroa*	Russia	*Urbanavichene* & *Urbanavichus* M-0311929 (M)	**MW523532**	**MW489436**	**MW506381**	**MW540443**	**MW522896**
JG169	*B. polychroa*	Russia	*Otte* GLM-0034608 (GLM)	**MW523533**	**MW489437**	**MW506382**	**MW540444**	**MW522897**
JG185	*B. polychroa*	Armenia	*Otte* GLM-0041577 (GLM)	**MW523534**				**MW522898**
JG186	*B. polychroa*	Russia	*Otte* GLM-0048845 (GLM)	**MW523535**				**MW522899**
JG187	*B. polychroa*	Russia	*Otte* GLM-0048844 (GLM)	**MW523536**				
JG188	*B. polychroa*	Russia	*Otte* GLM-0053439 (GLM)	**MW523537**	**MW489438**	**MW506383**		**MW522900**
JG189	*B. polychroa*	Russia	*Otte* GLM-0053126 (GLM)	**MW523538**	**MW489439**	**MW506384**	**MW540445**	**MW522901**
JG190	*B. polychroa*	Russia	*Otte* GLM-0048243 (GLM)	**MW523539**				**MW522902**
JG191	*B. polychroa*	Azerbaijan	*Otte* GLM-0052979 (GLM)	**MW523540**				
JG192	*B. polychroa*	Azerbaijan	*Otte* GLM-0053001 (GLM)	**MW523541**				
JG193	*B. polychroa*	Azerbaijan	*Otte* GLM-0039239 (GLM)	**MW523542**				
JG194	*B. polychroa*	Azerbaijan	*Otte* GLM-0038928 (GLM)	**MW523543**				**MW522903**
JG195	*B. polychroa*	Azerbaijan	*Otte* GLM-0039238 (GLM)	**MW523544**				**MW522904**
JG209	*B. polychroa*	Russia	*Urbanavichus* L-15342 (LE)	**MW523545**	**MW489440**	**MW506385**		**MW522905**
JG212	*B. polychroa*	Russia	*Urbanavichene* & *Urbanavichus* L-15343 (LE)	**MW523546**	**MW489441**	**MW506386**		
	B. polychroa	Sweden	*Knutsson* 91-215 (hb. Knutsson)	AF282089				
JG138	*B. rosella*	Russia	*Urbanavichene* & *Urbanavichus* L-15339 (LE)	**MW523556**		**MW506389**		**MW522909**
	B. rosella	Sweden	*Ekman* 3117 (BG)	AF282086	AY300829	AY300877	AY756412	AM292755
JG085	*B. rubella*	Russia	*Gerasimova* M-0182581 (M)	MH048630	MW493331	MW506353	MW540431	
JG142	*B. rubella*	Russia	*Ezhkin* M-0308499 (M)	MW491456	MW493332	MW506354	MW540432	MW522872

(*Continued*)

Table 1. (*Continued*)

DNA no. (JG)	Name	Country	Specimen voucher/isolate	GenBank Accession Number				
				nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2
JG133	*B. rubella*	Russia	*Gerasimova* M-0308494 (M)	**MW523524**				
JG134	*B. rubella*	Russia	*Gerasimova* M-0308495 (M)	**MW523525**	**MW489430**	**MW506375**		**MW522888**
JG171	*B. rubella*	Armenia	*Otte* GLM-0041636 (GLM)	**MW523526**	**MW489431**	**MW506376**		**MW522889**
JG173	*B. rubella*	Russia	*Otte* GLM-0031588 (GLM)					**MW522891**
JG174	*B. rubella*	Armenia	*Otte* GLM-0041554 (GLM)	**MW523527**				**MW522892**
JG207	*B. rubella*	Russia	*Urbanavichus* M-0311936 (M)	**MW523529**	**MW489433**	**MW506378**		**MW522894**
	B. rubella	Poland	AFTOL-ID 1793	HQ650644	DQ986793	DQ986808		DQ992422
	B. rubella	Switzerland	*van den Boom* (LG DNA 578)	JQ796852	JQ796843	JQ796830		
	B. rubella	Sweden	*Ekman* 3021 (BG)	AF282087		AY567723		
	B. rubella	Switzerland	*van den Boom* (LG DNA 581)			JQ796831		
	B. rubella	Switzerland	LIFU076-16	KX132984				
	B. rubella	Hungary	*Hur* H06122	EU266078				
JG082	*B. sachalinensis*	Russia	*Ezhkin* M-0182619 (M)	MH048621				
JG097	*B. sachalinensis*	Russia	*Ezhkin* M-0182623 (M)	MH048622	MW493333	MW506355	MW540433	MW522873
JG098	*B. sachalinensis*	Russia	*Ezhkin* L-12963 (LE)	MH048623	MW493334	MW506356		MW522874
JG099	*B. sachalinensis*	Russia	*Ezhkin* L-12964 (LE)	MH048624				
JG100	*B. sachalinensis*	Russia	*Ezhkin* M-0182624 (M)	MH048625				
JG014	*B. schweinitzii*	Russia	*Gerasimova* M-0182579 (M)	MW491454	MW493327			
JG015	*B. schweinitzii*	Russia	*Gerasimova* M-0182580 (M)	MH048613	MW493327	MW506350	MW540429	MW522869
	B. schweinitzii	USA	*Wetmore* 72619 (MIN)	AF282080	MG926045		MG926146	MG926235
	B. schweinitzii	USA	AFTOL-ID 642	DQ782850	DQ782911	DQ972998	DQ782830	DQ782872
	B. schweinitzii	USA	AFTOL-ID 4969		KJ766527	KJ766354		
	B. schweinitzii	USA	*Shaheen* (NY1451)	MG461696				
	B. schweinitzii	USA	*Tripp* 2614 (NY1448)	KX151762		KX151750		
	B. schweinitzii	USA	*Lendemer* 29364 (NY1449)	KX151763		KX151751		
	B. schweinitzii	USA	*Lendemer* 31230A (NY1450)	KX151766				
	B. schweinitzii	USA	*Lendemer* 31238 (NY1451)	KX151764		KX151752		
	B. schweinitzii	USA	*Lendemer* 30548 (NY1452)	KX151761		KX151749		
	B. schweinitzii	USA	*Lendemer* 31855 (NY1453)	KX151765		KX151753		
	B. scopulicola	Sweden	*Ekman* 3106 (BG)	AF282084				
	B. sipmanii	Spain	*Sérusiaux* (LG DNA 361)	JQ796853	JQ796844	JQ796832		

(*Continued*)

Table 1. (*Continued*)

DNA no. (JG)	Name	Country	Specimen voucher/isolate	GenBank Accession Number				
				nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2
	B. sorediata	USA	*Lendemer* 31692 (NY1389)	KX151768		KX151755		
	B. sorediata	USA	*Lendemer* 31527 (NY1397)	KX151771		KX151758		
	B. sorediata	USA	*Lendemer* 33702 (NY1539)	KX151767		KX151754		
	B. sorediata	USA	*Lendemer* 33787 (NY1544)	KX151772		KX151759		
	B. sorediata	USA	*Lendemer* 33869 (NY1546)	KX151773		KX151760		
	B. sorediata	USA	*Lendemer* 35031 (NY1747)	KX151769		KX151756		
	B. sorediata	USA	*Lendemer* 35386 (NY1748)	KX151770		KX151757		
	B. sorediata	USA	*Lendemer* 38909 (NY2294)	KX151774				
	B. sorediata	USA	*Barton* 658 (NY2496)	KX151775				
	B. squamulosula	Ecuador	*Kalb* SE-314, *Lich. Neotropici* No. 405	MG925955	MG926051	MG925856	MG926152	
	B. suffusa	USA	*Wetmore* 74771 (MIN)	AF282091				
JG038	*B. suffusa*	Russia	*Gerasimova* M-0182593 (M)	MH048616		MW506359	MW540435	
JG039	*B. suffusa*	Russia	*Gerasimova* M-0182594 (M)	MH048617		MW506360		
JG051	*B. suffusa*	Russia	*Gerasimova* M-0182601 (M)	MH048615		MW506361		MW522876
JG080	*B. suffusa*	USA	*Tucker* 17000 (M)	MH048618				
JG081	*B. suffusa*	USA	*Wetmore* 40219 (M)	MH048619				
JG176	*B. suffusa*	Azerbaijan	*Otte* GLM-0052934 (GLM)	**MW523547**				
JG177	*B. suffusa*	Azerbaijan	*Otte* GLM-0052906 (GLM)	**MW523548**				**MW522906**
JG178	*B. suffusa*	Azerbaijan	*Otte* GLM-0052950 (GLM)	**MW523549**	**MW489442**			
JG179	*B. suffusa*	Russia	*Otte* GLM-0055113 (GLM)	**MW523550**	**MW489443**	**MW506387**		**MW522907**
JG180	*B. suffusa*	Russia	*Otte* GLM-0048445 (GLM)	**MW523551**				**MW522908**
JG181	*B. suffusa*	Russia	*Otte* GLM-0048460 (GLM)	**MW523552**				
JG183	*B. suffusa*	Russia	*Otte* GLM-0048483 (GLM)	**MW523554**				
JG184	*B. suffusa*	Russia	*Otte* GLM-0048464 (GLM)	**MW523555**				
	B. suffusa	USA	*Lumbsch* 19190c (AFTOL-ID 5785)		KJ766528	KJ766355	KJ766836	
	B. suffusa	Korea	KBA-L-0000359	ON352605				
	B. suffusa	Korea	KBA-L-0002776	ON352614				
	B. suffusa	Korea	KBA-L-0002835	ON352616				
	Sporacestra borbonica	Reunion	*Krog & Timdal* RE08,12 (isolate 511)	MG925988	MG926086	MG925890	MG926184	
	S. pertexta	Cuba	*Pérez-Ortega* s. n. (isolate 1040)	MG926000	MG926093	MG925903	MG926194	MG926268

ined. and *S. pertexta* (Nyl.) Stapnes & Timdal as outgroup species based on the results of Kistenich *et al.* (2018).

