


## Research Article

Phylogenetic relationships within *Pyrenodesmia* sensu lato and the role of pigments in its taxonomic interpretationIvan Frolov<sup>1,2\*</sup> , Jan Vondrák<sup>2,3</sup>, Jiří Košnar<sup>2</sup>, and Ulf Arup<sup>4</sup><sup>1</sup>Russian Academy of Sciences, Ural Branch: Institute Botanic Garden, Vosmogo Marta 202a st., Yekaterinburg 620144, Russia<sup>2</sup>Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 1760, České Budějovice CZ-370 05, Czech Republic<sup>3</sup>Institute of Botany of the Czech Academy of Sciences, Zámek 1, Průhonice CZ-252 43, Czech Republic<sup>4</sup>Botanical Museum, Lund University, Box 117, Lund SE-221 00, Sweden

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**Abstract** Most lichens of the family Teloschistaceae (Ascomycota) produce yellow-orange-red anthraquinone pigments. However, the genus *Pyrenodesmia* encompasses species in which anthraquinones are absent and replaced by a gray pigment Sedifolia-gray. It was shown recently that these species are related to taxa with both anthraquinones and Sedifolia-gray (*Caloplaca xerica* group, *C. haematites* group, and *C. cretensis*) and to species with a brown pigment instead of both anthraquinones and Sedifolia-gray (*C. demissa*, *C. obscurella*, and *C. reptans*). Nevertheless, relationships between mentioned anthraquinone-containing and anthraquinone-lacking species remained unclear. In total, 8 DNA loci from 41 species were used here to resolve these uncertainties. We concluded that *C. demissa*, *C. obscurella*, and *C. reptans* are rather distant from the core of *Pyrenodesmia*, and we place them outside of *Pyrenodesmia* sensu lato. Within *Pyrenodesmia* sensu lato, three lineages were revealed and recognized on a generic level: the genus *Pyrenodesmia* sensu stricto (21 species), the genus *Kuettlingeria* (14 species), which is resurrected here, and the genus *Sanguineodiscus* (4 species), which is newly described here. The genus *Pyrenodesmia* includes taxa that never contain anthraquinones, but Sedifolia-gray. It matches with the former *C. variabilis* group. Taxa of the genera *Kuettlingeria* and *Sanguineodiscus* have anthraquinones in their apothecia and Sedifolia-gray in their thalli. The genus *Kuettlingeria* includes the former *C. xerica* group plus *C. cretensis* and *C. diphyodes*. The genus *Sanguineodiscus* includes the former *C. haematites* group and *C. bicolor*. The identity of *Kuettlingeria* (*Caloplaca*) *diphyodes* was clarified and the name *Pyrenodesmia helygeoides* was resurrected. Twenty-four new combinations were proposed.

**Key words:** anthraquinones, *Caloplaca haematites* group, *Caloplaca variabilis* group, *Caloplaca xerica* group, *Kuettlingeria*, *Pyrenodesmia* sensu stricto, *Sanguineodiscus*, Sedifolia-gray, Teloschistaceae.

## 1 Introduction

The majority of lichens belonging to the family Teloschistaceae produce yellow-orange-red anthraquinone pigments in their superficial tissues (e.g., Søchting, 1997). Some Teloschistaceae species, however, lack anthraquinones in their thalli or both thalli and apothecia. Instead of anthraquinones (or together with them), they synthesize different pigments (green, gray, brown, and in some exotic species others) of an unknown structure such as Cinereorufa-green (Wetmore, 1996; Arup et al., 2007) and Sedifolia-gray (e.g., Meyer & Printzen, 2000; Vondrák et al., 2012), which may have the same function as anthraquinones, namely protection against UV radiation (e.g., Hauck et al., 2007). These pigments are not extracted in acetone and cannot be revealed by TLC, but they are detectable in sections of tissue. Sedifolia-gray is gray in section and has a violet reaction with potassium hydroxide and with nitric acid. Cinereorufa-green is green in section and has a purple reaction with nitric acid only. Species lacking anthraquinones in thalli or both thalli

and apothecia do not form a monophyletic group (e.g., Wunder, 1974; Kärnefelt, 1989; Wetmore, 1994; Vondrák et al., 2012; Arup et al., 2013), but belong to different lineages within Teloschistaceae, for example, the genera *Blastenia*, *Caloplaca* sensu stricto, and *Parvoplaca*, or have an unresolved generic position, for example “*Caloplaca*” *ahtii* and “*C.*” *conversa*.

*Pyrenodesmia* is another generic name originally employed for members of the Teloschistaceae characterized by the total absence of anthraquinones. Author of the genus, Massalongo (1852), used the name for a small group of lichens with clear morphological and ecological characteristics. He accommodated there four species (*P. agardhiana*, *P. chalybaea*, *P. olivacea*, and *P. variabilis*) and three infraspecific taxa (*P. variabilis* β. *lilacina*, *P. variabilis* δ. *pulchella*, and *P. variabilis* γ. *fusca*) lacking anthraquinones and with Sedifolia-gray both in their thallus and apothecia, which inhabit calcareous outcrops. However, later lichenologists used this generic name much wider including to the genus also species with anthraquinones (e.g., *Caloplaca*

*monacensis* and *Flavoplaca citrina*) which are not related to the taxa of *Pyrenodesmia* sensu Massalongo as it was shown by Vondrák et al. (2009), Šoun et al. (2011), Arup et al. (2013), etc.

Zahlbruckner (1930–1931) included *Pyrenodesmia* in *Caloplaca*, but numerous later authors maintained the species without anthraquinones on limestone as a distinct infrageneric group. Wunder (1974) and Kärnefelt (1989) named it “*Caloplaca variabilis* group”. Clauzade and Roux (1985) called it “subgenus *Pyrenodesmia*”; however, they also included species that are not related to *C. variabilis* (e.g., *C. conversa* and *C. turkuensis*). Rudolph (1955) kept the genus *Pyrenodesmia* separately, but included many unrelated species with anthraquinones (e.g., *Athallia pyracea*, *Gyalolechia flavovirescens*, and *Polycauliona bolacina*). Above-mentioned concepts were revised by the analysis of three DNA loci by Arup et al. (2013), who resurrected the genus *Pyrenodesmia*, as it was understood by Massalongo (1852). However, in the phylogeny inferred by Arup et al. (2013), the genus did not seem to be monophyletic unless the species of the so-called *Caloplaca xerica* group with orange apothecia were incorporated. As a result, the authors recognized the genus *Pyrenodesmia* sensu stricto and the informal group *Pyrenodesmia* sensu lato. In their three loci phylogenetic reconstruction, *Pyrenodesmia* sensu stricto did not form a monophyletic clade, but *Pyrenodesmia* sensu lato did. The former includes the genus type *P. chalybaea* and some closely related species that lack anthraquinones, but possess Sedifolia-gray; the latter also includes species with Sedifolia-gray in the thallus, but with anthraquinones in the apothecia—the *C. xerica* group (also see Gaya et al., 2008; Vondrák et al., 2012). Finally, Arup et al. (2013) kept in the genus *Pyrenodesmia* six species, whereas taxa of the *C. xerica* group remained under the formal generic name “*Caloplaca*”, pending more robust data. However, already in 1857, Trevisan established the separate genus *Kuettlingeria* for some species of this currently informal group.

According to some other authors, *Pyrenodesmia* sensu lato may include other species with Sedifolia-gray in the thallus, but with anthraquinones in the apothecia: the *C. haematites* group (Hodkinson & Lendemer, 2012; Vondrák et al., 2012) and *C. cretensis*, an endolithic calcareous lichen occurring in the Mediterranean (Muggia et al., 2008).

It was also demonstrated that some species lacking both anthraquinones and Sedifolia-gray, but possessing other unknown brown pigments, namely *C. demissa*, *C. obscurella*, and *C. reptans*, may belong to *Pyrenodesmia* sensu lato. *Caloplaca demissa*, placed there by Arup et al. (2013), is a lobate sorediate species known only as a sterile crust on dry vertical faces of siliceous rocks in Europe and North America. *Caloplaca obscurella*, an epiphytic sorediate crust, which occurs mainly in boreal and temperate forests of Holarctic, formed a sister lineage with an unsupported clade of *Pyrenodesmia* in the study of Vondrák et al. (2012) and was included in the *Pyrenodesmia* clade by Muggia et al. (2008). *Caloplaca reptans*, a crustose sorediate lichen that is rarely fertile, is widespread in humid habitats on non-calcareous, sheltered rocks in Appalachian forests. Hodkinson and Lendemer (2012) showed that *C. reptans* is close to *Pyrenodesmia*.

To elucidate the taxonomy and phylogenetic relationship among taxa putatively belonging to *Pyrenodesmia*, we tried to answer following questions:

1. Do the species completely without anthraquinones, but with Sedifolia-gray, form a monophyletic group that merits recognition at generic rank as *Pyrenodesmia*?
2. Are the anthraquinone-containing groups, the *C. haematites* group and the *C. xerica* group, monophyletic, and do they merit recognition at generic rank? Can we resurrect the generic name “*Kuettlingeria*” for the *C. xerica* group?
3. Are the species lacking both anthraquinones and Sedifolia-gray, *C. demissa*, *C. obscurella*, and *C. reptans*, related to *Pyrenodesmia*?

## 2 Material and Methods

### 2.1 Sampling

Specimens were collected mainly by the first two authors and were deposited in PRA (J. Vondrák) and I. Frolov's personal herbarium. Other specimens for molecular investigations were kindly provided by the herbaria KW, NY, TSB, UCR, XJU, and by Mehmet Gökhan Halıcı and Toby Spribille from their personal collections.

### 2.2 DNA extraction and amplification

DNA was extracted with a CTAB-based protocol (Aras & Cansaran, 2006). For each sample, we sequenced as many as possible of eight DNA loci: (i) two nuclear ribosomal markers included the internal transcribed spacer regions 1 and 2 with the embedded 5.8S region (ITS), the nuclear ribosomal large subunit (nucLSU), (ii) mitochondrial ribosomal small subunit (mtSSU), and (iii) five protein-coding nuclear loci, parts of the largest and second largest subunits of RNA polymerase II (RPB1 and RPB2, respectively), a part of DNA replication licensing factor minichromosome maintenance complex component 7 (MCM7), a partial sequence of transcription elongation factor 1 alpha (EF1a), and a part of the beta-tubulin gene making up microtubules, major components of the cytoskeleton (TUBB). Polymerase chain reactions (PCRs) were performed in a reaction mixture containing 2.5  $\mu$ M MgCl<sub>2</sub>, 0.2  $\mu$ M of each dNTP, 0.3  $\mu$ M of each primer, 0.5 U Taq polymerase (Top-Bio, Praha, Czech Republic) in the manufacturer's reaction buffer, and sterile water to make up a final volume of 10  $\mu$ L. Primers and annealing temperatures used are listed in Table 1. Each sequence is provided with a GenBank accession number (Table 2).

