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New crustose *Teloschistaceae* in Central Europe

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Abstract: Central Europe in general is poor in *Teloschistaceae* lichen crusts (*Caloplaca* s. lat.). Diversity of these lichens is increased by the occurrence of some Arctic, Mediterranean and continental species, which are here close to the limits of their range. Examples include:

1) *Caloplaca interfulgens*, previously known from arid territories of northern Africa and western Asia, is recorded, surprisingly, from Austria, Czech Republic, Germany, Slovakia and southern Russia. In Central Europe, it is restricted to scattered xerothermic limestone outcrops.

2) *Caloplaca scabrosa*, previously known only from Svalbard, is recorded from the Sudetes in the Czech Republic. It is similar to, but not conspecific with, *C. furfuracea*. Its diagnostic characters include a blastidiate thallus and the presence of atranorin. Our results show that atranorin is absent in the majority of taxa related to *C. furfuracea* with only two exceptions: the sample from Eastern Carpathians, here called *C.* aff. *scabrosa*, and in one Sudetan sample identified as *C. crenularia*.

3) *Caloplaca emilii*, newly described below, is closely related to the Mediterranean *C. areolata*. We consider *C. emilii* a Mediterranean species rarely occurring in higher latitudes in Austria, the Czech Republic and Germany. It is distinguished from *C. areolata* mainly by the presence of vegetative diaspores (blastidia); a possible role of blastidia in the distribution pattern of *C. emilii* is discussed below. Status of the names *Caloplaca areolata*, *C. isidiigera* and *C. spalatensisis*, formerly used for the new taxon, is clarified.

4) *Caloplaca molariformis*, newly described below, belongs to the *Pyrenodesmia* group (a lineage of *Caloplaca* without anthraquinones). It is a continental species, frequently collected on limestone or lime-rich tuffs in steppes or deserts in Turkey, Iran, western Kazakhstan and southern Russia, and is also known from eastern Ukraine and southern Slovakia. *Caloplaca molariformis* is characterized by its thick thallus with fungal and algal tissues arranged in high stacks.

5) *Caloplaca substerilis*, newly described below, is distinguished from the closely related *C. ulcerosa* by its endophloeodal or minutely squamulose thallus with soralia formed in bark crevices or on margins of squamules. While *C. ulcerosa* has a maritime distribution in Europe, *C. substerilis* is typically a continental species. North American continental lichens called "*C. ulcerosa*" are phylogenetically closer and more similar to *C. substerilis*.

The positions within *Teloschistaceae* of the taxa considered are demonstrated by ITS phylogenies. The distributions of *C. areolata*, *C. emilii* and *C. interfulgens* are mapped. The new species are fully described using more than a hundred phenotype characters, and diagnostic characters are indicated separately.

Key words: biodiversity, biogeography, ITS phylogeny, lichen phenotype evaluation, species recognition, vegetative reproduction

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Introduction

Teloschistaceae, with its 1000 or more species (Arup *et al.* 2013), has highest biodiversity in temperate regions (Feuerer 2011). In Central Europe, hot spots of *Caloplaca* diversity are restricted to habitats with sun-exposed calcareous or base-rich siliceous outcrops in alpine zones of the Alps and high Carpathians (e.g. Poelt 1953*a*, *b*, 1954, 1955, 1960, 1964; Wilk & Flakus 2006; Vondrák *et al.* 2008), or in dry and warm rocky steppes (e.g. Poelt 1975; Vondrák *et al.* 2007). In other Central European habitats, only the common epiphytic and epilithic species are found; the highest number of these common species is found on lime-rich artificial substrata (e.g. Vondrák & Hrouzek 2006; Svoboda *et al.* 2007; Vondrák *et al.* 2010*a*).