BLAST searches in GenBank were performed to detect and exclude sequences from accessory and lichenicolous fungi and contaminants. We performed phylogenetic analyses on each locus separately ('single-locus' analyses) and on concatenated alignments of loci. In the concatenated analyses, we assembled one alignment with a minimum of two out of the five target loci (herein referred to as the 'two-locus' analysis) to retain a higher number of samples (88 samples). A second concatenated alignment was also assembled to test the effect of decreased missing data on the analyses; a minimum of three loci were included, but only 54 samples were retained in this alignment (herein referred to as the 'three-locus' analysis). An overview of the taxa number and newly produced sequences for each genetic marker and concatenated alignments are summarized in Table 2. Due to the higher number of samples included, we mainly focus on the results of the nrITS and two-locus analyses in this paper. Alignment from the single and concatenated datasets is available as Supplementary Material File S2 (available online).

Each locus was aligned using MUSCLE v. 3.8.31 using the default settings (Edgar 2004) implemented in the program PhyDE-1 v. 0.9971 and optimized manually. Ambiguous regions of nrITS1 were aligned using MAFFT v. 7.505 (Katoh & Standley 2013). Sites with more than 95% gaps were excluded, and alignments for the two-locus and three-locus analyses were concatenated manually. Substitution models for the concatenated and single locus datasets were selected using jModelTest v. 2 (Guindon & Gascuel 2003; Darriba *et al.* 2012) for BI, and ModelFinder (Kalyaanamoorthy *et al.* 2017) for ML analyses using IQ-TREE. Partition models were implemented for the concatenated alignments, allowing each partition to have its substitution model. Identical sequences were excluded from the subsequent analyses but are listed in Table 1.

We performed Bayesian inference (BI) and maximum likelihood (ML) analyses in RAxML and IQ-TREE on the single-locus and concatenated alignments of nrITS, nrLSU, mtSSU, *RPB*1 and *RPB*2. Bayesian inference was carried out using the Markov chain Monte Carlo method (MCMC) using MrBayes v. 3.2.6 (Ronquist *et al.* 2012). A GTR substitution model with gamma-distributed rate variations across sites and a proportion of invariable sites was selected based on the result of jModelTest. Two parallel runs were performed (two cold chains), with a single tree saved every 10th generation for a total of 1 000 000 generations. The convergence of the Markov chain was examined according to the trends in likelihood values; the initial 10% was discarded as burn-in, and the results were summarized as a 50% majority-rule consensus tree.

ML analysis was performed with RAxML v. 8.2.4 following a GTRGAMMA model of molecular evolution with bipartitions drawn onto the most likely tree topology using multiple non-parametric bootstraps (Stamatakis 2014) on the CIPRES web portal (Miller *et al.* 2010).

Further tree reconstruction using ML analysis was performed in IQ-TREE v. 1.6.12 using standard bootstrap approximation with 1000 bootstraps (Felsenstein 1985; Nguyen *et al.* 2015). Substitution models for concatenated (partitioned) and single-locus datasets were selected using ModelFinder (Kalyaanamoorthy *et al.* 2017).

The ML trees based on the different substitution models from single and concatenated datasets were congruent and in accordance with the Bayesian tree topology. Therefore, only the RAxML tree for the nrITS and concatenated dataset are shown, with RAxML bootstrap values (BSr), Bayesian posterior probabilities (PP), and IQ-TREE bootstrap values (BSi) used. The phylogenetic trees were visualized using FigTree v. 1.4.2 (Rambaut 2009). Only clades that received BSr ≥ 70%, PP ≥ 0.95 and BSi ≥ 80% were considered highly supported and given in bold. The concatenated and individual gene trees obtained from RAxML, MrBayes and IQ-TREE are provided in Supplementary Material Figs S1–8 (available online).

Results

Morphology and taxonomy

Revision of the 237 herbarium specimens showed that the most common species of *Bacidia* s. str. in our Caucasus collection is *B. polychroa* (16.5%), while *B. fraxinea* (7%), *B. arceutina* (5.5%), *B. laurocerasi* (3.8%), *B. absistens* (*c.* 1%) and *B. biatorina* (*c.* 1%) are least frequent. Only one herbarium specimen of *B. herbarum* was studied, which was collected in Krasnodarskiy Krai at 2115 m a.s.l. (GLM-L-0054141).

Our examination of herbarium material found the first record of *Bacidia heterochroa* (Müll. Arg.) Zahlbr. for Caucasus and Russia. Based on morphological and anatomical analyses, one new species, *Bacidia caucasica* sp. nov. (Suffusa group) was described (see 'Taxonomy'), and two putative taxa were defined: *Bacidia inconspicua* ined. (Rubella group), and *B. maritima* ined. (Rubella group). The systematic revision of the *Bacidia* species list provided by Urbanavichus (2010) and their current taxonomic status are given in Table 3. Observations of the complex morphology of the Rubella group are summarized in Table 4.

Ecology

All studied specimens were collected mainly in old mixed coniferous-broad-leaved forest communities in floodplains and river valleys as well as in the drier habitats such as fruit orchards,

Table 2. Overview of the number of taxa and newly produced sequences for each genetic marker and concatenated alignments (excluding outgroup).

	nrITS	nrLSU	mtSSU	*RPB*1	*RPB*2	2-locus dataset	3-locus dataset
Number of taxa	136	47	83	25	48	85	54
Newly produced sequences	52	23	26	10	31	–	–
Length with gaps (bp)	486	861	730	672	1083	3835	3832
Constant sites	219	703	533	337	575	2391	2406
Parsimony informative sites	233	122	177	302	478	1294	1260
Number of distinct site patterns	306	149	260	352	531	1551	1495

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Table 3. Revised *Bacidia* species list based on the checklist of Urbanavichus (2010), including recently found or newly described species.

Former name	Current name or related genus	Reference
Bacidia absistens	*Bacidia absistens*	Urbanavichene & Urbanavichus (2016)
B. albogranulosa	*Bacidia albogranulosa*	Malíček *et al.* (2018)
B. arceutina	*Bacidia arceutina*	
B. auerswaldii	*Scutula effusa*	Kistenich *et al.* (2018); reported as *Bacidia effusa* (Barkhalov 1975)
B. bagliettoana	*Toniniopsis bagliettoana*	Cannon *et al.* (2021)
B. beckhausii	*Biatora beckhausii*	Printzen (2014)
B. biatorina	*Bacidia biatorina*	
	Bacidia caucasica	Described as a new species in this study
B. circumspecta	*Scutula circumspecta*	Kistenich *et al.* (2018)
B. coprodes	*Toniniopsis coprodes*	Cannon *et al.* (2021), Urbanavichus & Urbanavichene (2014)
B. fraxinea	*Bacidia fraxinea*	
B. freshfieldii	*Catillaria* s. str.	Gerasimova & Ekman (2017)
B. friesiana	*Bacidina friesiana*	Ekman (2023)
B. herbarum	*Bacidia herbarum*	
B. heterochroa	*Bacidia heterochroa*	Reported as new to the Caucasus in this study
B. igniarii	*Scutula igniarii*	Cannon *et al.* (2021)
B. illudens	*Toniniopsis illudens*	Kistenich *et al.* (2018)
B. incompta	*Bellicidia incompta*	Kistenich *et al.* (2018)
B. laurocerasi	*Bacidia laurocerasi*	
B. notarisiana	*Bacidia notarisiana*	Ekman (2014), Urbanavichene & Urbanavichus (2018); belongs to *Bacidia* s. lat.
B. polychroa	*Bacidia polychroa*	
B. propinqua	*Bilimbia* s. str.	Ekman *et al.* (2021)
B. rosella	*Bacidia rosella*	
B. rubella	*Bacidia rubella*	
B. subincompta auct.	*Toniniopsis dissimilis*/*T. separabilis*	Kistenich *et al.* (2018), Gerasimova *et al.* (2021*a*)
B. suffusa	*Bacidia suffusa*	Otte (2007*a*)
B. trachona	*Aquacidia trachona*	Aptroot *et al.* (2018)
B. vermifera	*Bibbya vermifera*	Kistenich *et al.* (2018)
B. viridifarinosa	*Aquacidia viridifarinosa*	Aptroot *et al.* (2018)

deciduous forests without conifers, and recently clearcut young coppices. The main phorophytes included *Abies nordmanniana*, *Acer campestre*, *Carpinus betulus*, *Quercus* spp. (*Q. pubescens*, *Q. petraea* and *Q. robur*), *Juniperus* spp. (*J. excelsa*, *J. oxycerdrus* and *J. foetidissima*), and *Pistacia mutica*. Due to the proximity of the Caspian and Black Seas, the dense river system and the high groundwater level, the average relative humidity in all the studied areas was very high. The average annual rainfall ranged from 400 mm (Samursky National Park) and 600 mm (Utrish Nature Reserve) to 2000–3000 mm in the forest belt of the Caucasian Reserve. Most of the *Bacidia* species in the Caucasus are confined to humid environments, except *B. rubella* and *B. fraxinea*, which occur in a broader range of habitats from dry and warm to humid subtropics with high levels of sunlight. While both species could be present in dry areas, *Bacidia rosella* is one of the most hygrophilous species. It has been collected in the western and north-western Caucasus in old-growth forest habitat with *Abies nordmanniana*, *Acer trautvetteri* and *Fagus orientalis* at 1060–1600 m a.s.l., the most humid and shaded areas of all the studied localities due to the predominance of *Abies nordmanniana*.

Phylogeny

The BI and ML analyses for the single and concatenated datasets recovered highly concordant topologies of the phylogenetic groups (with a few exceptions discussed below). Both two-locus and three-locus trees resulted in well-supported nodes throughout the tree (the three-locus tree is provided in Supplementary Material Fig. S2, available online). In total, we produced 142 new sequences for this study for the various genetic markers. The nrITS comprised 40% of the alignment of a total dataset of 340 sequences, mtSSU comprised 24.7%, nrLSU 14%, *RPB*2 14%, and *RPB*1 7.3%.