### 2.3 Sequence alignment and phylogenetic reconstructions

Sequences were edited in FinchTV 1.4.0 (Geospiza, Inc.; Seattle, WA, USA; <http://www.geospiza.com>) and BioEdit 7.2.5 (Hall, 1999) and aligned online by MAFFT 7 (Katoh & Standley, 2013; available at <http://mafft.cbrc.jp/alignment/server/>) with the L-INS-i method (Katoh et al., 2005). Alignments were checked for obvious errors and corrected in BioEdit 7.2.5 when needed. To exclude ambiguously aligned positions, alignments were subsequently cleared by

**Table 1** Polymerase chain reaction primers used in this study

Name	Sequence (5'–3')	Annealing temperature (°C)	Source
ITS 1F	CTTGGTCATTTAGAGGAAGTAA	55	Gardes & Bruns (1993)
ITS 4	TCCTCCGCTTATTGATATGC	55	White et al. (1990)
Bt3LM	GAACGTCTACTTCAACGAG	55	Myllys et al. (2001)
Bt10LM	TCGGAAGCAGCCATCATGTTCTT	55	Myllys et al. (2001)
Mcm7-CF2	GGTCAACGCCTACACCTG	55	Designed here
Mcm7-CR2	GATGTCGCCACGIATCTT	55	Designed here
RPB1_191F	ACCGTGGTATTAGGTGTGGGACTTG	54	Designed by F. Fernández-Mendoza
RPB1_1082R	TCCATGTAGGTTCGCAACGTGGAATT	54	Designed by F. Fernández-Mendoza
RPB2-CF1	CTCTTCCAAAAGCTGACAAA	54 or 57	Designed here
RPB2-CR2	CCCATAGCGGATTGGTAIGT	54 or 57	Designed here
nu-LSU-155-5'	GGGTCCGAGTTGTAATTTGT	56	Arup et al. (2013)
LR5	TCCTGAGGGAACTTCG	56	Arup et al. (2013)
mtSSU1	AGCAGTGAGGAATATTGGTC	52	Arup et al. (2013)
mtSSU7	GTCGAGTTACAGACTACAATCC	52	Arup et al. (2013)
EFA_713F	GTCACCGCGATTTTCATCAAGA	58	Designed by F. Fernández-Mendoza
EFA_1453R	CCACGACGGATTTTCCTTGAC	58	Designed by F. Fernández-Mendoza

the *automated1* algorithm, as implemented in the trimAl software package (Capella-Gutierrez et al., 2009). Concatenated alignments were deposited in TreeBASE (Submission ID 23651).

To circumscribe *Pyrenodesmia* sensu lato, we compiled the Caloplacoideae alignment with five concatenated DNA loci: ITS, mtSSU, nuLSU, RPB1, and RPB2. This included 78 specimens (76 species; Table 2) and consisted of 148 single-locus sequences from 37 specimens published by Gaya et al. (2015), together with our 200 single-locus sequences from 41 specimens. The main Caloplacoideae groups and potential members of *Pyrenodesmia* sensu lato are represented in the alignment. The tree was rooted using several lineages of Teloschistoideae and Xanthorioideae as an outgroup.

To check the obtained phylogenetic scheme within *Pyrenodesmia* sensu lato, we compiled the *Pyrenodesmia* alignment with eight concatenated DNA loci including all the loci presented in the Caloplacoideae alignment plus EF1a, MCM7, and TUBB. The *Pyrenodesmia* alignment consists of 40 specimens (=species) involving 230 single-locus sequences. Eight-loci coverage was complete for 16 specimens, seven loci were obtained for 19 specimens, six loci were obtained for three specimens, and five and/or four loci for one specimen (Table 2). The species were selected on the basis of the previously analyzed Caloplacoideae alignment to include species of the *Pyrenodesmia* sensu lato clade (Fig. 1). The tree was rooted using *Caloplaca conversa* and *C. reptans* as an outgroup.

For both alignments, phylogenetic reconstructions were carried out using maximum likelihood (ML) and Bayesian inference (BI). The ML phylogenetic analysis was performed using RAxML v8.2.10 (Stamatakis, 2014) and BI using MrBayes 3.2.6 (Ronquist & Huelsenbeck, 2003). Analyses were run on the CIPRES Web Portal (<http://www.phylo.org/portal2/>). Optimum partitioning of the data sets and the optimum substitution models per partition were calculated in PartitionFinder2 using greedy algorithm and corrected Akaike Information Criterion (Lanfear et al., 2016). In the input file for PartitionFinder, we created partitions (i) for intronic and exonic fractions separately, with the three codon positions independently in the protein-coding genes, and (ii) for ITS1, ITS2, and 5.8S separately in ITS,

and (iii) mtSSU and nuLSU were analyzed as whole fragments. PartitionFinder retained four subsets of partitions for the Caloplacoideae alignment and five subsets of partitions for the *Pyrenodesmia* alignment. Results of the analyses in PartitionFinder are shown in Table S1. In MrBayes, analyses were performed using two independent runs with four MCMC chains. Trees were sampled after every 500th generation. The analyses were stopped when the average standard deviation of the split frequencies between the simultaneous runs dropped below 0.01. The first 25% of trees were discarded as the burn-in phase, and the remaining trees were used for construction of a 50% majority-rule consensus tree. The ML analysis was employed using the GTR+G model. Bootstrap support was calculated on 1000 bootstrap pseudoreplicates using rapid bootstrapping. A clade is considered to be supported with posterior probability  $\geq 0.95$  in BI and bootstrap value  $\geq 70\%$  in ML.

To check for topological incongruences, single-gene alignments were analyzed separately using BI, as described above. The differences in topology of single-gene trees were considered for the branches with posterior probability support values  $\geq 0.95$ . If the incongruences were due to odd clustering of a few individual samples, repeated PCR and sequencing were used to exclude the possibility of sample contamination.

## 2.4 Chemistry

Anthraquinones in the apothecial disc and the true exciple were identified using thin-layer chromatography (TLC). Although the TLC detects primarily the major substances, it is sufficient for separation of the main chemosyndromes in Teloschistaceae (sensu Søchting, 1997, 2001). We carried out the TLC in solvents A, B, and C according to Orange et al. (2001).

## 3 Results

### 3.1 Circumscription and content of *Pyrenodesmia* sensu lato: results from the five-loci Caloplacoideae data set

Both BI (Fig. 1) and ML (Fig. S1) analyses of the concatenated alignment showed the same result referring to clades

**Table 2** Voucher information and GB accession numbers of samples included in this study

Species	Locality (country, region)	Vouchers	Source	ITS	mtSSU	nucLSU	RPB1	RPB2	EF1a	MCM7	TUBB
<i>Athalia nesodes</i>	USA, California	DUKE s.n.	Gaya et al. (2015)	KT291457	KT291495	KT291548	KT291585	KT291635	–	–	–
<i>Blastenia</i>											
<i>catalinae</i>	USA, California	DUKE s.n.	Gaya et al. (2015)	KT291445	KT291477	KT291532	KT291572	–	–	–	–
<i>Blastenia</i>	Sweden,	BCN s.n.	Gaya et al. (2015)	JQ30166	JQ301489	–	JQ301711	–	–	–	–
<i>crenularia</i>	Bohuslän										
<i>Caloplaca</i>											
<i>cerina</i>	USA, Alaska	DUKE s.n.	Gaya et al. (2015)	–	JQ301483	JQ301549	–	JQ301744	–	–	–
<i>Caloplaca</i>	Chile, P.N. Fray										
<i>chilensis</i>	Jorge	SGO s.n.	Gaya et al. (2015)	JQ301660	JQ301485	JQ301551	JQ301709	–	–	–	–
<i>Caloplaca</i>	Mexico, Baja										
<i>cinnabarina</i>	California	DUKE s.n.	Gaya et al. (2015)	–	–	KT291538	KT291578	KT291624	–	–	–
<i>Caloplaca</i>	Iceland, Sudur-										
<i>cinnamomea</i>	Thingeyjarsysla	DUKE s.n.	Gaya et al. (2015)	–	JQ301487	JQ301552	JQ301710	–	–	–	–
<i>Caloplaca</i>	Mexico, Baja										
<i>conversa 1</i>	California	DUKE s.n.	Gaya et al. (2015)	KT291450	KT291504	KT291554	KT291589	KT291643	–	–	–
<i>Caloplaca</i>		J. Vondrák									
<i>conversa 2</i>	Iran, Hashpar	5538 (PRA) J. Vondrák	Original	<b>MH104924</b>	<b>MH100782</b>	<b>MH100750</b>	–	<b>MH119818</b>	<b>MH153698</b>	<b>MH119855</b>	<b>MH153729</b>
<i>Caloplaca</i>											
<i>demissa</i>	Spain, Tenerife	(PRA) 13127	Original	<b>MH104937</b>	<b>MH100784</b>	<b>MH100752</b>	–	<b>MH119844</b>	–	–	–
<i>Caloplaca</i>											
<i>gloriae</i>	Spain, Almería	P.v.d. Boom Herb. 38420	Gaya et al. (2015)	–	–	JQ301555	JQ301712	JQ301752	–	–	–
<i>Caloplaca</i>	Slovakia, Low										
<i>Caloplaca</i>	Tatras										
<i>isidigera</i>	mountains	PRA s.n.	Gaya et al. (2015)	KT291460	JQ301492	JQ301556	JQ301713	JQ301753	–	–	–
<i>Caloplaca</i>		J. Vondrák									
<i>obscura</i>	Russia, Tuapse	7641 (PRA)	Original	<b>MH104938</b>	–	<b>MH100762</b>	–	–	–	–	–
<i>Caloplaca</i>	Mexico, Baja										
<i>peludella</i>	California	DUKE s.n.	Gaya et al. (2015)	–	KT291505	KT291555	KT291590	KT291644	–	–	–
<i>Caloplaca</i>		J. Lendemer									
<i>reptans</i>	USA, Virginia	48186 (NY)	Original	<b>MH104934</b>	<b>MH100796</b>	<b>MH100766</b>	<b>MH141573</b>	<b>MH119819</b>	–	–	–
<i>Caloplaca</i>											
<i>santessoniana</i>	Chile, P.N. Pan										
ad int.	de Azúcar	DUKE s.n.	Gaya et al. (2015)	KT291463	KT291508	KT291558	KT291592	KT291647	–	–	–
<i>Gyalolechia</i>	Estonia,	P. Alanko									
<i>bracteata</i>	Saaremaa	121555 (H)	Gaya et al. (2015)	AF277666	JQ301502	JQ301566	–	–	–	–	–