Altogether, more than one hundred *Caloplaca* species occur in Central Europe (Vondrák & Wirth 2013), but about two thirds of these are rare species, known from very few localities. In other words, the generally low *Caloplaca* species diversity in Central Europe is partly enriched by marginal occurrences of some 'exotic' taxa further distributed in the Mediterranean basin, western Asia or in the Arctic. Known examples are *C. exsecuta* (Nyl.) Dalla Torre & Sarnth., *C. haematites* (Chaub.) Zwackh, *C. pollinii* (A. Massal.) Jatta (Vondrák & Wirth 2013), *C. raesaenenii* Bredkina (e.g. Søchting & Stordeur 2001), *C. tominii* Savicz (Vondrák *et al.* 2011), and many others.

Here we report several taxa newly discovered in Central Europe. *Caloplaca interfulgens* and *C. scabrosa* were previously known only from very distant areas and their occurrence in Central Europe was not expected. *Caloplaca emilii*, *C. molariformis* and *C. substerilis* are newly described from elsewhere, but also occur in Central Europe.

Materials and Methods

Sampling

Lichen samples were collected by the authors from various European and Asian localities between 1994 and 2012. We list information regarding locality, habitat, collection and deposition of specimens. Citations of the older herbarium samples from BRA and STU (in *Caloplaca interfulgens* and *C. emilii*) are as complete as we can make them. Specimens from CBFS, PRA and GZU used for comparative studies are cited more briefly in the text.

Phenotype evaluation

More than 100 phenotype characters were assessed before preparing descriptions of the three new taxa. The list of characters and the way in which they were studied is provided in Vondrák *et al.* (2013). All observations were carried out on dead, stabilized material, on hand-cut sections mounted in water, without any chemical treatments. Measurements are accurate to 0·5 µm for cells and 10 µm for larger structures. All measurements of cells include their walls, except for tissues with glutinized cell walls. In *Caloplaca molariformis*, the widths of algal and fungal stacks are measured at the mid-point of their vertical extent. In each sample, ten measurements were made for each measurable character. Results of the measurements are given as (min.–) $\bar{x}_1$–$\bar{x}_2$–$\bar{x}_3$ (–max.), where min/max are extremes from all measurements, $\bar{x}_1$ is the lowest specimen arithmetic mean observed, $\bar{x}_2$ is the arithmetic mean of all observations, $\bar{x}_3$ is the highest specimen arithmetic mean observed. In cases where measurements were made from one sample, only $\bar{x}_2$ is recorded. Total number of measurements (*n*), number of samples asessed (N), and standard deviation from all measurements (SD) are given in square parenthesis for each character measured [*n*; N; SD]. General morphological terminology follows Smith *et al.* (2009); the term "alveolate cortex" is adopted from Vondrák *et al.* (2009*a*).

Chemistry

Spot tests with KOH (K), sodium hypochlorite (C), paraphenylenediamine (P) and UV light were performed in each new species. Tissues were also tested for amyloidity by the reaction with Lugol's solution (I). Pigments insoluble in acetone were evaluated following Meyer & Printzen (2000). Extracellular crystals were examined by the reaction with concentrated H_2SO_4 for detection of Ca. HPLC was used for identification of acetone-soluble compounds. The anthraquinone contents were analyzed on a LichroCART 250-4 RP18-e (5 µm) column using an Agilent 1100 Series Chromatograph after Søchting (1997), but using the wavelength (240 nm). Whole absorption spectra in the range 200–600 nm were monitored. The presence of atranorin in the samples was determined after Feige *et al.* (1993) on the same column and chromatographic system.

DNA extraction, amplification and sequencing

The simple NaOH extraction (Werner *et al.* 2002) was used for DNA isolations. Primers for PCR amplification were ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). PCR cycling parameters follow Ekman (2001). A total of 51 nuclear ITS sequences were newly generated (Table 1).