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Table 4. Main characters separating taxa of *Bacidia rubella* s. lat. group. Information for *Bacidia fraxinea* and *B. rubella* are given by Ekman (1996), Ekman & Nordin (1993), Smith *et al.* (2009) and Llop (2007); *B. iberica* and *B. parathalassica* are from Llop (2007) and Aragón & Martínez (2003); *B. thyrrenica* from Llop *et al*. (2007); *B. obtecta* and *B. elongata* are from Gerasimova *et al.* (2018, 2021*b*). Measurements for Caucasian taxa are newly provided (see taxa with 'Caucasus' in brackets after the species name. Measurements from the present study are given as (min–) mean ± SD (–max), and are otherwise are taken from the relative references. Taxa are ordered according to their morphological similarity.

	Thallus structure	Hymenium: size (μm)	Hypothecium: colour	Exciple: size (μm)	Exciple: cell layers	Exciple cells: size (μm)	Crystals: presence & distribution	Crystals: colour & solubility	Ascospores size (μm)	Ascospores: number of septa
B. rubella (North America)	Coarsely granular; consists of globose or ± flattened, almost squamulose and slightly incised granules; pale grey to greyish green	(67–)69–86–97(–109)	Almost colourless or pale yellowish to orange	(59–)79 (–103)	0–1	up to 6 × 6	Sometimes with radiating clusters of minute crystals (up to 1 μm)	Colourless (reaction is not provided)	(31–)44–52–63(–104) × (2.1–)2.4–2.7–3.2(–4.3)	(3–)3.2–7.1– 8.7(–13)
B. rubella (Europe)	Thinly to richly granular isidiate to coralloid; grey to yellow-green	70–115	Colourless, or upper part pale yellow or orange-straw	-	1	to 3–5	Sometimes with radiating streaks of minute crystals in exciple and minor crystals in hymenium	Colourless, K+, N–	(35–)40–70 (–84) × 2.5–3 (–4)	3–7(–13)
B. rubella (Caucasus)	As above	(64)74.1 ± 9(–95)	Yellow-brown, brownish, orange	(51.5–) 69.15 ± 14.4(–91)	1–3	up to 5.5 × 12	Sometimes with radiating clusters of minute crystals in lateral exciple	Colourless to pale yellow, K+, N–	(31–)47.8 ± 6.6(–75) × (1.5–)2.7 ± 0.4 (–4)	(1–)5.5 ± 3 (–12)
B. maritima ined. (Caucasus): JG206 & 208	Consists of scattered ± globose granules or ± flattened, almost squamulose warts; whitish to green	73.5–120	Yellow-brown to pale brown	50–103	1–3	up to 6 × 13	With radiating clusters of minute crystals in lateral exciple	Colourless, K+, N–	(34–)48 ± 6.7 (–65) × (2–) 2.65 ± 0.3(–3.5)	(1–)4.7 ± 2.6 (–10)
B. maritima ined. (Caucasus): JG131 & 172	Consists of scattered or contiguous, ±globose or flattened, irregular granules; green	81–91	Yellow-brown	73.5–91	1–3	up to 5 × 11	Not observed	-	(35–)41.5 ± 6.2(–55) × (2–) 2.65 ± 0.47(–3)	1–3–6
B. rubella (Far East)	Coarsely granular, consists of separate or contiguous, ±globose granules	(49–)74.2 ± 15.8(–97)	Pale straw to orange	(61–) 95.8 ± 25(–122.5)	2-3	up to 6 × 12	Without or with clusters or crystals in lateral exciple	Yellow, not observed	(36–)58.8 ± 9.2(–72) × (2.5–)3.0 ± 0.3 (–4)	(1–)6 ± 3.7 (–12)
B. iberica (Spain)	Minutely squamulose, whitish to greenish grey; squamules ascending, with crenate to subdigitiform margins	(50–)63–78(–94)	Colourless or pale yellowish	(55–) 65–80 (–97)	1	4.0–5.5	With crystals in lateral exciple and medulla	Colourless to pale yellow, K–, N+	(42–)45.5–46–46.7(–50) × (2.5–) 2.9–3.0–3.1 (–3.5)	5–9
B. fraxinea s. str. (Europe)	Thin and smooth to thick and verrucose, areolate or irregularly cracked, grey	76–89–103	Straw to pale orange	-	0–1	up to 6 × 6	Sometimes with radiating clusters of minute crystals in exciple rim and medulla	Colourless to pale yellow, K–, N+	(42–)50–67–85(–109) × (2.5–)2.6–3.0–3.4(–4.3)	3–17

(*Continued*)

Table 4. (*Continued*)

	Thallus structure	Hymenium: size (μm)	Hypothecium: colour	Exciple: size (μm)	Exciple: cell layers	Exciple cells: size (μm)	Crystals: presence & distribution	Crystals: colour & solubility	Ascospores size (μm)	Ascospores: number of septa
B. fraxinea (Caucasus): JG170 & 205	Thick, consists of irregular warts, wrinkled; warts adnate to the surface, grey-green to dirty green	70–93	Pale straw to pale yellow-brown	80–95	1–3	up to 6 × 7	Clusters of minute crystals in lateral exciple	Colourless, not observed	(35–)50 ± 6.7 (–66) × (2–) 2.7 ± 0.3(–3)	(1–)5 ± 3(–9)
B. elongata (Far East)	Thin to thick, smooth to areolate, wrinkled and warted; grey to dark grey-green	62.5–92–110	Colourless, pale yellow to orange-brown	55–79.5–87.5–110	up to 4 layers	up to 7 × 20	Not observed	-	(39–)59 ± 8(–80) × (2.0–) 2.5 ± 0.5(–4.0)	(2–)5–7–12(–16)
B. obtecta (Far East)	Thick, wrinkled, warted; grey-green to yellowish green	73.5–108–135	Orange-brown	86–94.3–98	up to 4 layers	up to 5 × 13	Throughout lateral part of exciple and upper hymenium	Colourless, K+, N–	(47–)61.2 ± 7.0(–79) × (2.0–)3.0 ± 0.36(–4.0)	(1–)6 ± 3(–11)
B. inconspicua ined. (JG130)	Thin, forming continuous patches, greenish to greenish grey; mostly endophloeodal	80–103	Pale straw to yellow-brown	80–90	0	-	Minor crystals in medullar part and hypothecium	Colourless or yellowish K–, N–. Occasionally crystals in lateral exciple, K–, N+	(45–)59.6 ± 5.5(–68) × (2–) 2.9 ± 0.4(–4)	(3–)8 ± 3(–13)
B. inconspicua ined. (*Vondrak* 12200, PRA)	Thin, mainly consists of patches of aggregated warts	103–115	Pale orange	86–103	2–3	up to 5 × 8	Along lateral exciple, medulla, and hypothecium	Yellow, K–, N–	(43–)56.4 ± 5.3(–65) × (2–) 2.6 ± 0.3(–3.2)	(3–)7 ± 3(–13)
B. parathalassica (Spain)	Warted, verruculose-squamulose, with individual squamules attached to the substratum, and having rounded margins	(60–)70(–75)	Colourless to yellowish	-	1	up to 4 × 10	Clusters in medulla	Colourless to pale yellow, K–, N+	(26–)33.6–52.2(–59) × (1.5–)2.1–2.9 (–3.0)	(3–)5–7(–9)
B. thyrrenica (Mediterranean)	Continuous to cracked, surface warted to areolate	(50)60–75 (85)	Colourless to yellowish	-	-	-	Evenly distributed in marginal area, occasionally clusters in medulla, in upper hymenium	Colourless to yellowish, K+, N–; medulla K–, N+	(32.8)40–55 (60.8) × 2–3 (3.6)	(3)7(10)

All the sequences from the Caucasus obtained for this study nested in the correspondent clades recovered in the last multilocus phylogeny of *Bacidia* s. str. (Gerasimova *et al.* 2021*a*). *Bacidia heterochroa* from the Caucasus formed a new group (Figs 1 & 2). The two-locus and nrITS trees were congruent with the topology of the three-locus phylogeny, but while we retrieved high support in the nrITS tree for nodes towards the tips, the backbone in the multilocus phylogenies was better supported (Figs 1 & 2; Supplementary Material Fig. S2).

The main groups obtained from single and concatenated data in both ML and BI analyses are congruent and correspond to those obtained from the previous phylogenies (Ekman 2001; Gerasimova *et al.* 2018, 2021*b*). Furthermore, similar to previous results, our phylogenies revealed two highly supported major clades in the two- and three-locus phylogenies. Clade I included the Laurocerasi, Schweinitzii, Suffusa, and Heterochroa groups from the Caucasus (BSr/PP/BSi: 100/1/100 in both phylogenies). Several sequences of *B. heterochroa* from South Korea formed a sister clade to *B. laurocerasi* in the nrITS phylogeny but with low support (BSr/PP/BSi: 44/0.75/43) (see 'Discussion'). Clade II included the Arceutina (BSr/PP/BSi: 75/1/87, and 73/1/75), Rubella (BSr/PP/BSi: 85/1/82, and 86/1/88), Polychroa (BSr/PP/BSi: 100/1/100 in both phylogenies), and *B. rosella* groups (BSr/PP/BSi: 100/1/100 in both phylogenies). *Bacidia lutescens* Malme (referred to as *B. thiersiana* Lendemer by Lendemer (2020)), *B. hostheleoides* (Nyl.) Zahlbr., and recently described *B. fuscopallida* B.G. Lee & T.I. Heo formed a separate group within Clade II but without support in the nrITS phylogeny (Fig. 2). All clades in the multilocus phylogenies received strong support throughout the tree (i.e. with BSr ≥ 70%, PP ≥ 0.95 and BSi ≥ 80%). However, in the multilocus trees poor support was retrieved for the sister relationship of the Suffusa and Heterochroa groups (BSr/PP/BSi: 62/0.92/65, and 71/0.94/72), the subclades of the Schweinitzii group (not present in the Caucasus, discussed in detail in Gerasimova *et al.* (2021*b*)), the position of the *Bacidia rubella* s. str. clade (BSr/PP/BSi: 72/0.55/66, and 54/-/37), the placement of *B. inconspicua* ined. (BSr/PP/BSi: 79/0.74/73, and 55/-/36), and the retrieval of the *B. albogranulosa* clade as sister to *B. polychroa* (JG188) (BSr/PP/BSi: 77/0.91/56 in the two-locus tree).