Continued

Table 2 Continued

Species	Locality (country, region)	Vouchers	Source	ITS	mtSSU	nucLSU	RPB1	RPB2	EF1a	MCM7	TUBB
<i>Gyalolechia canariensis</i>	Spain, Canary Islands	TFC Lich: 3593, duplic.	Gaya et al. (2015)	EU639587	KT291516	KT291562	KT291599	KT291655	–	–	–
<i>Gyalolechia flavorubescens</i>	unidentified	unidentified	Gaya et al. (2015)	AF279887	AY143403	AF279887	–	–	–	–	–
<i>Gyalolechia stipitata</i>	Mexico, Baja California	DUKE s.n. U. Søchting	Gaya et al. (2015)	KT291465	KT291490	KT291543	KT291582	KT291630	–	–	–
<i>Huea cerussata</i>	South America	s.n. A. Aprroot 56827 (ABL)	Gaya et al. (2015)	–	KT291519	–	KT291601	KT291658	–	–	–
<i>Ioplaca pindarensis</i>	China, Yunnan prov.	DUKE s.n.	Gaya et al. (2015)	JQ301672	–	–	JQ301718	JQ301763	–	–	–
<i>Kuettlingeria atroflava</i> 1	USA, California	DUKE s.n.	Gaya et al. (2015)	KT291444	KT291511	KT291560	KT291593	KT291650	–	–	–
<i>Leprolaca proteus</i>	Spain, Catalonia	BCN 13706 T. Spribille 12970 (B)	Gaya et al. (2015)	EU639613	KT291507	KT291557	–	KT291646	–	–	–
<i>Leprolaca xantholyta</i>	Greece, Crete	BCN s.n.	Gaya et al. (2015)	JQ301670	JQ301501	JQ301565	–	JQ301761	–	–	–
<i>Polycauliona candalaria</i>	Sweden, Halland	BCN s.n.	Gaya et al. (2015)	EU639625	JQ301528	JQ301587	JQ301732	JQ301782	–	–	–
<i>Pyrenodesmia chalybaea</i> 1	Sweden, Gotland	BCN s.n.	Gaya et al. (2015)	JQ301659	JQ301484	JQ301550	JQ301708	JQ301745	–	–	–
<i>Rufoplaca scotoplaca</i>	Sweden, Bohuslän	BCN s.n.	Gaya et al. (2015)	JQ301665	JQ301497	JQ301561	JQ301715	JQ301756	–	–	–
<i>Seiophora californica</i>	Mexico, Baja California	DUKE s.n. U. Søchting	Gaya et al. (2015)	KT291470	KT291521	KT291564	KT291602	KT291660	–	–	–
<i>Seiophora contortuplicata</i>	Tajikistan	s.n.	Gaya et al. (2015)	KT291471	KT291522	–	KT291603	KT291661	–	–	–
<i>Seiophora lacunosa</i>	Spain, Alacant	BCN, herb. Gaya 391	Gaya et al. (2015)	JQ301683	JQ301517	JQ301575	JQ301724	JQ301771	–	–	–
<i>Teloschistes nodulifer</i>	Peru, Tarma province	DUKE s.n.	Gaya et al. (2015)	–	KT291524	KT291566	KT291605	KT291663	–	–	–
<i>Usnochroma carphinea</i>	Spain, Catalonia	BCN 13714 P.v.d. Boom	Gaya et al. (2015)	EU639595	JQ301482	JQ301548	JQ301707	KT291621	–	–	–
<i>Usnochroma scoriophila</i>	Spain, Almería	Herb. 38386	Gaya et al. (2015)	JQ301664	JQ301496	JQ301560	JQ301714	JQ301755	–	–	–
<i>Variospora aurantia</i>	Spain, Catalonia	BCN 13326	Gaya et al. (2015)	EU639602	KT291479	–	–	KT291616	–	–	–
<i>Variospora cancarixiticola</i>	Spain, Castilla-La Mancha	MUB, holotype	Gaya et al. (2015)	EU639608	KT291482	–	–	KT291620	–	–	–

Continued

Table 2 Continued

Species	Locality (country, region)	Vouchers	Source	ITS	mtSSU	nucLSU	RPBI	RPB2	EF1a	MCM7	TUBB
<i>Variospora paulii</i>	Spain, Catalonia	BCN s.n.	Gaya et al. (2015)	EU639606	KT291503	–	–	KT291642	–	–	–
<i>Variospora thallicola</i>	Sweden, Halland	BCN s.n. U. Arup	Gaya et al. (2015)	JQ301667	JQ301498	JQ301563	KT291595	JQ301758	–	–	–
<i>Variospora velana</i>	Italy, Veneto East Antarctica, Hallett	L07123 (LD)	Gaya et al. (2015)	KT291467	KT291515	–	KT291598	–	–	–	–
<i>Xanthomendoza borealis</i>	Peninsula	DUKE s.n.	Gaya et al. (2015)	KT291473	KT291526	KT291567	–	KT291665	–	–	–
<i>Xanthomendoza mendozae</i>	Bolivia, Potosi	DUKE s.n.	Gaya et al. (2015)	JQ301688	JQ301523	JQ301581	–	–	–	–	–
<i>Kuettlingeria albulitescens</i>	Italy, Toscana	J. Vondrák 8849 (PRA) J. Vondrák 10843	Original	MN305804	MN305824	–	MN311941	MN311948	MN311926	MN311933	MN311954
<i>Kuettlingeria areolata</i>	Italy, Sicily	(PRA)	Original	MN305805	MN305825	MN305847	MN311942	MN311949	–	MN311934	MN311955
<i>Kuettlingeria atroflava</i> 2	Greece, Meteora	J. Vondrák 8723 (PRA)	Original	MH104921	MH100775	MH100744	MH141559	–	MH153700	MH119858	MH153732
<i>Kuettlingeria cretense</i>	Portugal France, Haute- Vienne, topotype	I. Frolov s.n. I. Frolov 1430	Original	MH104925	MH100783	MH100751	MH141560	MH119821	MH153701	MH119845	MH153733
<i>Kuettlingeria diphyodes</i>	Czech Republic, Pavlovské vrchy hills	J. Vondrák 9358 (PRA)	Original Vondrák et al. (2013) and original	MH104926	MH100785	MH100753	MH141561	–	MH153702	MH119846	MH153734
<i>Kuettlingeria emili</i>	Russia, Black Sea coast	J. Vondrák 6650 (PRA)	Original	KC416102	MH100787	MH100754	MH141575	MH119822	MH153704	MH119847	MH153735
<i>Kuettlingeria erythrocarpa</i>	Greece, Peloponnese	J. Vondrák 8714 (PRA) J. Vondrák 10805	Original	MN305806	MN305826	–	MN311943	MN311950	MN311927	MN311935	MN311956
<i>Kuettlingeria fuscoatroides</i>	Italy, Sardinia	(PRA)	Original	–	MN305827	–	MN311944	–	MN311928	MN311936	–
<i>Kuettlingeria neotaurica</i>	Ukraine, Black Sea coast	J. Vondrák 7213 (PRA) J. Vondrák	Original	MN305807	MN305829	MN305849	MN311946	MN311951	MN311930	MN311938	MN311958
<i>Kuettlingeria percrocata</i>	Italy, Dolomites	4634 (PRA)	Original	MH104931	MH100794	MH100763	MH141563	MH119823	MH153705	MH119848	MH153736
<i>Kuettlingeria soralfjera</i>	France, Maritime Alps	J. Vondrák 10813	Original	MN305808	MN305830	MN305850	MN311947	MN311952	MN311931	MN311939	MN311959

Continued

Table 2 Continued

Species	Locality (country, region)	Vouchers	Source	ITS	mtSSU	nucl.SU	RPB1	RPB2	EF1a	MCM7	TUBB
<i>Kuettlingeria teicholyta</i>	Ukraine, Kherson	(PRA) in J. Vondrák 6943 (PRA) J. Vondrák 14544	Original	MH104935	MH100797	MH100767	MH141576	–	MH153706	MH119849	MH153737
<i>Kuettlingeria xerica</i>	Russia, Dagestan	(PRA) I. Frolov	Original	MN305809	MN305831	MN305851	–	MN311953	MN311932	MN311940	MN311960
<i>Kuettlingeria sp.2.</i>	Ritsinsky	1456	Original	MH104932	MH100786	MH100764	MH141562	–	MH153703	MH119859	MH153728
<i>Pyrenodesmia albopruinosa</i>	Italy, Verona	TSB 37658 J. Vondrák 10463 (PRA)	Muggia et al. (2008) and original Vondrák et al. (2013) and original Muggia et al. (2008) and original	EF093577	MH100770	–	MH141578	MH119824	MH153708	MH119851	KR912027
<i>Pyrenodesmia albopustulata</i>	Turkey, Black Sea region	TSB 37735 T. Spribille s.n.	original	MH104918	MH100771	MH100741	MH141564	MH119825	MH153709	–	KC615301
<i>Pyrenodesmia alociza</i>	Italy, Ascoli Piceno	TSB 37735 T. Spribille s.n.	original	EF090931	MH100772	MH100742	MH141587	MH119826	MH153710	MH119860	MH153739
<i>Pyrenodesmia atroalba</i>	USA, Montana	s.n.	Original	MH104920	MH100774	MH100743	MH141565	MH119827	MH153711	MH119861	MH153740
<i>Pyrenodesmia badioaregens</i>	Italy, Foggia	TSB 36422	Muggia et al. (2008) and original Frolov et al.	EF081035	MH100776	MH100745	MH141566	MH119828	MH153712	MH119862	MH153741
<i>Pyrenodesmia chalybaea 2</i>	Greece, Crete	J. Vondrák 4059 (PRA) M.G. Halici s.n.	original	KC884498	MH100779	MH100747	MH141584	MH119830	MH153714	MH119864	KC615292
<i>Pyrenodesmia circumalbata</i>	Turkey, Mersin	s.n.	Original	MH104923	MH100780	MH100748	MH141567	MH119831	MH153715	MH119865	MH153742
<i>Pyrenodesmia concreticola</i>	Kazakhstan, Mangistau	J. Vondrák 9443 (PRA) J. Vondrák 12733	Frolov et al. (2016) and original	KC884506	MH100781	MH100749	MH141568	MH119832	MH153716	MH119852	KC615277
<i>Pyrenodesmia erodens</i>	Turkey, Kahramanmaraş	(PRA) I. Frolov	Original	MH104927	MH100788	MH100755	MH141569	MH119833	MH153717	MH119853	MH153743
<i>Pyrenodesmia helfygeoides</i>	Switzerland, Ticino	I. Frolov 1414	Original	MH104929	MH100790	MH100757	MH141570	MH119834	MH153718	MH119866	MH153744
<i>Pyrenodesmia micromarina</i>	Ukraine, Black Sea coast	J. Vondrák 7236 (PRA)	Frolov et al. (2016) and original	KC611248	MH100791	MH100758	–	MH119835	MH153719	MH119867	KC615269