TABLE 1. *New* Caloplaca *ITS sequences generated during this study*

Labels of phylogenetic tree terminals	Voucher	GenBank Accession No.
Caloplaca aff. *crenularia* Canary Islands	GZU (1993, *Poelt & Sanchez-Pinto*)	KC416116
C. areolata Croatia	CBFS JV7950	KC416098
C. areolata Montenegro	GZU (2008, *Mayrhofer*)	KC416097
C. areolata Spain	CBFS JV6314	KC416096
C. crenularia Bulgaria	CBFS JV2065	KC416112
C. crenularia Crete 1	GZU (*Mayrhofer* 18045)	KC416113
C. crenularia Crete 2	CBFS JV4137	KC416119
C. crenularia Hungary	CBFS JV6409	KC416117
C. crenularia Iran	CBFS JV5608	KC416115
C. crenularia Spain	CBFS JV6255	KC416114
C. crenularia Turkey	CBFS JV6064	KC416118
C. emilii Bulgaria, holotype	CBFS JV6600	KC416101
C. emilii Bulgaria, Rhodopes	CBFS JV2223	KC416099
C. emilii Czech Republic	CBFS JV9358	KC416102
C. emilii Czech Republic 2	CBFS JV9357	KC416103
C. emilii France	Hb. Clauzade 23475	KC416100
C. emilii Greece	CBFS JV8832	KC416104
C. ferrarii s.lat. Czech Republic 1	CBFS JV8782	KC416139
C. ferrarii s.lat. Czech Republic 2	CBFS JV9150	KC416132
C. ferrarii s.lat. Czech Republic 3	CBFS JV9043	KC416137
C. ferrarii s.lat. Czech Republic 4	CBFS JV9151	KC416140
C. furfuracea Austria	PRA (*Palice* 12390)	KC416120
C. fuscorufa Ukraine	CBFS JV6204	KC416111
C. herbidella Turkey	PRA (*Palice* 11832)	KC917268
C. interfulgens Czech Republic 1	CBFS JV9399	KC416134
C. interfulgens Czech Republic 2	CBFS JV9153	KC416131
C. interfulgens Czech Republic 3	CBFS JV9156	KC416129
C. interfulgens Czech Republic 4	CBFS JV9155	KC416130
C. interfulgens Czech Republic 5	CBFS JV9144	KC416138
C. interfulgens Slovakia 1	CBFS JV9260	KC416136
C. interfulgens Slovakia 2	CBFS JV9186	KC416135
C. interfulgens southern Russia	CBFS JV9396	KC416133
C. interfulgens Turkey	CBFS JV8552	KC416125
C. interfulgens Turkey	CBFS JV8557	KC416126
C. interfulgens Turkey	CBFS JV8539	KC416127
C. lactea Greece	CBFS JV8331	KC416128
C. lactea Italy	CBFS JV8679	KC416124
C. molariformis Kazakhstan	CBFS JV7635	KC416146
C. molariformis Slovakia, holotype	CBFS JV10192	KC416142
C. molariformis Turkey	CBFS JV9787	KC416144
C. molariformis Ukraine 1	KV (Luhansk, *Nadyeina* 132)	KC416143
C. molariformis Ukraine 2	KV (Luhansk, *Nadyeina* 134)	KC416145
C. scabrosa Czech Republic	CBFS JV1908	KC416122
C. "*scabrosa*" Ukraine 1	CBFS JV6198	KC416121
C. "*scabrosa*" Ukraine 2	CBFS JV6199	KC416123
C. substerilis Austria	CBFS JV7257	KC416107
C. substerilis Bulgaria	CBFS (Exs. of *Caloplaca*, nr 11)	KC416108
C. substerilis Czech Republic, holotype	CBFS JV7920	KC416109
C. substerilis Slovakia	PRA (*Palice* 13441)	KC416110
C. "*ulcerosa*" USA	GZU (*Wetmore* 93230)	KC416105
C. "*ulcerosa*" USA 2	GZU (*Advaita* 4915)	KC416106
C. sp. southern Russia	CBFS JV8181	KC416141

TABLE 2. *Summary of phylogenetic analyses: length of alignments (including gapped positions) and model selected for the purpose of MrBayes calculation*