The retrieved groups are discussed in detail in previous studies (Gerasimova *et al.* 2021*b*); therefore, we focus on those with Caucasian representatives below. As phylogenies are congruent in the topology of the groups, the Results and Discussion are based on the two-locus and nrITS trees, as those are the most species-inclusive. Trees from the single and concatenated phylogenies not shown in the manuscript can be found in Supplementary Material Figs S1–8 (available online).

Laurocerasi group. In concatenated phylogenies, *B. biatorina*, *B. laurocerasi* and *B. kurilensis* Gerasimova, A. Ezhkin & A. Beck (Sakhalin endemic) formed one clade with high support of all subclades (Fig. 1). Two sequences of *B. biatorina* from the Caucasus formed a highly supported clade (BSr/PP/BSi: 100/1/100), including a sequence from Sweden (Fig. 2).

The sequences from the Caucasus formed a well-supported clade in the multilocus phylogenies and formed a clade together with the representatives from the Far East and the USA in the two-locus and nrITS phylogenies (Fig. 1 & 2). In all phylogenies, the sequence from Alaska (*Spribille* 26334) was placed as sister to all others with maximum support in the multilocus phylogenies (BSr/PP/BSi: 100/1/100) and high support in the nrITS tree (BSr/PP/BSi: 92/0.99/99).

Bacidia heterochroa *clades from South Korea and the Caucasus.* *Bacidia heterochroa* inhabits tropical and subtropical areas worldwide (Ekman 1996) and was recently found in South Korea (Lee & Hur 2022). To include nrITS sequences of *B. heterochroa* from South Korea and keep the informative part of the nrITS alignment, we constrained our alignment to *Bacidia* Clade I (Supplementary Material Fig. S3, available online). Three sequences of *B. heterochroa* from Korea (GenBank ON352606, ON352612 and ON352613) formed a sister clade to *B. laurocerasi*, but with support in RAxML and BI analyses only (BSr/PP/BSi: 74/1/65). Instead, *Bacidia heterochroa* sequences from the Caucasus formed a separate clade sister to the Suffusa and Schweinitzii groups in all the phylogenies but with uncertain sister relationships (Fig. 2). In the multilocus phylogenies, it was sister to the Suffusa group with low support (BSr/PP/BSi: 62/0.92/65, and 71/0.94/72; Fig. 1 & Supplementary Material Fig. S2). In the nrITS tree, it was sister to the Schweinitzii group on a long branch and with low support (BSr/PP/BSi: 63/0.91/61; Fig. 2).

Suffusa group. The *Bacidia suffusa* sequences from the Caucasus formed a clade together with those from North America (JG080 and JG081; Figs 1 & 2) and a sequence from South Korea (ON352616) in the nrITS phylogeny (Fig. 2). They formed a sister clade to the representatives from the Far East and South Korea with strong support values in all phylogenies. The sequences from the Caucasus differ from the Far East individuals by 3% (up to 15 nucleotides); however, as we could not observe any strong morphological differences between the specimens from these two clades, we chose not to recognize these individuals as new species.

One sequence from the Caucasus (JG182) formed a separate clade in all phylogenies with strong support. Based on this phylogenetic evidence and its distinct morphology, a new species, *Bacidia caucasica*, is described (see 'Taxonomy').

Schweinitzii group. The taxa from the Schweinitzii group are mostly known from North America and the coast of the Russian Far East (see details in Gerasimova *et al.* (2021*b*)) and have not been found in the Caucasus to date.

Rubella group. The highly supported Rubella group (BSr/PP/BSi: 85/1/82) forms four distinct clades comprising sequences of *Bacidia fraxinea*, *B. rubella*, *B. elongata* Gerasimova & A. Beck, *B. obtecta* Gerasimova *et al.*, *B. inconspicua* ined. and *B. maritima* ined. (Fig. 1). *Bacidia rubella* sequences from the west coast of the Caspian Sea (JG172, JG206), and the north-east coast (JG208) and south-east coast (JG131) of the Black Sea formed a sister clade to *Bacidia rubella* s. lat. clades in all reconstructed phylogenies with maximum support; these are provisionally defined as *Bacidia maritima* ined. here. However, JG131 and JG172 are represented by only one sequence: nrITS and *RPB2*, respectively. The difference of nrITS sequences of JG206 and JG208 is almost 3% compared to other sequences from the *B. rubella* s. str. clade; however, this difference does not seem to be correlated with a difference in studied morphological characters (see 'Discussion', Table 4, and Fig. 3).

Sequences from the Caucasus (JG130) and Ukraine (*Vondrák* 12200, PRA; identified and published as *Bacidia* cf. *rubella* by Malíček *et al.* (2018)) formed a highly supported clade sister to

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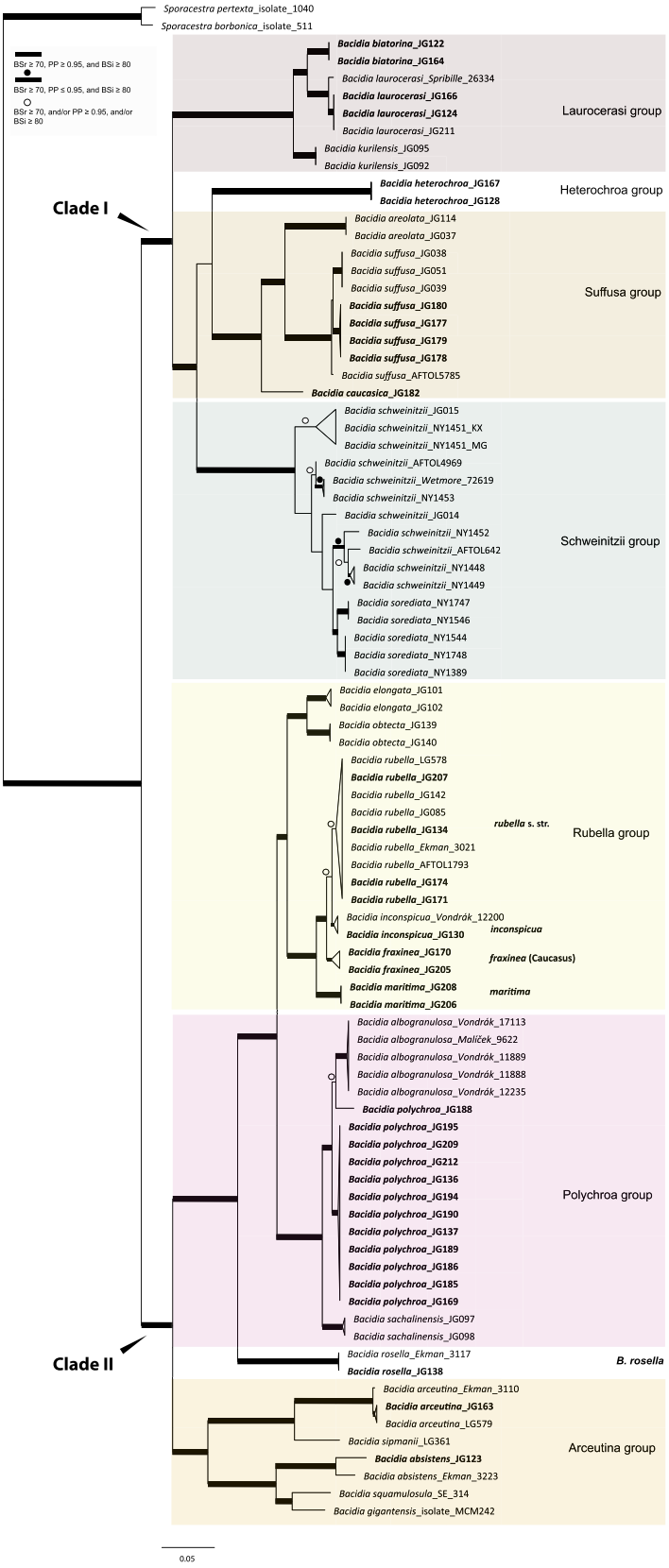

Figure 1. Maximum likelihood (ML) tree of *Bacidia* s. str. resulting from a RAxML analysis of the concatenated multilocus dataset with a minimum of two loci included (out of nrITS, nrLSU, mtSSU, *RPB*1 and *RPB*2). RAxML bootstrap values (BSr), Bayesian posterior probabilities (PP) and IQ-TREE bootstrap values (BSi) are indicated. Highly supported branches with BSr ≥ 70%, PP ≥ 0.95, and BSi ≥ 80% are marked in bold; strongly supported branches with BSr ≥ 70% and BSi ≥ 80% are also marked in bold with a dot above the branch; branches with BSr ≥ 70%, and/or PP ≥ 0.95, and/or BSi ≥ 80% are marked with a white dot. Major groups within clades are indicated, as are species within or outside groups. New sequences are in bold. For further information about sequences, see Table 1. Single phylogenetic trees resulting from the concatenated multilocus datasets from RAxML, BI, and IQ-TREE analyses are in Supplementary Material Figs S1 and S2, (available online). In colour online.

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B. rubella s. str. in the two-locus phylogeny (BSr/PP/BSi: 90/1/87; Fig. 1), and are provisionally placed in *Bacidia inconspicua* ined. The nrITS sequences alone are insufficient to resolve the species relationships within *B. rubella*, thus appearing paraphyletic but without support for the paraphyly (Fig. 2).

The nrITS sequence of *Bacidia fraxinea* from Sweden (*Johansson* 1620) and one from Caucasus (JG170) were nested in a clade of *B. rubella* sequences in the nrITS phylogenies (Fig. 2), revealing paraphyletic status of the species as two other *B. fraxinea* sequences from the Caucasus formed a clade with high support in the two- and three-locus phylogenies (BSr/PP/BSi: 85/1/86, and 87/-/73).