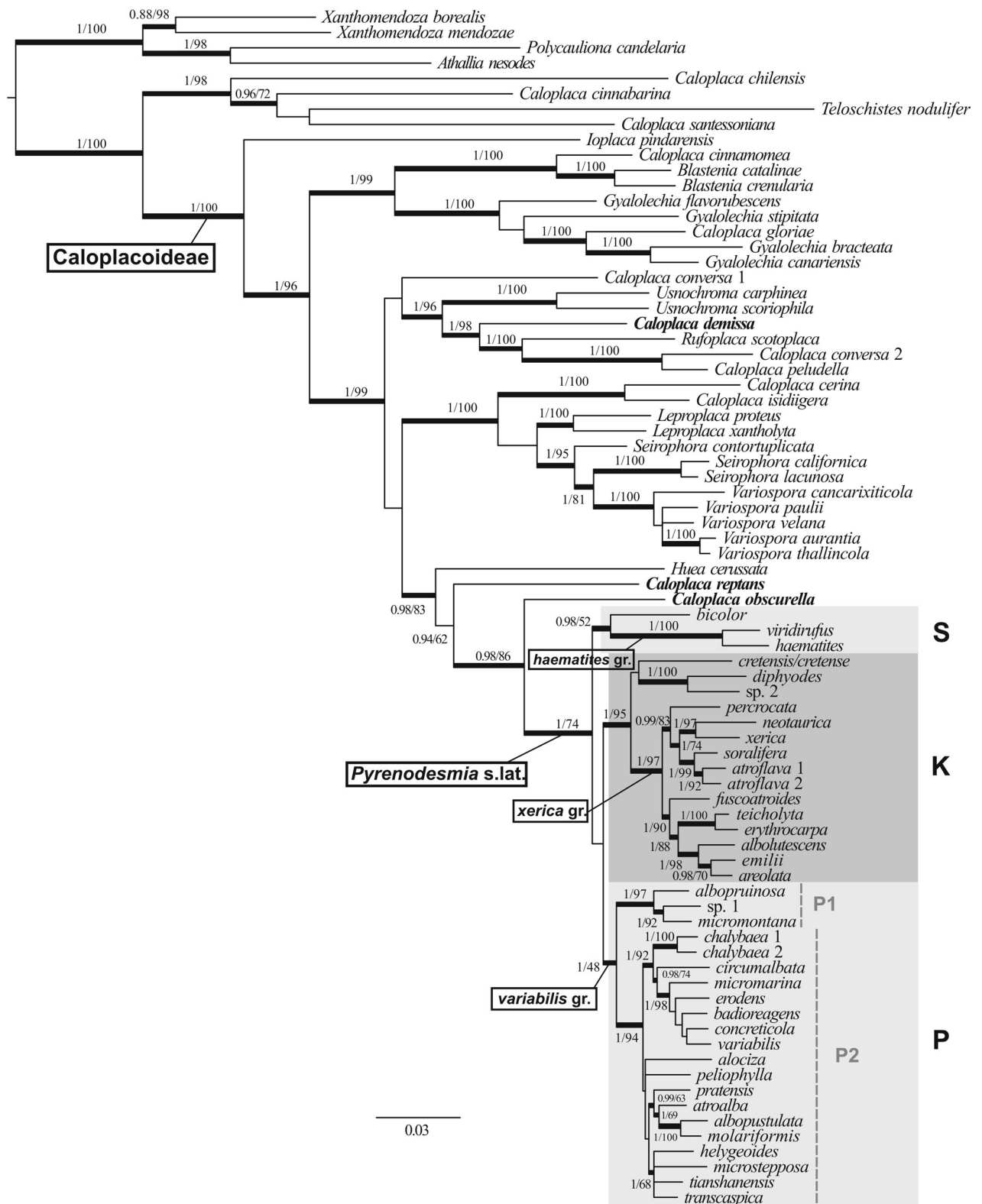
Continued

Table 2 Continued

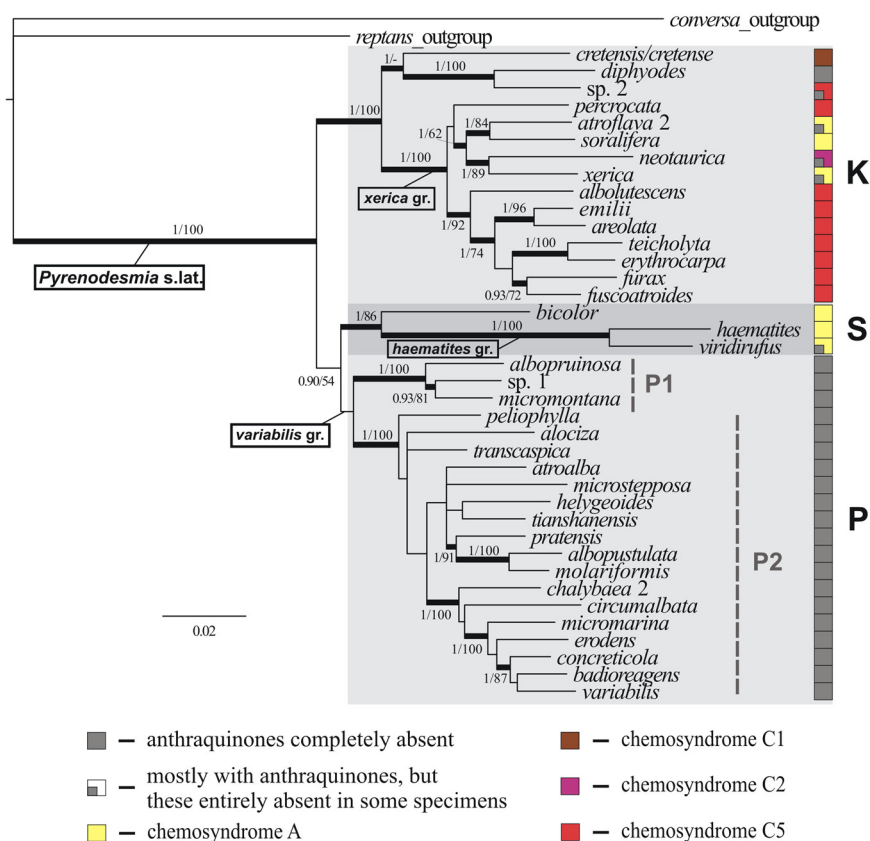
Species	Locality (country, region)	Vouchers	Source	ITS	mISSU	nucLSU	RPB1	RPB2	EF1a	MCM7	TUBB
<i>Pyrenodesmia micromontana</i>	Russia, Southern Ural, holotype	J. Vondrák 9467 (PRA)	Frolov et al. (2016) and original	KC346303	MH100792	MH100759	MH141580	MH119836	MH153720	MH119868	KC615299
<i>Pyrenodesmia microstepposa</i>	Czech Republic, Bohemian karst, holotype	J. Vondrák 9141 (PRA)	Frolov et al. (2016) and original	KC984530	–	MH100760	MH141581	MH119837	MH153721	MH119869	KT013276
<i>Pyrenodesmia molariformis</i>	Ukraine, Luhansk	O. Nadyeina 132 (KW) K. Knudsen 13557	(2013) and original	KC416143	MH100793	MH100761	MH141582	MH119838	MH153722	–	MH153745
<i>Pyrenodesmia peltophylla</i>	USA, California	(UCR) in MIN	Original	MH104930	–	–	MH141571	MH119839	MH153723	MH119870	MH153746
<i>Pyrenodesmia pratensis</i>	USA, Wyoming	891605	Original	MH104933	MH100795	MH100765	MH141583	MH119840	MH153724	MH119871	MH153747
<i>Pyrenodesmia tianshanensis</i>	China, Xinjiang, holotype	XJU 1691	Xahidin et al. (2010) and original	GU552277	MH100798	–	MH141585	MH119841	MH153725	MH119872	MH153748
<i>Pyrenodesmia transcaspica</i>	Kazakhstan, Mangistau	J. Vondrák 9430 (PRA)	Original	MH104936	MH100799	MH100768	MH141572	MH119842	MH153726	MH119873	MH153749
<i>Pyrenodesmia variabilis</i>	Czech Republic, Horažďovice	J. Vondrák 5114 (PRA)	Frolov et al. (2016) and original	KC884500	MH100800	–	MH141586	MH119843	MH153727	MH119854	KC615273
<i>Pyrenodesmia</i> sp.1	Czech Republic, Bohemian karst	J. Vondrák 9673 (PRA) J. Vondrák 10373	Frolov et al. (2016) and original	KC884525	MH100778	–	MH141579	MH119829	MH153713	MH119863	KC984549
<i>Sanguineodiscus bicolor</i>	Russia, Altai	(PRA)	Original	MH104922	MH100777	MH100746	MH141577	–	MH153707	MH119850	MH153738
<i>Sanguineodiscus haematites</i>	Ukraine, Black Sea coast	J. Vondrák 7278 (PRA)	Original	MH104928	MH100789	MH100756	MH141558	MH119820	–	MH119856	MH153730
<i>Sanguineodiscus viridifufus</i>	Czech Republic, Hanušovice	J. Vondrák 6702 (PRA)	Original	MH104919	MH100773	–	MH141574	–	MH153699	MH119857	MH153731

Sequences with bold accession numbers were newly obtained during this study. All samples were used in the Caloplacoideae alignment; *Pyrenodesmia* s.lat. specimens used in the *Pyrenodesmia* alignment start after *Xanthomendoza mendozae*.





**Fig. 1.** Position and content of *Pyrenodesmia s.lat.* within the Caloplacoideae clade. Bayesian phylogeny of the concatenated data set of five loci: ITS, mtSSU, nuLSU, RPB1, and RPB2. Bayesian posterior probabilities (values  $\geq 0.90$ ) and bootstrap support from the maximum likelihood analysis (after slashes; values  $\geq 70$ ) are shown above branches. Branches supported at least in one analysis are thickened. *Caloplaca demissa*, *C. obscurella*, and *C. reptans* are in bold. K, the genus *Kuettlingeria*; P, the genus *Pyrenodesmia s.str.*; S, the genus *Sanguineodiscus*.



**Fig. 2.** The clade of *Pyrenodesmia* s.lat. Bayesian phylogeny of the concatenated data set of eight loci: EF1a, ITS, MCM7, mtSSU, nuLSU, RPB1, RPB2, and TUBB. Bayesian posterior probabilities (values  $\geq 0.90$ ) and bootstrap support from the maximum likelihood analysis (after slashes; values  $\geq 70$ ) are shown above branches. Branches supported at least in one analysis are thickened. K, the genus *Kuettlingeria*; P, the genus *Pyrenodesmia* s.str.; S, the genus *Sanguineodiscus*.

included in *Pyrenodesmia* sensu lato, which consists of *Pyrenodesmia* sensu stricto, the *Caloplaca haematites* group, the *C. xerica* group, *C. bicolor*, and *C. cretensis*. *Caloplaca obscurella* seems to be the closest lineage to *Pyrenodesmia* sensu lato.

*Pyrenodesmia* sensu lato, together with *Caloplaca obscurella*, *C. reptans*, and *Huea cerussata*, forms a supported clade in both BI and ML reconstructions. Relationships among “*Pyrenodesmia* s.lat. + *Caloplaca obscurella*”, *C. reptans*, and *Huea cerussata* were not resolved. *Caloplaca demissa* is considerably distant from *Pyrenodesmia* sensu lato in our phylogenetic reconstructions and belongs to the highly supported clade, which consists of the genera *Usnochroma* and *Rufoplaca* and the species *Caloplaca conversa* and *C. peludella*.

Within *Pyrenodesmia* sensu lato, three main lineages could be distinguished (Figs. 1, S1; groups K, P, S), but relationships among them are not supported.

The lineage P (*Pyrenodesmia*) is highly supported in the BI tree (but not supported by ML; Fig. S1) and includes all species belonging to the *Caloplaca variabilis* group. Two internal branches are recognized—(P1) *C. albopruinosa* + *C. micromontana* + *Caloplaca* sp. 1 and (P2) the rest of the species. The lineage K (*Kuettlingeria*) is highly supported in the BI and ML trees and includes the supported clade of

the *C. xerica* group and *C. cretensis*, *C. diphynes*, and *Caloplaca* sp. 2. The lineage S (*Sanguineodiscus*) is well supported in the BI tree (but not supported by ML) and includes the fully supported *C. haematites* group and *C. bicolor*.

### 3.2 Phylogeny within *Pyrenodesmia* sensu lato: results from the eight-loci *Pyrenodesmia* data set

As in the analysis of the *Caloplacoideae* data set, the same three main lineages could be distinguished within the *Pyrenodesmia* sensu lato clade: K (*Kuettlingeria*), P (*Pyrenodesmia*), and S (*Sanguineodiscus*). Relationships among the lineages are not supported (Figs. 2, S2).

Unlike the analysis of the *Caloplacoideae* alignment, the lineage P lacks support in both BI and ML analyses of the *Pyrenodesmia* alignment. As in the *Caloplacoideae* tree (Fig. 1), it matches with the *Caloplaca variabilis* group and consists of two highly supported branches: (P1) involving *C. albopruinosa* + *C. micromontana* + *Caloplaca* sp.1 and (P2) involving the rest of the species.

The lineage K is highly supported in both analyses. As in the *Caloplacoideae* tree, it consists of a clade of the *C. xerica* group (also supported in both analyses) and *C. cretensis*, *C. diphynes*, and *Caloplaca* sp. 2. The latter two species always group together. *Caloplaca cretensis* forms a highly

supported clade with *C. diphyodes* and *Caloplaca* sp. 2 in the BI tree, but its relationships within the lineage K are not supported in the ML tree. The lineage S is supported in both analyses. As in the *Caloplacoideae* tree, it consists of a clade of the *C. haematites* group (highly supported in both analyses) and *C. bicolor*.

Eight *Pyrenodesmia* single-locus alignments were analyzed separately using BI (Fig. S3). The phylogenetic trees often have an unresolved backbone with few supported branches. Therefore, only two supported topological conflicts were observed (see below). The lineage P was monophyletic and supported in two single-locus trees, RPB1 and RPB2. A supported topological conflict was found in MCM7, with the P1 clade of *Pyrenodesmia* being more closely related to clades K and S than to the members of the P2 clade. The lineage K was resolved and supported in five loci (EF1a, MCM7, RPB1, RPB2, and TUBB) and resolved but not supported in one locus (mtSSU). Out of the four trees involving all the three analyzed taxa of the lineage S, the group was detected in MCM7 and ITS, but without support. A topological conflict was found in mtSSU, where two taxa *C. haematites* group formed a well-supported clade together with two members of the lineage K (sequences of all four taxa were verified using repeated PCR and sequencing).