Target Group	Phylogenetic tree	Length of alignment	Model
Caloplaca crenulatella group	Fig. 2	525 positions	SYM+ADGamma
C. crenularia group	Fig. 3	486 positions	GTR+ADGamma
C. xerica group	Fig. 4	501 positions	SYM+ADGamma
Pyrenodesmia group	Fig. 5	535 positions	SYM+ADGamma
C. ulcerosa and related taxa	Fig. 6	519 positions	GTR+ADGamma

Phylogenetic analyses

Five independent phylogenetic analyses of the nuclear ITS region were made to cover the individual groups studied. All analyses followed almost the same design; differences are listed in Table 2. Sequences were aligned using the MAFFT v6 server (http://mafft.cbrc.jp/alignment/server; Katoh & Toh 2008) according to the L-INS-i strategy. The resulting alignments required some manual adjustments (done in BioEdit; Hall 1999) and, in the case of the *C. crenularia* group, also trimming of unalignable positions (using TrimAl-automated1 algorithm, Capella-Gutierrez *et al.* 2009). The length of datasets submitted to further analyses ranged from 486–535 positions. Final alignments were submitted to TreeBase http://treebase.org/treebase-web/home.html.

Molecular phylogenies were estimated by Bayesian inference as incorporated in MrBayes 3.0b4 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Model selection was committed to the Kakusan4 algorithm (Tanabe 2011), whereas the baseml software (Adachi & Hasegawa 1996) served as the computational core. With reference to the Bayesian information criterion (Schwartz 1978), we opted for SYM or GTR models with rate variation across sites simulated by discrete gamma distribution (Γ8) and autocorrelated by the AdGamma rates prior (Table 2.). The increased probability of transitions over transversions, well documented in many rDNA datasets (see e.g. Keller *et al.* 2007), was reflected by setting the substitution rates prior (revMatPr) to dirichlet with values 1 and 3 for these two mutational types, respectively. Each analysis comprised two independent runs, each of which encompassed four Metropolis-coupled MCMC chains with 10 000 000 generations sampled after every 1000th generation. In every run, one Markov chain was cold and three were incrementally heated by the parameter of 0·3. To eliminate trees sampled before reaching apparent stationarity, the first 25% of entries were discarded as burn-in and the rest were used to compute majority-rule consensus, where the relative occurrences of nodes are identified with the Bayesian posterior probabilities (Figs 2–6). Bayesian posterior probabilities ≥50 are shown, branches with lower posterior probabilities are collapsed.

Nomenclature

Arup *et al.* (2013) proposed a new nomenclature within *Teloschistaceae* and split the crustose genus *Caloplaca* into numerous genera. We do not follow the new nomenclature in this paper, because generic names are still missing for many *Teloschistaceae* taxa, including *Caloplaca emilii* and *C. substerilis* described here. Names of other lichen taxa follow the Index Fungorum http://www.indexfungorum.org/names/names.asp

Records new to Central Europe

Caloplaca interfulgens (Nyl.) J. Steiner

Verh. zool.-bot. Ges. Wien **52:** 479 (902). – *Lecanora interfulgens* Nyl. *Flora* **56:** 340 1878.

Images of some Czech and German specimens are available on the lichenological web page at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5.

Diagnostic characters. Thallus well-developed, consisting of yellow areoles and often with squamules at the margin. Ascospores polarilocular, *c*. 15–19 × 5·0–7·5 µm with septa up to 4 µm wide. Prothallus indistinct. Occurs on calcareous rocks.

Similar taxa are *Caloplaca crenulatella* s. lat. (the yellow thallus usually reduced), *C. diffusa* Vondrák & Llimona (on non-calcareous rocks, yellow thallus with thin diffuse margin, with grey-white prothallus, squamules absent) and species of the *Caloplaca velana* complex (ascospores shorter with thicker septa).

Distribution (Fig. 1A). *Caloplaca interfulgens* was previously known only from deserts, semi-deserts or steppes in North Africa (Nylander 1878; Navarro-Rosinés & Hladun 1996), Mediterranean Europe (Italy: Nimis & Martellos 2008; Spain: Nimis *et al.* 1998), Iran, Kazakhstan (Vondrák *et al.* 2011) and continental Turkey (Vondrák *et al.* 2012*a*). The new records are surprisingly from less arid territories in Austria, the Czech Republic, Germany, southern Russia and Slovakia.