Polychroa group. The Polychroa group comprises a highly supported clade of *Bacidia polychroa*, *B. sachalinensis* Gerasimova *et al.*, *B. diffracta* S. Ekman and *B. albogranulosa* in the two-locus trees (Figs 1 & 2). All Caucasian *B. polychroa* sequences formed one clade with high support, including a sequence from Sweden in the nrITS phylogeny (BSr/PP/BSi: 93/1/98).

One sequence from Caucasus (JG188) was placed as a sister to the *B. albogranulosa* clade in the two-gene phylogeny with low support (BSr/PP/BSi: 77/0.91/56) but with high support in the nrITS tree (BSr/PP/BSi: 89/0.99/99).

Rosella group. The sequences from the Caucasus (JG138) and Norway (*Ekman* 3117) formed a highly supported clade in all phylogenies. In the two- and three-gene phylogenies, these sequences are retrieved in Clade II with maximum support, together with the Polychroa and Rubella groups (BSr/PP/BSi: 100/1/100 in both phylogenies).

Arceutina group. The *B. arceutina* sequences from the Caucasus (JG126 and JG163) and Switzerland (AFTOL LG579) formed a well-supported clade sister to the *B. arceutina* clade from Sweden in the two- and three-locus trees (BSr/PP/BSi: 100/1/100, and 99/1/98). The sequences differ by *c.* 2.5% (7–8 nucleotides) in nrITS. *Bacidia arceutina* is distributed in the western part of the Caucasus (viz. Krasnodarskiy Krai, Republic of Adygea, Georgia), with its southern-most limit recorded in a valley in the Lenkaran district of Azerbaijan (GLM-L-529756). Throughout its range, it is found at elevations of up to 1000 m in warm, well-lit and relatively dry lowlands and habitats with very high rainfall (from 1500 to 3000 mm per year). The *B. absistens* sequence from the Caucasus (JG123) was placed with the sequence from Norway as a sister to *B. squamulosula* (Nyl.) and *B. gigantensis* Lendemer *et al.*, with high support in the multilocus phylogenies (BSr/PP/BSi: 100/1/99, and 73/1/75). *Bacidia absistens* in the Caucasus is recorded from shaded habitats at elevations of 700 m a.s.l. with very high humidity (rainfall of *c.* 1000 mm per year).

Figure 2. Maximum likelihood (ML) nrITS tree of *Bacidia* s. str. resulting from a RAxML analysis. RAxML bootstrap values (BSr), Bayesian posterior probabilities (PP), and IQ-TREE bootstrap values (BSi) are indicated. Highly supported branches with BSr ≥ 70%, PP ≥ 0.95, and BSi ≥ 80% are marked in bold; strongly supported branches with BSr ≥ 70% and BSi ≥ 80% are also marked in bold with a dot above the branch; branches with BSr ≥ 70%, and/or PP ≥ 0.95, and/or BSi ≥ 80% are marked with a white dot. Major groups within clades are indicated, as are species within or outside groups. New sequences are in bold. For further information about sequences, see Table 1. Single phylogenetic trees resulting from the concatenated multilocus datasets from RAxML, BI, and IQ-TREE analyses are in Supplementary Material S4 (available online). In colour online.

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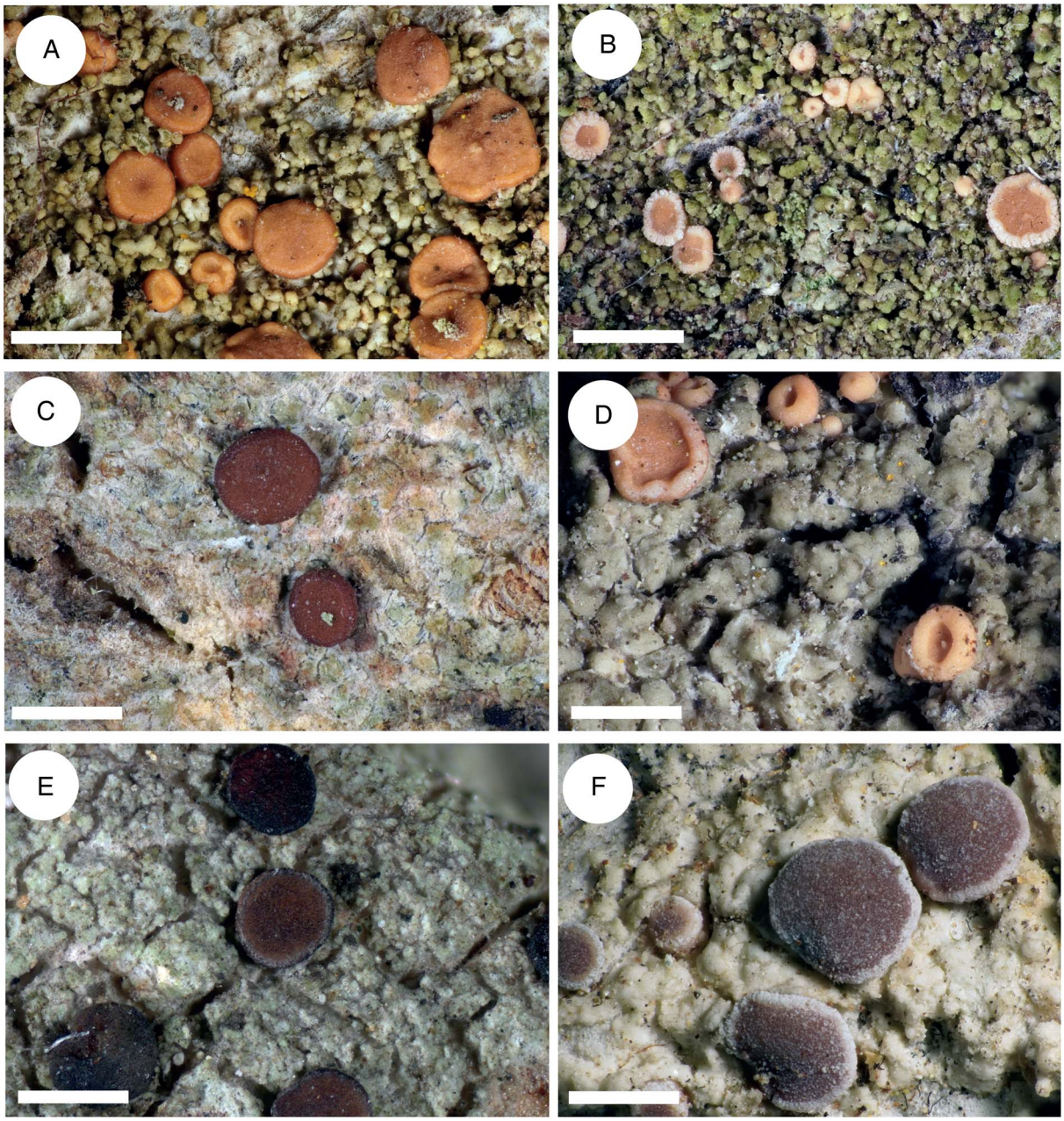

Figure 3. Thallus structure and apothecia variability of the most typical representatives of the Rubella group. A, *Bacidia rubella* s. str. from Caucasus (JG171, GLM-0041636). B, *B. maritima* ined. (JG206, M-0311935). C, *B. inconspicua* ined. (JG130, M-0311925). D, *B. fraxinea* from Caucasus (JG170, GLM-0044145). E, *B. elongata* (JG101, M-0182625). F, *B. obtecta* (JG141, M-0308496—holotype). Scales: A–E = 1 cm; F = 0.5 cm. In colour online.

Discussion

Two main clades correlated with apothecia pigmentation

Our phylogenies of *Bacidia* with 142 additional sequences from the Caucasus were congruent with previous results based on nrITS and multilocus phylogenies (Ekman 2001; Gerasimova *et al.* 2018, 2021*b*). In line with previous studies, we retrieved two large clades: Clade I includes the Laurocerasi, Schweinitzii and Suffusa groups, as well as the newly defined Heterochroa group (that consists of representatives from the Caucasus), and Clade II includes the Rubella, Polychroa and Arceutina groups. In a previous work, phylogenies mainly included specimens from temperate regions (Gerasimova *et al.* 2021*b*), while in this study, we also included representatives from the subtropics. Only the nrITS phylogeny included *B. lutescens* (*B. thiersiana*), *B. hostheleoides*, and the recently described *B. fuscopallida* (Lee & Hur 2022), which formed an unsupported group nested in Clade II. The former two taxa are widespread in south-eastern North America and the Neotropics (Malme 1935; Ekman 1996; Lendemer 2020), while *B. fuscopallida* is known only from the Gangwon Province in South Korea (Lee & Hur 2022), characterized by a moist, warm, temperate climate (Sayre *et al.* 2020). Further analyses are necessary to clarify the phylogenetic position of this group.

Similar to previous results, two main clades can be separated based on apothecial pigment. Specimens from Clade I have dark brown, red-brown or green pigments (Laurocerasi-brown

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and Bagliettoa-green), or a combination thereof, in the upper part of the hymenium and lateral exciple. The herein-defined Heterochroa group from the Caucasus also supports this differentiation; the Caucasian specimens are characterized by a dark purplish epithecium corresponding to the type specimen of *B. heterochroa*. The specimens from South Korea have a dark brown epithecium corresponding to the Laurocerasi group, where South Korean sequences were nested. In contrast, representatives from Clade II have a mixture of yellow, orange and/or brown apothecial pigments (Arceutina-yellow, Polychroa-brown and Rubella-orange) in the upper part of hymenium and lateral exciple. The specimens from the Caucasus in Polychroa and Rubella groups also supported the apothecial pigment differentiation. The representatives from the Lutescens-Hostheleoides group have been characterized by almost colourless or faintly and diffusely pigmented internal apothecial structures (Ekman 1996; Gerasimova *et al.* 2021*b*). In contrast, recently described *B. fuscopallida* is characterized by the clearly pigmented orange-brown to brown hypothecium (Lee & Hur 2022). However, this clade was inferred to have very long branches in our analyses, suggesting that their relationship warrants further investigation in future studies, including additional samples.