### 3.3 Chemistry

In the analyzed samples, we identified chemosyndromes A (Søchting, 1997) and C1, C2, C5 (Søchting, 2001). Chemosyndrome A is characterized by strong dominance of parietin. Chemosyndrome C belongs to syndromes with chlorinated anthraquinones. C1 is characterized by strong dominance of 7-Cl-emodin, C2 by dominance of 7-Cl-emodin and a higher proportion of 7-Cl-citreorosein, and C5 by 7-Cl-emodin as the dominant compound in association with a substantial proportion of fragilin. Chemosyndromes are given in the taxonomical part under each species with anthraquinones in the apothecia as well as in Fig. 2.

## 4 Discussion

### 4.1 *Pyrenodesmia* sensu lato; three-generic scenario

The clade *Pyrenodesmia* sensu lato (Figs. 1, 2) encompasses species with a similar morphology, chemistry, geography, and ecology—crustose lichens that always contain the pigment Sedifolia-gray in outer tissues and occur mostly in xerothermic sun-lit conditions of temperate Northern Hemisphere. Nevertheless, the group has large internal variability in phenotype and genotype and could be divided into several supported lineages. In our opinion, a division into three groups (lineages K, P, and S in Figs. 1, 2) is reasonable and biologically relevant, as the lineages are monophyletic and supported at least in some of the multi-loci analyses (see the Results) and can be characterized by specific though partly overlapping sets of morphological, chemical, geographical, and ecological features. The lineage P consists of the species always lacking anthraquinones both in their thalli and apothecia, growing mainly on calcareous outcrops. The lineage has the Holarctic distribution with three main centers of its diversity (regions with sets of taxa occurring only there): the Mediterranean basin, Central Asia, and arid

regions of western North America. Taxa of the lineages K and S normally contain anthraquinones in the apothecia (chemosyndromes A, C1, C2, and C5 in the lineage K and chemosyndrome A in the lineage S); however, specimens completely lacking anthraquinones are rarely known in a few species. The lineage K is Holarctic; all currently known species occur in the Mediterranean basin, whereas just a few of them are distributed outside this region. It prefers base-rich siliceous (sometimes pure limestone) outcrops. The lineage S is absent in North America; it is known from the Mediterranean basin, adjacent regions and Northern Europe, and Central Asia. It is the only lineage in the *Pyrenodesmia* sensu lato clade that includes both saxicolous (mainly base-rich siliceous outcrops) and corticolous species.

As these three lineages are closely related and form a monophyletic group, it would be possible to unite them all within a single genus *Pyrenodesmia* including species of the currently informal *Caloplaca haematites* and *C. xerica* groups, and therefore extending the original concept of *Pyrenodesmia* proposed by Massalongo (1852) and accepted by Arup et al. (2013) to species with anthraquinones in the apothecia. This option was chosen by Kondratyuk et al. (2020a,b). However, uniting all the lineages into one genus will result in a loss of information. In this case, the large genus would have an unreasonably high internal variability, and we would still have to talk about *C. haematites*, *C. variabilis*, and *C. xerica* groups when dealing with *Pyrenodesmia* sensu lato. In our opinion, three-generic scenario corresponding to three main lineages of *Pyrenodesmia* sensu lato contains more information than one genus; it makes most sense even if some of the genera features are partly overlapping. The most powerful and also practical difference is the lack of anthraquinones in the lineage P as compared with the species from other two lineages (except *C. diphyodes*). There is also a rather strong difference between the lineage P and the lineages K and S in the substrate preferences, strongly calcareous in the former and, in general, calciferous or siliceous substrates in the latter two (with only a few species growing on pure limestone).

Differences between the other two lineages, K and S, are not as distinct as delimitation of the lineage P. However, uniting them into a single genus is not suitable, as they do not form a monophyletic group in any of our phylogenetic reconstructions and show differences in morphology, chemistry, geography, and ecology. The lineage S always has only chemosyndrome A (the lineage K has a mixture of chemosyndromes A, C1, C2, and C5, and also complete absence of anthraquinones in *C. diphyodes*); true exciple of the taxa of the lineage S is often without anthraquinones and gray (in the lineage K, it is always with anthraquinones, orange); the lineage S is absent in North America (the lineage K has Holarctic distribution) and includes a corticolous species (the lineage K is exclusively saxicolous).

Moreover, during the last 170 years, these three lineages were at least partly regarded as informal groups (*C. haematites*, *C. xerica*, and *C. variabilis* groups) or even genera (*Pyrenodesmia* and *Kuettlingeria*). In the context of the current taxonomy of the lichenized fungi (Crespo et al., 2010; Nordin et al., 2010; Spribille et al., 2011; Ekman & Svensson, 2014; Buaruang et al., 2015), and particularly of the family Teloschistaceae (Fedorenko et al., 2012;

**Table 3** Characters of the genera within the *Pyrenodesmia* sensu lato clade

	<i>Pyrenodesmia</i> s.str. (lineage P)	<i>Kuettlingeria</i> (lineage K)	<i>Sanguineodiscus</i> (lineage S)
No. of species accepted in the paper	21	14	4
Former groups and species included	<i>Caloplaca variabilis</i> group	<i>Caloplaca xerica</i> group plus <i>C. cretensis</i> and <i>C. diphyodes</i>	<i>Caloplaca haematites</i> group plus <i>C. bicolor</i>
Vegetative propagules	Blastidia, soredia, soredia-like minute granules, pustulate outgrowths	Blastidia, soredia	Not known
Color of apothecial disc and true exciple	Brown to black	Yellow-orange to dark red or brown-red, exceptionally black or brown	Disk pale to dark red, true exciple of the same color or gray-black, exceptionally whole apothecium black (Fig. 3C, right)
Pigments	Only Sedifolia-gray in thallus and apothecia	Sedifolia-gray in thallus and thalline exciple; anthraquinones in apothecial disc and true exciple (chemosyndromes A, C1, C2, and C5); in some individuals only Sedifolia-gray in apothecia	Sedifolia-gray in thallus, thalline exciple and sometimes in true exciple; anthraquinones in apothecial disc and sometimes in true exciple (chemosyndrome A); in some individuals only Sedifolia-gray in apothecia
Geography	Holarctic; three biodiversity centers—Mediterranean basin, Central Asia, and arid regions of western North America	Holarctic; one biodiversity center—Mediterranean basin	Eurasia and Northern Africa; mainly in Mediterranean basin and Central Asia
Ecology	Saxicolous; mainly calcareous (rarely base-rich siliceous) outcrops in xerothermic sun-lit conditions; exceptionally on acidic outcrops in wet conditions	Saxicolous; mainly calciferous (sometimes pure limestone) outcrops in xerothermic sun-lit conditions; exceptionally on acidic outcrops in wet conditions	Saxicolous and corticolous; mainly calciferous (rarely pure limestone) outcrops or bark of different trees and shrubs in xerothermic sun-lit conditions

Arup et al., 2013; Søchting et al., 2014; Kondratyuk et al., 2017b, etc.), the three groups within *Pyrenodesmia* sensu lato should be treated at the genus rank, as they show a considerable phylogenetical and morphological differentiation.

The lineage P represents the genus *Pyrenodesmia* sensu stricto described by Massalongo (1852) and resurrected by Arup et al. (2013). The old generic name *Kuettlingeria* (Trevisan, 1857) can be used for designation of the lineage K, which includes *Caloplaca teicholyta*—current name for *Kuettlingeria visianica*, the type species of the genus *Kuettlingeria*. We were not able to find any appropriate existing name for the lineage S; consequently, it was formally described here as a new genus *Sanguineodiscus*. Differences between the three genera are summarized in Table 3.

The genus *Pyrenodesmia* sensu stricto (Fig. 3A) matches the *Caloplaca variabilis* group (Wunder, 1974; Kärnefelt, 1989; Vondrák et al., 2012). Our concept of the genus is the same as that proposed by Massalongo (1852) and Arup et al. (2013). Unlike the phylogeny by Arup et al. (2013), our analyses demonstrate that it is well separated from the *C. xerica* group. The genus is monophyletic in all of our phylogenetic trees (Figs. 1, 2, S1, S2); however, it is supported only in the BI phylogeny of the Caloplacoideae alignment (Fig. 1). In other cases, it could be subdivided into two groups corresponding

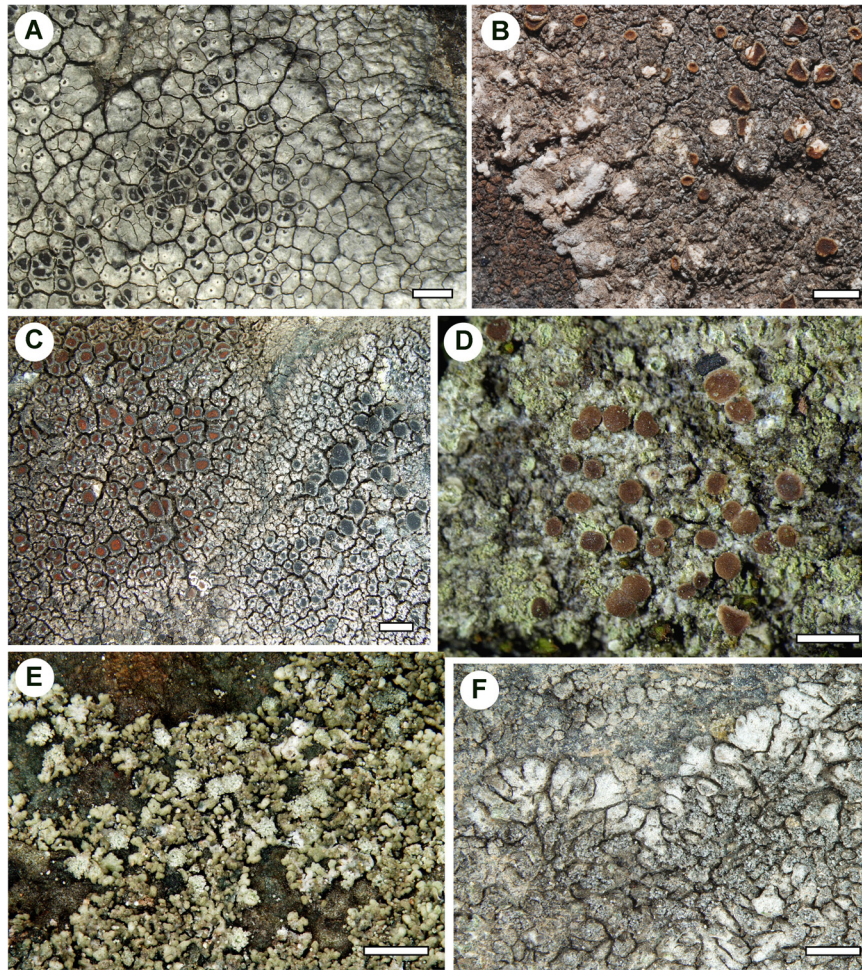
to highly supported clades P1 and P2. Nevertheless, these groups do not demonstrate any perceptible differences in morphology, anatomy, chemistry, or ecology. Hence, we prefer to keep them within the same genus *Pyrenodesmia*.

The genus *Kuettlingeria* (Fig. 3B) consists of a clade of the former *Caloplaca xerica* group (Vondrák et al., 2012; Arup et al., 2013) and *K. cretense*, *K. diphyodes*, and *Kuettlingeria* sp. 2. The genus *Sanguineodiscus* (Fig. 3C) consists of a lineage containing a single species *S. bicolor* and a lineage formed by the former *Caloplaca haematites* group.

#### 4.2 The name *Caloplaca diphyodes*

*Kuettlingeria diphyodes* is the only species of the genus lacking anthraquinones entirely. In addition, it differs from other *Kuettlingeria* species by its ecology, as it grows on periodically inundated acidic siliceous boulders in watercourses.

Formerly recognized as *Caloplaca diphyodes*, it was traditionally considered as widespread in the alpine belt and in the Arctic regions in the Holarctic (e.g., Wunder, 1974; Poelt & Hinteregger, 1993; Davydov et al., 2007; Gröner, 2016; Hafellner & Türk, 2016; McCune, 2016). However, the type material of *Lecanora* (= *Caloplaca*) *diphyodes* originates from low altitude (about 600 m a.s.l.) of the Massif Central in France (Nylander, 1872). Our investigation of the material recently



**Fig. 3.** Representatives of the genera in *Pyrenodesmia* sensu lato (A–C) and the species indicated to be outside *Pyrenodesmia* sensu lato (D–F). **A**, *Pyrenodesmia chalybaea* (PRA Vondrák 9686). **B**, *Kuettlingeria teicholyta* (holotype of *Blastenia visianica*, VER, photo by U. Arup). **C**, *Sanguineodiscus viridirufus*, thallus with red apothecia with anthraquinones on the left and thallus with black anthraquinone-lacking apothecia on the right (PRA Vondrák 9600). **D**, *Caloplaca obscurella* (PRA Vondrák 7641). **E**, *Caloplaca reptans* (NY Lendemer 48186). **F**, *Caloplaca demissa* (PRA Vondrák 19188). All scales: 1 mm.

collected by us in the locus classicus (specimens Frolov 1430, Vondrák 15096) placed it into *Kuettlingeria* and showed that this taxon is not related to the Arctic–alpine specimens and is so far known only from a few collections from the Massif Central in France. Instead, the Arctic–alpine specimens belong to *Pyrenodesmia* sensu stricto, and *P. helygeoides* is the earliest appropriate name for that species we found (see Section 5).

#### 4.3 Species not included in *Pyrenodesmia* sensu lato

*Caloplaca obscurella* (Fig. 3D), which is considered as the closest lineage to *Pyrenodesmia* sensu lato, could be possibly included in the ingroup. Such a decision was made by Choisy (1951), who proposed the combination *Pyrenodesmia obscurella*, and Muggia et al. (2008), who placed *C. obscurella* within their “*Pyrenodesmia*” clade. However, the chemistry of this species does not correspond with that of *Pyrenodesmia*, as both anthraquinones and Sedifolia-gray are absent. Moreover, *C. obscurella* is an epiphytic taxon distributed mainly in boreal and temperate forests, which is

uncharacteristic for *Pyrenodesmia* sensu lato. A distinct secondary chemistry, ecology, and an outlying position in the phylogenetic trees (Figs. 1–3) led us to place *C. obscurella* outside *Pyrenodesmia* sensu lato.

*Caloplaca reptans* (Fig. 3E) is widespread in moist habitats on non-calcareous rocks in forests of eastern North America (Hodkinson & Lendemer, 2012). It is characterized by lacking both anthraquinones and Sedifolia-gray in the thallus. Hodkinson & Lendemer (2012) observed immature apothecia with reddish-brown discs lacking anthraquinones, but did not mention Sedifolia-gray, and we did not see fertile specimens. In the five-loci tree, *C. reptans* is even more distant from the *Pyrenodesmia* core than *C. obscurella* (Fig. 1), and we consider it being outside *Pyrenodesmia* sensu lato.

The genus *Huea* was erected by Dodge & Baker (1938) to encompass Antarctic species of Teloschistaceae without anthraquinones. *Huea* is known by its complicated typification (Fryday, 2011), and the genus was not regarded by Arup et al. (2013). We did not study any specimens of *Huea* and do not have any information about its pigments, but we

included the species *H. cerussata* into our five-loci phylogenetic analysis and confirmed the result of Gaya et al. (2015) that it is close to *Pyrenodesmia* sensu lato. Its position in the tree (Fig. 1) is, however, as distant from the *Pyrenodesmia* core as the position of *C. reptans*.

Our phylogenetic data do not support attribution of *C. demissa* (Fig. 3F) to *Pyrenodesmia* sensu lato. According to our five-loci phylogenetic analysis (Fig. 1), it belongs to a supported clade including the genera *Rufoplaca* and *Usnochroma* and the species *C. conversa* and *C. peludella*. As in *C. obscurella* and *C. reptans*, the chemistry of *C. demissa* differs from that of *Pyrenodesmia* sensu lato by the absence of both anthraquinones and Sedifolia-gray in the thallus (apothecia are unknown in that species).

Apparently, *C. demissa*, *C. obscurella*, and *C. reptans* currently form three monotypic genera. Kondratyuk et al. (2015) already proposed the genus *Olegblumia* to accommodate *C. demissa*, but it is not legitimate, because the basionym, *Placodium demissum* Körb. ex Flotow, was not cited within the combination. Formal taxonomic proposals concerning these three taxa require further research.

Previous studies proved that the absence of anthraquinones, as well as the presence of other pigments, is not a phylogenetically reliable indication of relationship, as the loss of anthraquinone production occurs in unrelated lineages of Teloschistaceae (e.g., Vondrák et al., 2012). However, according to our results, pigments can play a crucial role in the taxonomy of some particular groups within the family. For example, *Pyrenodesmia* sensu lato consists of species that always possess Sedifolia-gray in thallus, whereas anthraquinones are either absent or, in some species, restricted to the apothecia; species without both Sedifolia-gray and anthraquinones (e.g., *C. demissa*, *C. obscurella*, and *C. reptans*) do not belong there. Within *Pyrenodesmia* sensu lato, species completely without anthraquinones form a monophyletic lineage—the genus *Pyrenodesmia* sensu stricto. Two other genera of *Pyrenodesmia* sensu lato, *Kuettlingeria* and *Sanguineodiscus*, have Sedifolia-gray in their thalli and anthraquinones in their apothecia, but anthraquinones are exceptionally absent from apothecia of some individuals.

## 5 Taxonomy

### 5.1 *Kuettlingeria* Trevis., *Revista Periodica dei Lavori della Imperiale Regia Accademia di Padova* 5: 72. 1857

Fig. 3B

Type: *Kuettlingeria visianica* (A. Massal.) Trevis., *Revista Periodica dei Lavori della Imperiale Regia Accademia di Padova* 5: 73. 1857.

Bas.: *Blastenia visianica* A. Massal., *Atti Ist. Veneto Sci. Lett. Arti*, ser. 2, vol. 3 (app.): 117. 1852.

Syn.: *Kuettlingeria teicholyta* (Ach.) Trevis., *Revista Periodica dei Lavori della Imperiale Regia Accademia di Padova* 5: 73. 1857.

Diagnosis: Apothecial disc and true exciple yellow-orange to dark red or brown-red with anthraquinones of the chemosyndromes A, C1, C2, or C5 (sensu Søchting, 1997, 2001), exceptionally lacking anthraquinones and brown or black. Thallus and thalline exciple with Sedifolia-gray, lacking

anthraquinones. Distribution: Holarctic with biodiversity center in the Mediterranean region. Saxicolous.

Description: *Morphology and anatomy*: Thallus crustose, epiphytic or rarely endolithic, white or gray; cortex paraplectenchymatous, usually represented by alveolate cortex (sensu Vondrák et al., 2013); some species with vegetative propagules (blastidia, soredia, isidia, or minute lobules). Apothecia zeorine, rarely biatorine, sometimes appearing lecanorine, but thin true exciple is always present; thalline exciple of the same color as thallus, disc and true exciple usually of different tinges of red and yellow, but in some individuals, within a population true exciple and disc may be black, gray, or brown; ascospores polariblastic, medium to broadly ellipsoid, with medium long septum; pycnidia present or absent, gray-black; conidia bacilliform to subglobose.

Chemistry: Thallus and thalline exciple are always without anthraquinones, but with Sedifolia-gray. Epiphyllum and upper part of true exciple are usually with anthraquinones (either dominated by non-chlorinated parietin or by chlorinated 7-Cl-omodrin, fragilin, or 7-Cl-citreorsein; Section 2). Sometimes epiphyllum and true exciple contain both anthraquinones and Sedifolia-gray; in this case, Sedifolia-gray could be seen when anthraquinones are washed out by KOH in the apothecial section. In some species, two chemotypes are known within the same species—with red-colored apothecia (with anthraquinones) and rarer with black-colored apothecia (without anthraquinones, only with Sedifolia-gray). *Kuettlingeria diphyodes* is the only exception in the group—the chemotype entirely without anthraquinones is only known.

Distribution and ecology: Northern Hemisphere. All currently known species occur in the Mediterranean regions and Macaronesia, some of them distributed also in non-Mediterranean Europe, Asia, and North America. One record is known from Ecuador (*K. aff. soralifera* on concrete; herb. Zdeněk Palice 4836). The genus consists of exclusively saxicolous taxa, which grow both on limestone and base-rich siliceous outcrops in sun-lit conditions mostly from sea coasts to the mid-altitudinal zone. Few species (*K. diphyodes* and sometimes *K. atrofava*) grow on rather acidic siliceous boulders in streams. *Kuettlingeria percrocata* is a single species confined to the montane-alpine zone.

Remarks: Currently, 14 species are included in the genus, but this group is more diverse and contains other unnamed species (Vondrák et al., 2012). We did not consider taxa that probably belong to the genus, if their taxonomic status is unclear (e.g., *Caloplaca aetnensis* and *C. sbarbaronis*). Author of the genus *Kuettlingeria*, Trevisan (1857), included there three species—*K. lallavei*, *K. visianica*, and *K. teicholyta*. Currently, the former two species are synonymized under the latter species (see below under *K. teicholyta*). Apart from Trevisan, C.W. Dodge has been the only author describing or combining species names to *Kuettlingeria*. Some of them were already moved to other genera by Arup et al. (2013): *K. elegantissima* (Nyl.) C.W. Dodge to *Stellarangia* and *K. physcioides* (A. Massal.) C.W. Dodge to *Dufourea*. Other species (*K. crozetica*, *K. fuegiensis*, *K. macquariensis*, *K. rufa*, *K. rutilans*, and *K. siplei*) are lichens with yellow to red thallus (Zahlbruckner, 1906a; Dodge & Baker, 1938; Dodge, 1968, 1970; Kantvilas & Seppelt, 1992),

and they do not belong to *Kuettlingeria* in its present meaning.

***Kuettlingeria albolutescens*** (Nyl.) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828678

≡ *Lecanora albolutescens* Nyl., *Flora* (Regensburg) 64: 177. 1881 (basionym).

Type: [England]. Northumberland in Anglia, supra saxa quarcitosa ad Stocksfield, *W. Johnson* (holotype, H-NYL 29845!).  
Chemistry: Chemosyndrome C5.

***Kuettlingeria areolata*** (Zahlbr.) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828679

≡ *Caloplaca cerina* var. *areolata* Zahlbr., *Öst. bot. Z.* 53: 289. 1903 (basionym).

Type: [Montenegro]. Bocche di Cattaro: Devesite bei Castelnuevo [Herceg Novi], altitude about 600–700 m, an Kalkfelsen, 1902, *J. Baumgartner* (holotype, W 7068!).

Chemistry: Chemosyndrome C5.

***Kuettlingeria atroflava*** (Turner) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828680

≡ *Lecidea atroflava* Turner, *Trans. Linn. Society Lond.* 9: 142. 1808 (basionym).