The clade containing *Bacidia absistens*, *B. gigantensis* and *B. squamulosa* is exceptional because it has highly variable pigmentation. This evidence may be related to the exceptional diversity of secondary compounds in this group detected by TLC, such as 4-*O*-methylcryptochlorophaeic and homosekikaic acids (Tønsberg *et al.* 1995; Lendemer 2020). This combination is so far unknown for species in other *Bacidia* s. str. groups, which contain atranorin as the main known secondary compound (Ekman 1996; Gerasimova *et al.* 2022).

As a result of morphological and/or phylogenetic analyses, the current list of *Bacidia* s. str. in Caucasus includes 13 species, namely *B. absistens, B. albogranulosa*, *B. arceutina*, *B. biatorina*, *B. caucasica*, *B. fraxinea*, *B. herbarum*, *B. heterochroa*, *B. laurocerasi*, *B. polychroa*, *B. rosella*, *B. rubella* and *B. suffusa*, which is almost 68.4% of the 19 species of *Bacidia* s. str. known from Russia (Ekman 2009; Gerasimova *et al.* 2018).

Laurocerasi group

The known distribution of *Bacidia biatorina* in Russia includes the European part, Far East, and Caucasus (Gerasimova 2016; Gerasimova *et al.* 2018). However, only a small number of herbarium specimens were confirmed to belong to the species; therefore, its distribution in Russia remains insufficiently studied. *Bacidia laurocerasi* has a cosmopolitan distribution, having been recorded in Russia (Caucasus, Ural, Siberia, and the Far East), Europe, Macaronesia, Africa, North and South America, Asia, Australia, and New Zealand (Smith *et al.* 2009; Urbanavichus 2010). Both *B. biatorina* and *B. laurocerasi* are restricted to forests with high humidity in the Caucasus. *Bacidia biatorina* is mainly found in undisturbed, beech-dominated, humid, shaded forests of the middle mountain forest belt of the north-western Caucasus, while *B. laurocerasi* is found in cooler, humid middle and even upper beech- and fir-dominated mountain forest belts but also inhabits stream valleys and lowlands.

Suffusa group: several species or different populations?

Bacidia suffusa is mainly known from the eastern temperate region of North America, the Caucasus and Russian Far East (Ekman 1996; Otte 2007*a*; Gerasimova *et al.* 2018), and it was also recently recorded in South Korea (Lee & Hur 2022). The closely related *B. areolata* Gerasimova & A. Beck is known only from the Far East and is thus still considered endemic. The finding of *B. suffusa* in the Caucasus was surprising, as it indicates the species has a disjunct distribution across eastern North America and parts of Eurasia, including the Caucasus, but is absent in Europe (Otte 2007*a*). The species inhabits lower mountain belts of oak and beech, indicating it could be restricted to Tertiary relict floras that are common in parts of the Caucasus.

To confirm the relationship between North American, Far Eastern and Caucasian representatives, we included several specimens from different parts of the Caucasus in our phylogeny (Table 1). Our results indicate that sequences of *B. areolata* and *B. suffusa* form a strongly supported clade. In previous work, single-locus and combined nrLSU, mtSSU and *RPB*1 phylogenies indicate that Far Eastern *B. suffusa* and North American *B. suffusa* sequences are not monophyletic (Gerasimova *et al.* 2021*b*). Intriguingly, in our analyses, the newly sequenced Caucasian specimens of *B. suffusa* form a clade with the North American individuals that is sister to the Far Eastern *B. suffusa* clade. The nrITS sequences in these two clades differed by 3% (up to 15 nucleotides), suggesting substantial genetic differentiation; however, no significant morphological differences were found between them. Therefore, we suggest clades containing sequences from 1) the Far East and South Korea and 2) Caucasus, North America and South Korea are two populations of *B. suffusa* on the cusp of divergence into separate species.

Importantly, one of the sequences (JG182) was consistently retrieved as a sister to *B. areolata* and *B. suffusa* subclades in all phylogenies with the highest support. Morphological examination indicates clear differentiation from *B. areolata* and *B. suffusa* s. lat., strongly supporting the recognition of this individual as a new species. As a result, a new species, *Bacidia caucasica*, is described below (see 'Taxonomy').

Rubella group: the complex morphology of taxa

Bacidia rubella is one of the most widespread species of *Bacidia* s. str., occurring in the Holarctic and known from Europe, Macaronesia, Africa, Asia and North America (Ekman 1996; Llop 2007; Smith *et al.* 2009). In the Caucasus, it occurs in habitats with a wide range of humidity levels and light intensities, from dry, subtropical coastlines with *Juniperus,* to humid, dense, mid-mountain forests with *Abies nordmanniana*. It occurs in open upper mountain forest belts and has also been recorded from humid stream valleys, with evidence of natural or anthropogenic disturbance. Similar to *B. rubella*, *B. fraxinea* occurs across a wide range of habitats, found in the open, Mediterranean-like, drought-adapted forest vegetation of the Black Sea coast, in forest patches throughout agricultural areas of the forest-steppe region, and in lower mountain forest belts and higher-humidity habitats, in broad-leaved mesophilic forests. In lower mountain forest belts, *B. fraxinea* usually occurs in areas of relatively high humidity but is especially abundant in logged forests. Interestingly, the provisionally defined *B. inconspicua* ined. was also collected in young, dry, and warm secondary forest. This evidence leads to the conclusion that species from the Rubella group are most adapted to dry conditions, contrary to other *Bacidia* species.

This study included 14 additional specimens of both *Bacidia rubella* s. lat. and *B. fraxinea* s. lat. for sequencing and phylogenetic analysis. Whereas in the nrITS phylogeny, the Rubella group renders paraphyletic (viz. nesting *B. rubella*, *B. fraxinea*, and

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B. inconspicua ined.), the two- and three-locus phylogenies reveal six supported clades: 1) a large *B. rubella* s. str. clade comprising sequences from North America, Caucasus, Northern and Central Europe, and the Far East; 2) a newly defined *B. maritima* ined. from Caucasus (JG206 and JG208); 3) a clade of *B. fraxinea* from Caucasus (JG170 and JG205); 4) a clade of newly defined *B. inconspicua* ined. species from Caucasus (JG130) and Ukraine (*Vondrák* 12200, PRA); 5) a clade of endemic *B. elongata* from the Far East; 6) a clade of *B. obtecta*, endemic to the Far East (Figs 1 & 2). As we were not able to study the type material of the Mediterranean-European specimens of *Bacidia rubella* s. lat. and there are no sequence data available, we intend to obtain and include this data in our future studies. Nevertheless, we discuss the morphology of the Mediterranean representatives based on the literature summarized in Table 4.

Morphologically, *B. fraxinea* was mainly separated from *B. rubella* by thallus structure (Ekman & Nordin 1993). This separation was supported in the first phylogenetic study on *Bacidiaceae*, where the two species formed two sister clades (Ekman 2001), with a 1% (4 nucleotides) difference in the nrITS sequences. More recent studies of the nrITS2 secondary structure of *B. fraxinea* (*Johansson* 1620) and *B. rubella* (*Ekman* 3021) revealed one hemi-compensatory base change (hemi-CBC) in the structurally conserved regions of helix III (Gerasimova *et al.* 2018), also supporting the distinction of the species. However, subsequent single-gene and multilocus phylogenetic analyses resulted in a paraphyletic *Bacidia rubella* clade, where *B. fraxinea* (*Johansson* 1620) was frequently nested within the *B. rubella* s. str. clade (Gerasimova *et al.* 2018, 2021*b*); this result is consistent with our results from the analysis of an enlarged dataset.

As previously mentioned, the thallus structure is an essential character for distinguishing species in the Rubella group more broadly (Table 4). Thus, *B. fraxinea* is characterized by a thin, inconspicuous to thick, verrucose, wrinkled, and warted thallus (Ekman & Nordin 1993). In contrast, *B. rubella* s. str. is characterized by a granular thallus with isidia- to coral-like structures. Further delimitation based on thallus characteristics in later studies led to a description of two new taxa from the Mediterranean area: *Bacidia iberica* Aragón & I. Martínez and *B. parathalassica* Llop & Gómez-Bolea (Llop & Gómez-Bolea 1999; Aragón & Martínez 2003). The morphology of *B. iberica* and *B. parathalassica* is similar to *B. rubella*, but *B. iberica* has a thallus formed by the adpressed squamules, and *B. parathalassica* has a continuous, smooth to warted thallus, somewhat closer to *B. fraxinea* (Llop & Gómez-Bolea 1999; Aragón & Martínez 2003).

In addition to the thallus structure, the presence and distribution of crystals were used by Llop *et al.* (2007) to separate the taxa in the Rubella group, leading to the description of a new species, *B. thyrrenica* Llop. The authors distinguished two main groups: the first included *B. thyrrenica*, *B. rosella* and *B. rubella*, and the second was composed of *B. fraxinea*, *B. iberica* and *B. parathalassica*. The first group have crystals equally distributed in the upper part of the exciple, dissolving in K. However, sometimes *B. rubella* has been observed to have scarce crystals restricted to the uppermost part of the exciple (Llop *et al.* 2007). A second group have clusters of colourless to pale yellow crystals in the medullary part of the exciple that dissolve in acid solution (HNO_3). In all specimens, we observed colourless crystals, except for JG142 (Far East, *B. rubella* s. str. clade) and *B. inconspicua* ined. (*Vondrák* 12200, PRA) with yellow crystals in the exciple. *Bacidia obtecta* is also characterized by having crystals in the upper part of the hymenium and exciple, but these are colourless. However, as crystals are only occasionally present, we suggest this character is not consistent enough to differentiate the Rubella group taxa.