Type: England. Flints on the Sussex Downs, Turner (holotype, BM 730327!).

Chemistry: Chemosyndrome A; rarely anthraquinones completely absent.

***Kuettlingeria cretense*** (Zahlbr.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828681

≡ *Blastenia cretensis* Zahlbr., *Sitzungsber. Kais. Akad. Wiss. Wien, math.-naturw.* 115: 519. 1906b (basionym).

Type: Griechenland. Kreta: an Kalkfelsen auf der kleineren Insel Paximadhia, 1904, *J. Dörfner* (holotype, W!).

Chemistry: Chemosyndrome C1.

***Kuettlingeria diphyodes*** (Nyl.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828682

≡ *Lecanora diphyodes* Nyl., *Flora* (Regensburg) 55: 353. 1872 (basionym).

Type: [France]. Haute-Vienne: Bessines[-sur-Gartempe], sur le rochere au bord de la Gartempe, *Ripart* (holotype, H-NYL 29379!).

Remarks: see the Discussion and notes under *Pyrenodesmia helygeoides*.

Chemistry: anthraquinones completely absent.

***Kuettlingeria emilii*** (Vondrák, Khodos., Cl. Roux & V. Wirth) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828683

≡ *Caloplaca emilii* Vondrák, Khodos., Cl. Roux & V. Wirth, *Lichenologist* 45: 709. 2013 (basionym).

Type: Bulgaria. Black Sea coast: Kavarna, limestone cliffs on seashore 15 km NE of Kamen Brjag, 43°27'58.76"

N, 28°33'55.02"E, on coastal limestone outcrop above supralittoral zone, 2007, *J. Vondrák* 6600 (holotype, PRA!; isotype, KHER).

Chemistry: Chemosyndrome C5.

***Kuettlingeria erythrocarpa*** (Pers.) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828685

≡ *Patellaria erythrocarpa* Pers., *Annalen der Wetter-atischen Gesellschaft für die Gesamte Naturkunde* 2: 12. 1811 (basionym).

Type: Galliae [France]. Ad lapides calcarios prope Dijon, *Persoon* (holotype, H-ACH 353!).

Chemistry: Chemosyndrome C5.

***Kuettlingeria furax*** (Egea & Llimona) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB832249

≡ *Caloplaca furax* Egea & Llimona, *Collnea bot., Barcinon. Bot. Instit.* 14: 266. 1983 (basionym).

Type: [Spain.] Lectus loco Cañada del Conejo dicto, ad pedem Sierra del Relumbrar, prope Bienservida (Albacete), altitude 350 m, ad saxa schistosa metamorphica paulo inclinata, in dominio Pyro-Querceti, super *Aspicilia* cf. *epiglypta*, 27 May 1978, *J.M. Egea et X. Llimona* (isotype, GZU, Murc. lichenotheca no. 3039!).

Chemistry: Chemosyndrome C5.

***Kuettlingeria fuscoatroides*** (J. Steiner) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828686

≡ *Caloplaca fuscoatroides* J. Steiner, *Verh. zool.-bot. Ges. Wien* 69: 69. 1919 (basionym).

Type: [Greece]. Delos: Klein-Delos, auf herumliegendeuden Schieferplatten, 1911, *Schiffner* (holotype, WU 41148!).

Chemistry: Chemosyndrome C5.

***Kuettlingeria neotaurica*** (Vondrák, Khodos., Arup & Søchting) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828687

≡ *Caloplaca neotaurica* Vondrák, Khodos., Arup & Søchting, *Lichenologist* 44: 414. 2012 (basionym).

Type: Ukraine. Crimean Peninsula: Sudak, Karadag Mts, Mt Svyataya, altitude 320 m, 44°56'03.27"N, 35°13'06.17"E, on volcanic rock, 2007, *J. Vondrák* 5925 (holotype, PRA!).

Chemistry: Chemosyndrome C2; anthraquinones occasionally completely absent.

***Kuettlingeria percrocata*** (Arnold) I.V. Frolov, Vondrák & Arup, **comb. nov.**

Mycobank: MB828688

≡ *Blastenia percrocata* Arnold, *Verh. K. K. Zool.-Bot. Ges. Wien* 37: 120 (1887) (basionym).

Type: [Italy]. Südtirol: Auf Sandstein der Campiler Schichten ober dem Rolle-pass bei Paneveggio, 6 Aug 1882, *Arnold*, *Arn. Lich. Exs. No 924* (lectotype, M 0102293!), selected by *Wetmore*, 1996, p. 312).

≡ *Blastenia arenaria* var. *percrocata* Arnold, *Flora* (Regensburg) 67: 309. 1884, nom. nud.

Chemistry: Chemosyndrome C5.

***Kuettlingeria soralifera*** (Vondrák & Hrouzek) I.V. Frolov, Vondrák & Arup, **comb. nov.**

MycoBank: MB828689

≡ *Caloplaca soralifera* Vondrák & Hrouzek, *Graphis Scripta* 18: 8. 2006 (basionym).

Type: Czech Republic. Central Bohemia: Rakovník district, Křivoklát, Kalubice, by the small pond in the village, 50°02'56.3"N, 13°49'30.4"E, altitude 348 m, on horizontal side of concrete wall, 2004, *J. Vondrák 3332* (holotype, PRM!).

Chemistry: Chemosyndrome A.

***Kuettlingeria teicholyta*** (Ach.) Trevis.

Fig. 3B

≡ *Lecanora teicholyta* Ach., *Lichenographia Universalis*: 425. 1810 (basionym).

Type: Gallia [France]. *Dufour* (lectotype, H-ACH 1229!, selected by Vondrák & Vitikainen, 2008).

= *Blastenia visianica* A. Massal., *Atti Ist. Veneto Sci. Lett. Arti*, ser. 2, vol. 3 (app.): 117. 1852.

Type: [Italy. Padua?] *Viget ad saxa trachytica in horto botanico, cujus Praefecto* (R. Prof. Visiani) *speciem dicatam voluimos* (holotype, VER!).

= *Kuettlingeria visianica* (A. Massal.) Trevis., *Revista Periodica dei Lavori della Imperiale Regia Accademia di Padova* 5: 73. 1857.

= *Lecidea lallavei* Clemente ex Ach. *Syn. meth. lich.* (Lund): 45. 1814.

= *Kuettlingeria lallavei* (Clemente ex Ach.) Trevis., *Revista Periodica dei Lavori della Imperiale Regia Accademia di Padova* 5: 73. 1857.

Chemistry: Chemosyndrome C5.

***Kuettlingeria xerica*** (Poelt & Vězda) I.V. Frolov, Vondrák & Arup, **comb. nov.**

MycoBank: MB828691

≡ *Caloplaca xerica* Poelt & Vězda, *Mitteilungen aus der Botanischen Staatssammlung München* 12: 1. 1975 (basionym).

Type: [Italy]. Südtirol: Vintschgau, Südseitige trockene, Gneishänge am Eingang in das Schlanders, Jun 1966, *J. Poelt 12073* (holotype, GZU!).

Chemistry: Chemosyndrome A; rarely anthraquinones completely absent.

## 5.2 *Pyrenodesmia* A. Massal.

Fig. 3A

Type: *Pyrenodesmia chalybaea* (Fr.) A. Massal.

Diagnosis: Completely lacking anthraquinones, with *Sedifolia*-gray. Distribution: Holarctic with biodiversity centers in the Mediterranean basin, Central Asia, and arid regions of western North America. Saxicolous (mainly calcicolous).

Nomenclature: The name was resurrected by Arup et al. (2013).

Description: *Morphology and anatomy*: Thallus crustose, epi- or endolithic, white, gray or brown; cortex paraplectenchymatous, usually represented by alveolate

cortex (sensu Vondrák et al., 2013), rarely well developed and thick (known in some Central Asian taxa); some species with vegetative propagules (blastidia, soredia, minute granules and lobules, or pustulate outgrowths). Apothecia zeorine, rarely biatorine, sometimes appearing lecanorine, but a thin true exciple is always present; thalline exciple of the same color as thallus, disc and true exciple brown, gray or black; ascospores polardiblastic with short to large long septum. Pycnidia present or absent, gray or black; conidia bacilliform to subglobose.

Chemistry: Thallus, apothecia, and pycnidia always without anthraquinones, but with *Sedifolia*-gray. Unknown brown pigment (K–) sometimes present in epihymenium.

Distribution and ecology: Northern Hemisphere. The record from Antarctica (Øvstedal & Lewis Smith, 2001) needs confirmation. Mainly in Mediterranean region, Central Asia, and desert regions of western North America. There are just few taxa known in other parts of Europe, Asia, and North America. The genus consists of exclusively saxicolous taxa. In Europe, they grow only on calcareous outcrops (limestones and sandstones), and in Central Asia and the USA, both on calcareous and base-rich siliceous outcrops in sun-lit conditions from coast to alpine zone. *Pyrenodesmia helygeoides* often grows on acidic siliceous boulders in water.

Remarks: Currently, 21 species are included in the genus, but this group is more diverse and contains many unnamed taxa (our unpublished data). We did not consider taxa that probably belong to the genus, if their taxonomic status is unclear (e.g., *Caloplaca ayachina* and *C. ochromela*). We did not study the identity of the names *C. circumalbata* var. *bicolor* (Wunder, 1974) and *Pyrenodesmia variabilis* var. *ocellulata* (Hafellner & Türk, 2016). *Pyrenodesmia duplicata* (a new combination proposed by Kondratyuk et al., 2017a), in our opinion, belongs to the genus *Kuettlingeria*, but it has an unclear taxonomic status (Redchenko et al., 2012; Motiejūnaitė et al., 2016).

***Pyrenodesmia albopruinosa*** (Arnold) S.Y. Kondr. (for details, see Kondratyuk et al., 2020b)

***Pyrenodesmia albopustulata*** (Khodos. & S.Y. Kondr.) I.V. Frolov & Vondrák, **comb. nov.**

MycoBank: MB828622

≡ *Caloplaca albopustulata* Khodos. & S.Y. Kondr., *Graphis Scripta* 13: 6. 2002 (basionym).

Type: Ukraine. Crimean Peninsula: Alushta district, Mt Southern Demerdji, "Dolina Prividenij", on conglomerate, 2000, A. Khodosovtsev (holotype, KW; isotypes, KHER, LD).

***Pyrenodesmia albovariegata*** B. de Lesd., *Rev. Bryol. Lichénol.*, N.S. 12: 62. 1942.

Type: USA. New Mexico: Santa Fe Co., Santa Fe, Cienga Creek, 1890 m, sur roches volcaniques, 1930, *Arsène Brouard 21550* (lectotype, UPS!, selected by Wetmore, 1994, p. 816).

Remarks: Belonging to *Pyrenodesmia*, which was confirmed by data on MCM7 gene (Frolov, unpublished).

***Pyrenodesmia alociza*** (A. Massal.) Arnold (for details, see Arup et al., 2013)



***Pyrenodesmia atroalba*** (Tuck.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828625

≡ *Placodium atroalbum* Tuck., Proc. Amer. Acad. Arts & Sci. 12: 172. 1877 (basionym).

Type: USA. State unknown, [river] North Platte, Rocky Mts., cretaceous sandstones, Dr. Hayden (lectotype, FH!, selected by Wetmore, 1994: 816).

***Pyrenodesmia badioreagens*** (Tretiach & Muggia) Söchting, Arup & Frödén (for details, see Arup et al., 2013)

***Pyrenodesmia bullata*** (Müll. Arg.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828627

≡ *Calloposma bullatum* Müll. Arg., Hedwigia 31: 156. 1892 (basionym).

Type: Persien. Kuh Tscharmekam, altitude 3300 m, 1885, Dr. Stapf (lectotype, G 00110799!, selected by Wunder, 1974: 120).