In addition to crystals, *B. fraxinea*, *B. iberica*, *B. rubella* and *B. parathalassica* are characterized by having one layer of more or less globose cells along the exciple margin. In the provisionally defined *B. inconspicua* ined. specimens, this character varies in two specimens (Table 4). In contrast, *B. elongata* and *B. obtecta* are characterized by having four layers of enlarged lumina cells along the exciple margin. Additionally, all species differ based on characteristics of spore size, hymenium height and apothecia colour (Table 4).

The newly introduced Bacidia inconspicua *ined.* This is represented by two specimens: one collected in the Caucasus (JG130) and one in Ukraine (*Vondrák* 12200, PRA). The *B. inconspicua* ined. specimen was collected in a young, dry, and warm secondary forest with pine trees and *Cladonia rangiferina* undergrowth; the original primary forest of oak and hornbeam, probably logged and replaced by ash and pine plantations. *Bacidia inconspicua* ined. is characterized by a prosoplectenchymatic exciple without enlarged cells along the exciple rim (JG130), with sometimes up to three layers of enlarged lumina cells (*Vondrák* 12200, PRA), in contrast to *B. iberica*, *B. fraxinea* s. str., *B. parathalassica* and *B. rubella* s. str., which are characterized by one layer of more or less globose cells (Table 4 and references therein, Fig. 4). Based on thallus structure and phylogenetic evidence using a multilocus dataset, it seems that *B. inconspicua* ined. may represent a separate species belonging to the Rubella group. However, as only two specimens were studied and in light of the high plasticity of the phenotypic characters in the Rubella group, we refrain from describing a new species and thus define *B. inconspicua* provisionally. A detailed description of all distinguishing morphological characters for *B. inconspicua* ined. is given in Table 4 and Fig. 4.

The newly defined Bacidia maritima *ined.* This is known from four specimens: JG131, JG172, JG206, and JG208 (Figs 1 & 2); although, from the first two specimens, a sequence could be obtained from only one locus (nrITS and *RPB2*, respectively). Interestingly, most specimens were collected near the Black and Caspian Seas coasts, suggesting that the species may be confined to the maritime zone. In more detail, JG206 was collected on the west coast of the Caspian Sea, *c.* 3 km from the coast, in a shaded forest very rich in epiphytic lichens (82 species in 1 ha). JG208 was collected on a south-east slope, *c.* 750 m from the Black Sea coast in a *Juniperus-Pistacia* forest in dry subtropic conditions, in a sunny, warm locality but apparently influenced by the proximity of the sea. The fog and high humidity favoured a rich epiphytic composition of lichens in this locality (71 species for 10–12 trees). JG131 was collected in a shaded pine forest also close to the south-east coast of the Black Sea. However, JG172, collected in the southern Caucasus region of Azerbaijan, was found at a site much further inland, seemingly without maritime influence, in a pastured, coppice-like mixed forest. However, the number of specimens of *Bacidia maritima* ined. known to date is too small to characterize its overall distribution with certainty; it seems that the affinity for coastal sites is more strongly expressed in the somewhat harsher climate of the northern Caucasus.

Morphological examination indicates *B. maritima* ined. has a similar thallus structure and coloration of the upper and inner apothecia to *B. rubella*. However, *B. maritima* ined. has shorter

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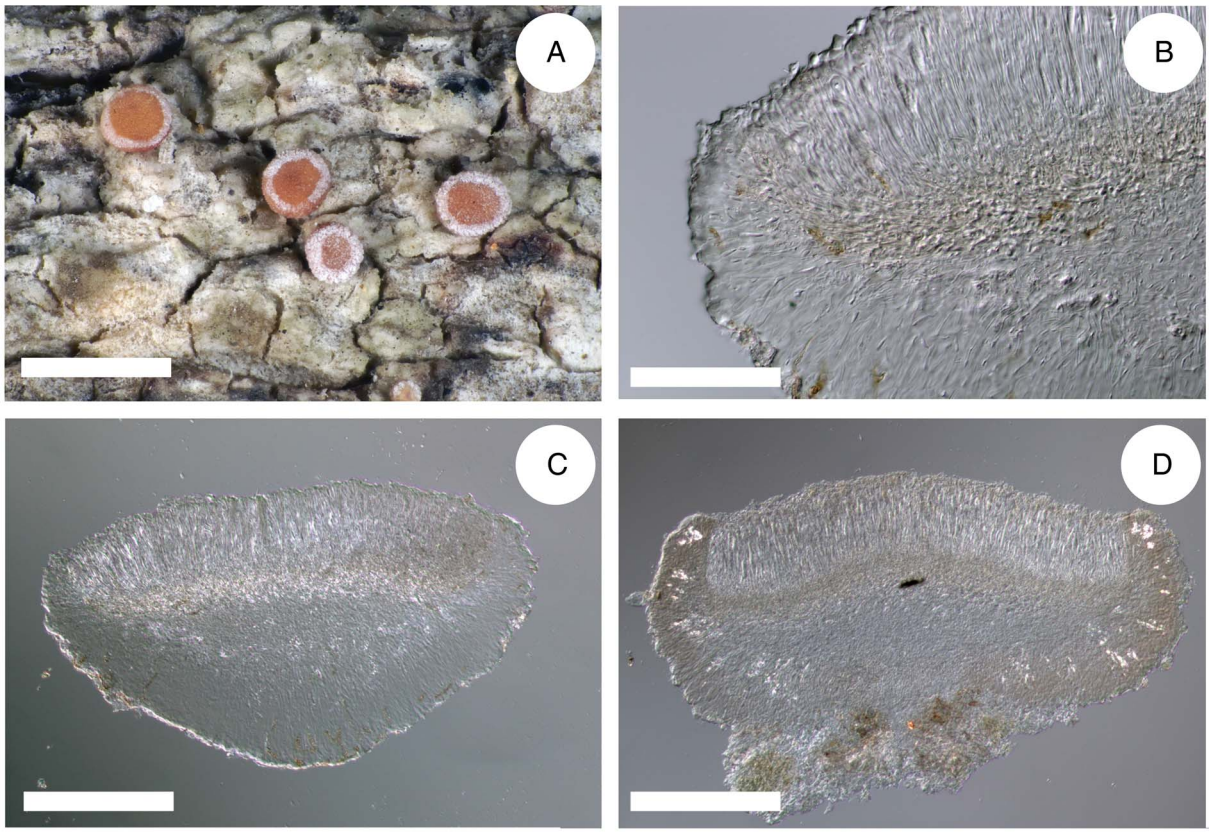

Figure 4. Cross-sections of apothecia and thallus structure of *Bacidia inconspicua* ined. (A–C, M-0182578; D, *J. Vondrák* 12200, PRA). A, smooth, inconspicuous thallus with orange pruinose apothecia. B, cross-section of apothecium with detailed exciple structure. C, cross-section of apothecium viewed using a polarized filter. D, cross-section of apothecium with yellow clusters of crystals arranged in the lateral part of the exciple viewed using a polarized filter. Scales: A = 1 cm; B–D = 100 µm. In colour online.

spores than *B. rubella*, similar to *B. iberica* and *B. parathalassica*. The mean spore size of *B. rubella* from the Caucasus is 47.8 ± 6.6 µm (up to 75 µm) × (1.5–)2.7 ± 0.4(–4) µm wide, and they have up to 12 septa. The mean spore size of European *B. rubella* individuals is 40–70 µm (up to 84 µm) × 2.5–3(–4) µm wide with up to 13 septa, and of *B. rubella* North American individuals is 44–63 µm (up to 104 µm) × (2.1–)2.4–2.7–3.2(–4.3) µm wide with up to 13 septa (Table 4). On the contrary, the spores of *B. maritima* ined. are 48 ± 6.7 µm (up to 65 µm) × (2–)2.65 ± 0.3(–3.5) µm wide with up to 10 septa. Nevertheless, to clearly distinguish between the taxa, additional specimens are necessary for a more detailed description and measurement of spores; therefore, we refrain from describing a new species here.

Polychroa group: the presence of an unpigmented member

Bacidia polychroa is another widespread species of *Bacidia* s. str., occurring in Europe, North and South America and Asia (Ekman 1996; Llop 2007; Smith *et al.* 2009). *Bacidia albogranulosa* is known from the Czech Republic, Poland, Ukraine and the Caucasus (Malíček *et al.* 2018). Conversely, *Bacidia diffracta* and *B. sachalinensis* are known only as endemics from North America and the Russian Far East, respectively. *Bacidia polychroa* is particularly common in stream valleys but also inhabits humid lower and middle mountain forest belts of the north-western Caucasus. It is the most abundant *Bacidia* species in these forest belts of the north-western Caucasus and is usually found in shaded places with the young regrowth of coppiced trees.

We included 16 specimens of *B. polychroa* from the Caucasus in our phylogeny, encompassing its observed morphological variation. The nrITS analysis also included a European sequence (Fig. 2) and resulted in a well-supported clade of *B. polychroa* in the multilocus phylogeny. All taxa within the Polychroa group share the pigment Polychroa-brown in the hypothecium, exciple and hymenium, and a distinguishing K+ purplish reaction in apothecial cross-sections. This purple reaction is unknown for *B. albogranulosa* since it is known only in its sterile form (Malíček *et al.* 2018) and was also not observed in the sister JG188, represented by pale or almost unpigmented apothecia. The specimen JG188 is characterized by its warted thallus similar to *B. polychroa*, but has very bright apothecia, which do not have a K+ purplish reaction. The lack of a K+ purplish reaction makes it easily confused with *B. fraxinea*. Other specimens of *B. polychroa* from the large clade also contained pale or unpigmented apothecia lacking the characteristic K + purplish reaction. Therefore, despite distinct morphological characters, we did not find enough evidence to support the circumscription of a new species in this study.

Taxonomy

Bacidia caucasica Gerasimova, Otte & A. Beck sp. nov.

MycoBank No.: MB 847536

Similar to *Bacidia suffusa* but differs by abundant colourless crystals above the exciple edge and upper hymenium, and the

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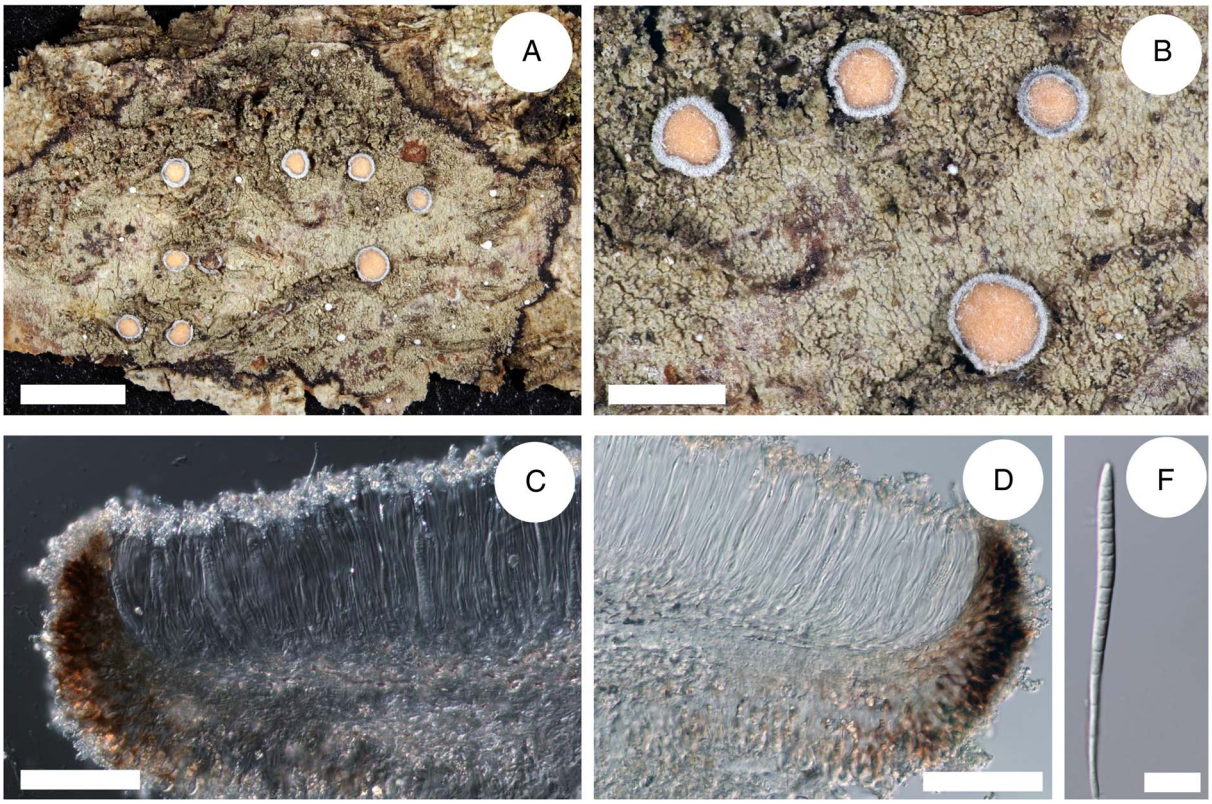

Figure 5. Cross-section of apothecia and thallus structure of *Bacidia caucasica* (GLM-0048447, holotype). A, general overview of apothecia and thallus structure with the distinct black prothallus. B, detail view of apothecia and thallus structure, yellow apothecia with a dark pruinose margin. C, clusters of crystals in the upper part of hymenium. D, cross-section of apothecia with detailed exciple structure. E, acicular multiseptate spore. Scales: A = 3 cm; B = 1 cm; C–D = 100 µm; E = 10 µm. In colour online.

prominent yellow coloration of the apothecia with darker, almost black, thinner margin.

Type: Russia, Adygea, Maykopskiy Rayon, im Sachraital, 44.12′N, 40.33′E, 715 m a.s.l., on the bark of *Corylus avellana*, 17 September 2015, *V. Otte* s. n. (GLM-L-0048447—holotype).

(Fig. 5)

Thallus indeterminate, thin, rimose, partly smooth, mainly consisting of single or contiguous, more or less roundish or irregularly shaped warts. Warts ±flat, adnate to and only slightly raised above the surface; when spreading on mosses, the thallus is more or less granular; green-grey to dark green. *Prothallus* presents as a black line bordering the thallus. *Photobiont* chlorococcoid.

Apothecia 0.7–1.1 mm diam. ($n_1 = 1$, $n_2 = 8$), ±flat or with a margin slightly above the disc. *Disc* dark yellow to orange, slightly pruinose. *Margin* dark brown to black, covered by thick white pruina. *Hymenium* 84–125–150 µm tall ($n_1 = 1$, $n_2 = 5$), with crystals in the upper part (from pruina) not dissolving in K and N. *Epithecium* pale orange, almost colourless. *Hypothecium* straw-coloured, almost colourless. *Exciple* 37–42.5 µm wide ($n_1 = 1$, $n_2 = 4$), without or with minor crystals along the rim (from pruina) not dissolving in K and N. Rim dark brown, with two layers of enlarged more or less globose lumina cells, 5–8 µm wide and 7–10 µm long ($n_1 = 55$, $n_2 = 10$); the lateral part brown to dark brown, paler closer to hymenium, with crystals less than 0.5 µm or up to 5 µm, not dissolving in K and N. Medullary part under hypothecium pale straw to almost colourless. *Paraphyses* simple, 1–2.5 µm wide with apices ±clavate or not swollen. *Ascospores* acicular, (48–)57.8 ± 9.6(–71) µm long and (2–)3.3 ± 0.6(–5) µm wide ($n_1 = 1$, $n_2 = 44$), with (3–)10 ± 4(–15) septa ($n_1 = 1$, $n_2 = 44$).

Chemistry. Hypothecium and exciple K+ yellow; brown parts of exciple N+ purplish brown.

Pigments. Rubella-orange in epithecium; Laurocerasi-brown in rim and lateral part of exciple.

Etymology. The epithet ‘caucasica’ refers to the locality where the species was collected.

Habitat and distribution. The specimen was collected in a moist, mixed forest in a valley on the bark of *Corylus avellana*. The species is so far known only from a single collection in the Caucasus area.

Comments. Bacidia caucasica differs from the closely related *B. suffusa* primarily by abundant colourless crystals along the exciple edge and upper hymenium, the prominent yellow coloration of the apothecia with darker, almost black, thinner margin, and a thallus consisting of single or contiguous, more or less roundish or irregularly shaped warts (Fig. 5).

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Bacidia heterochroa (Müll. Arg.) Zahlbr.

Bacidia heterochroa is distributed throughout the tropics and subtropics (Ekman 1996). It is recorded in India, Central and South America, Thailand, Macaronesia and North America (Ekman 1996; Breuss 2001, 2018; Aptroot *et al.* 2007; Diederich & Lawrey 2007; Joseph & Sinha 2012; Etayo & Berger 2013; Aptroot & Spielmann 2020), and it has recently been found in South Korea (Lee & Hur 2022). Here, we report *B. heterochroa* for the Caucasus and Russia for the first time, representing the northernmost subtropical locality for the species. The individuals of *B. heterochroa* from the Caucasus were collected in the warm-wet Colchic region in a humid floodplain locality. Interestingly, these individuals were nested in the clade, sister to the Suffusa and Schweinitzii groups, which are also particularly abundant in the oceanic and temperate warm climates of Asia and North America (Ekman 1996; Lendemer *et al.* 2016).

Bacidia heterochroa collected in the present study is characterized by having one layer of enlarged lumina cells along exciple edge (up to 6 × 8 µm); a thallus whitish, grey to green-grey, consisting of thin adnate warts, rimose; apothecia black or dark brown with a margin of the same colour, paler below; epithecium dark brown, almost black; exciple edge dark red-brown or brown; lateral part pale brown, yellow-brown, brown to reddish brown; medullar part yellow to nearly colourless, paler than hypothecium; hypothecium yellow; hymenium (61.5–)85.6 ± 16.1(–122.5) µm; exciple (49–)68.4 ± 13.4(–88) µm. The characteristics of thallus and apothecia correspond to those provided by Ekman (1996) for North America. However, the ascospores are shorter (22–56 × 2.5–4.3 µm) with up to 11 septa compared to ascospores of *B. heterochroa* from North America that are longer (32–73 × 2.5–4.3 µm) with up to 15 septa.

The studied type material of *B. heterochroa* is characterized by the dark brown, brown-purplish epithecium with a distinct K+ purplish reaction. In addition, the dark brown to black apothecia have brighter brown margins, at least in the lower part towards the base. These characteristics match those of *B. heterochroa* from the Caucasus. The specimens of *B. heterochroa* from South Korea have a dark brown epithecium (K+ purplish) and dark brown apothecia with concolourous margins (Lee & Hur 2022). These characters resemble the closely related *B. laurocerasi* s. str. and probably represent a separate species. Nevertheless, *B. heterochroa* from the Caucasus was retrieved on a very long branch, suggesting that additional lineages may be missing from the analysis and that further detailed examination of specimens is necessary.

Additional specimens examined. **Georgia:** *Ochamchirskiy Rayon*: the Abkhazian Research Forest Experimental Station, 22 viii 2012, *J. Gerasimova* (LE L-11663, LE L-12975, LE L-12974, M-0182575); *ibid*., 22 viii 2012, *L. Gagarina* (LE L-11635, LE L-11621, LE L-11625, LE L-11626, LE L-11979); *ibid*., 23 viii 2012, *L. Gagarina* (LE L-11980). *Gudautskiy Rayon*: Ritsa Strict Nature Reserve, 14 viii 2012, *J. Gerasimova* (LE L-11656).— **Russia:** *Krasnodarskiy Krai*: Schachetal oberhalb von Solochaul, 24 viii 2016, *V. Otte* (GLM-L-0048864, GLM-L-0048863); *ibid*., 25 viii 2016, *V. Otte* (GLM-L-0048909).

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Author Contribution. AB and JG designed the study; JG performed the experiments and wrote the first draft of the manuscript; VO, IU and GU provided specimens; all authors contributed to the draft and revised the manuscript.

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