None *Placodium bullatum* Müll. Arg., Proc. R. Soc. Edinb. 11: 459. 1882.

≡ *Pyrenodesmia bullata* (Müll. Arg.) Tomin, nom. inval., Sbor. Nauchn. Trud. Akad. Nauk. Byelorussk. SSR, Inst. Biol. 1: 85. 1950.

≡ *Caloplaca variabilis* var. *bullata* (Müll. Arg.) Wunder, Bibliotheca Lichenol. 3: 120. 1974.

Remarks: The name *Placodium bullatum* Müll. Arg. is a basionym for *Hepposora bullata* (Müll. Arg.) Lumbsch & Mies belonging to the family Ramalinaceae (Mies & Schultz, 2004). The combination *Pyrenodesmia bullata* (Müll. Arg.) Tomin is not valid; it was mentioned as a synonym to *Caloplaca bullata* by Tomin (1950) without any comments. We failed to find any record of that combination in other papers by Tomin.

So far, it is explicitly known only from the type material and we do not have any molecular data for it. It is placed here on the basis of morphology and chemistry (contains only Sedifolia-gray).

***Pyrenodesmia chalybaea*** (Fr.) A. Massal. (for details, see Arup et al., 2013)

Fig. 3A

***Pyrenodesmia circumalbata*** (Delile) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank MB828660

≡ *Lecidea circumalbata* Delile, Flore d'Égypte: 157 and tab. 59 (Fig. 8). 1813 (basionym).

Type: [Egypt]. Vallée de l'Égarement, Delile (lectotype, G 00290773!, selected by Wunder, 1974, p. 53).

≡ *Blastenia circumalbata* (Delile) Müll. Arg., Revue mycol., Toulouse 2(2): 78 (1880).

***Pyrenodesmia concreticola*** (Vondrák & Khodos.) Söchting, Arup & Frödén (for details, see Arup et al., 2013)

***Pyrenodesmia erodens*** (Tretiach, Pinna & Grube) Söchting, Arup & Frödén (for details, see Arup et al., 2013)

***Pyrenodesmia helygeoides*** (Vain.) Arnold, Verh. zool.-bot. Ges. Wien 47: 215. 1897.

≡ *Lecanora helygeoides* Vain., Meddn Soc. Fauna Flora Fenn. 6: 148. 1881 (basionym).

Type: [Russia. Murmansk Region]: Lapponia inarenis, Köngäs [Borisoglebsky], 1878, E. Vainio 07666 (holotype, TUR-V!).

= *Caloplaca diphyodes* auct. non Nylander (1872).

Remarks: We propose to use this name for most European specimens called *Caloplaca diphyodes* (see the Discussion for identity of *C. diphyodes*). The holotype of *Lecanora helygeoides* investigated by us fits the Arctic-alpine *C. diphyodes* auct. in morphology, anatomy, and chemistry. A specimen Frolov 644 was collected in the Murmansk region of Russia, not far from the type locality, and it is very similar to the type. The specimen groups with Arctic-alpine specimens of *C. diphyodes* auct. in the phylogeny based on several loci (Frolov, unpublished).

***Pyrenodesmia micromarina*** (I.V. Frolov, Khodos. & Vondrák) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828641

≡ *Caloplaca micromarina* Frolov, Khodos. & Vondrák, Annales Botanici Fennici 53: 251. 2016 (basionym).

Type: Turkey. Sea of Marmara coast: Tekirdağ, in valley of small brook near Gaziköy, 40°45'21"N, 27°20'04"E, altitude 20–40 m, on stones and pebbles of calcareous sandstone, 2007, J. Vondrák 8199 (holotype, PRA!).

***Pyrenodesmia micromontana*** (I.V. Frolov, Wilk & Vondrák) Hafellner & Türk (for details, see Hafellner & Türk, 2016)

***Pyrenodesmia microstepposa*** (I.V. Frolov, Nadyeina, Khodos. & Vondrák) Hafellner & Türk (for details, see Hafellner & Türk, 2016)

***Pyrenodesmia molariformis*** (I.V. Frolov, Vondrák, Nadyeina & Khodos.) S.Y. Kondr. (for details, see Kondratyuk et al., 2020a)

***Pyrenodesmia peliophylla*** (Tuck.) S.Y. Kondr. (for details, see Kondratyuk et al., 2020a)

***Pyrenodesmia pratensis*** (Wetmore) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828644

≡ *Caloplaca pratensis* Wetmore, Bryologist 112: 382. 2009 (basionym).

Type: USA. North Dakota: Oliver Co., about 3.2 km S, 6.4 km E of Hensler, The Nature Conservancy's Cross Ranch Preserve, Sangor Ghost Town, gentle slopes of mixed grass prairie, Missouri River Valley floodplain, 47°10'48"N, 100°59'42"W, altitude 515 m, on old concrete foundation, 2007, M. K. Advaita 6100 (holotype, MIN; isotype, GZU!).

***Pyrenodesmia tianshanensis*** (Xahidin, A. Abbas & J.C. Wei) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828645

≡ *Caloplaca tianshanensis* Xahidin, A. Abbas & J.C. Wei, Mycotaxon 114: 3. 2011 (basionym).

Type: China. Xinjiang: Mt. Nan-shan in Tianshan mountain chain, Miaoergou, altitude 1280 m, on limestone, 2009, A.

Abbas & H. Xahidin 20090001 (holotype, XJU!; isotype, HMAS-L).

*Pyrenodesmia transcaspica* (Nyl.) S.Y. Kondr. (for details, see Kondratyuk et al. 2020b)

*Pyrenodesmia variabilis* (Pers.) A. Massal. (for details, see Arup et al., 2013)

Type: Deutschland. [Nordrhein-Westfalen]: Kalkstein zu Buren [Büren], 1856, J. Lahm? (neotype, B 600011187!, selected by Wunder, 1974: 97).

### 5.3 *Sanguineodiscus* I.V. Frolov & Vondrák, gen. nov.

Mycobank: MB828647; Fig. 3C

Etymology: Included lichens often have deep red (sanguineous) apothecial discs.

Type: *Sanguineodiscus viridirufus* (Ach.) I.V. Frolov & Vondrák

Diagnosis: Apothecial disc pale to dark red with anthraquinones of the chemosyndrome A (sensu Søchting, 1997), exceptionally lacking anthraquinones and brown or black (Fig. 3C, right). True exciple often gray-black or the same color as disc. Thallus and thalline exciple with Sedifolia-gray, lacking anthraquinones. Distributed in Eurasia and Northern Africa, mainly in the Mediterranean basin and Central Asia. Saxicolous and corticolous.

Description: *Morphology and anatomy*: Thallus crustose, epilithic or epiphytic, white to dark gray; cortex paraplectenchymatous, well developed in lower part of thalline exciple, but only alveolate cortex (sensu Vondrák et al., 2013) developed in thallus; vegetative propagules not known. Apothecia zeorine, sometimes seemingly lecanorine, but thin true exciple is always present. Disc dark to pale red, but rarer some individuals have black or brown discs without anthraquinones (Fig. 3C, right). True exciple orange to red, but its outer rim often gray, darker than thallus and thalline margin. Thalline exciple of the same color as thallus. Ascospores polardiblastic, ellipsoid, with medium to large long septum; pycnidia often present, gray-black; conidia bacilliform.

Chemistry: Thallus and thalline exciple always without anthraquinones, usually with Sedifolia-gray. Epithymenium and inner rim of true exciple usually with anthraquinones. Outer rim of true exciple may contain only anthraquinones or both anthraquinones and Sedifolia-gray. Rare chemotypes with black-colored apothecia (without anthraquinones, only with Sedifolia-gray) are occasionally recorded within typical populations (Fig. 3C, right).

Distribution and ecology: Distributed in Europe, Northern Africa, and Asia, but main occurrence is in the Mediterranean basin and Central Asia. Saxicolous or corticolous. Saxicolous taxa occur on inland rain-sheltered base-rich siliceous rocks (*S. viridirufus*), seashore siliceous rocks (*S. aractinus*) in western Eurasia, or on calcareous outcrops in Central Asia (*S. bicolor*). Corticolous species grow on deciduous and coniferous trees and shrubs predominantly in Mediterranean regions and Macaronesia.

Remarks: Currently, four species are included in the genus, but this group is more diverse and contains unnamed taxa (both saxicolous and corticolous; Vondrák, unpublished).

*Sanguineodiscus aractinus* (Fr.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828648

≡ *Parmelia aractina* Fr., *Systema Orbis Vegetabilis* (Lundae) 1: 284. 1825 (basionym).

Type: Sweden. Halland: 1825 (holotype, UPS 63456!).

Chemistry: Chemosyndrome A; rarely anthraquinones completely absent.

*Sanguineodiscus bicolor* (H. Magn.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828649

≡ *Caloplaca bicolor* H. Magn., *Lichens from Central Asia* 1: 132. 1940 (basionym).

Type: [China. Gansu Province]: Erh-tao-ch'uan (Nan-shan), altitude about 4100 m, 1932, Bohlin 77 c, d (holotype, S).

Chemistry: Chemosyndrome A.

*Sanguineodiscus haematites* (Chaub.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828650

≡ *Lecanora haematites* Chaub., *Flore Agenaise*: 492. 1821 (basionym).

Type: [France]. Sur l'écorce de presque tous les arbres. CCC. Aux environs d'Agen. (type not located).

Chemistry: Chemosyndrome A.

*Sanguineodiscus viridirufus* (Ach.) I.V. Frolov & Vondrák, **comb. nov.**

Mycobank: MB828651; Fig. 3C

≡ *Lecidea viridirufa* Ach., *Lich. univ.*: 204. 1810 (basionym).

Type: Helvetiae [(Switzerland)]. Ad lapides schistosos, *Schleicher* 544 (holotype, H-ACH 336).

Remarks: The name refers to inland populations morphologically similar to *S. aractinus* from seashore rocks. Data from mtLSU and nucITS DNA loci suggest a close relationship but separation of coastal and inland populations (Vondrák, unpublished).

Chemistry: Chemosyndrome A; rarely anthraquinones completely absent.

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## Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12717/supinfo>:

**Fig. S1.** Position and content of *Pyrenodesmia* s.lat. within Caloplacoideae clade. Maximum likelihood phylogeny of the concatenated data set of ITS, mtSSU, nuLSU, RPB1, and RPB2 loci. Numbers at branches represent bootstrap values  $\geq 70\%$ . Branches with bootstrap values  $\geq 70\%$  are thickened. *Caloplaca demissa*, *C. obscurella*, and *C. reptans* are in bold. K, the genus *Kuettlingeria*; P, the genus *Pyrenodesmia* s.str.; S, the genus *Sanguineodiscus*.

**Fig. S2.** The clade of *Pyrenodesmia* s.lat. Maximum likelihood phylogeny of the concatenated data set of EF1a, ITS, MCM7, mtSSU, nuLSU, RPB1, RPB2, and TUBB loci. Numbers at branches represent bootstrap values  $\geq 70\%$ . Branches with bootstrap values  $\geq 70\%$  are thickened. Abbreviations: K, the genus *Kuettlingeria*; P, the genus *Pyrenodesmia* s.str.; S, the genus *Sanguineodiscus*.

**Fig. S3.** The clade of *Pyrenodesmia* s.lat. Bayesian single-gene phylogeny reconstructions. **A**, EF1a, ITS, MCM7, mtSSU. **B**, nuLSU, RPB1, RPB2, TUBB. Branches with posterior probabilities  $\geq 0.95$  are thickened.

**Table S1.** Subsets of partitions and the best substitution models per subset for the Caloplacoideae and the *Pyrenodesmia* alignments: PartitionFinder results.