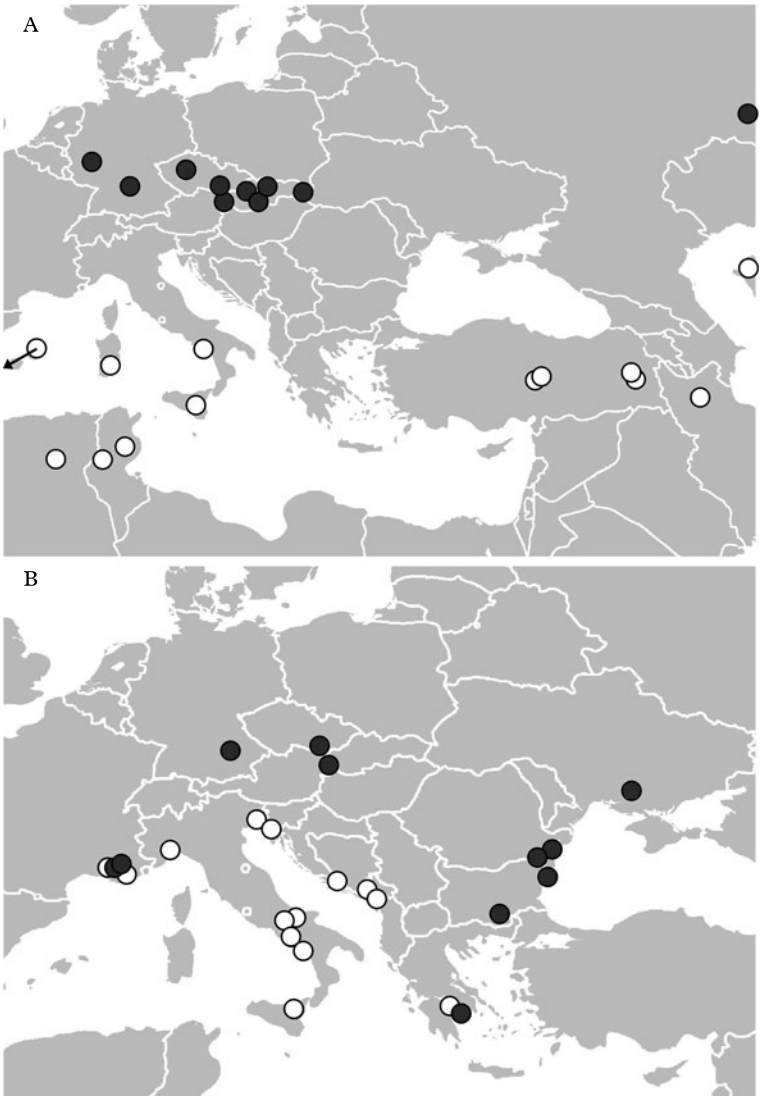

FIG. 1. Distribution maps. A, *Caloplaca interfulgens*, previously published data (white dots), new records (black dots); B, *C. emilii* (black dots), *C. areolata* (white dots).

In all Central European localities, *C. interfulgens* is restricted to limestone outcrops in xerothermic sites (often south-facing steppes).

Phylogeny. In the ITS phylogeny of the *Caloplaca crenulatella* group (Fig. 2), *Caloplaca interfulgens* forms a well-resolved sister clade to *Caloplaca tominii*, a sorediate species with a similar distribution pattern in Europe.

Taxonomic note. Although the *Caloplaca crenulatella* group has been studied recently (Navarro-Rosinés & Hladun 1996; Vondrák *et al.* 2011), it is still poorly understood and many lineages are not yet well characterized. Fortunately, its well-developed areolate thallus separates *C. interfulgens* from the many taxa with reduced thalli. However, some Central Asian taxa have a thallus similar to

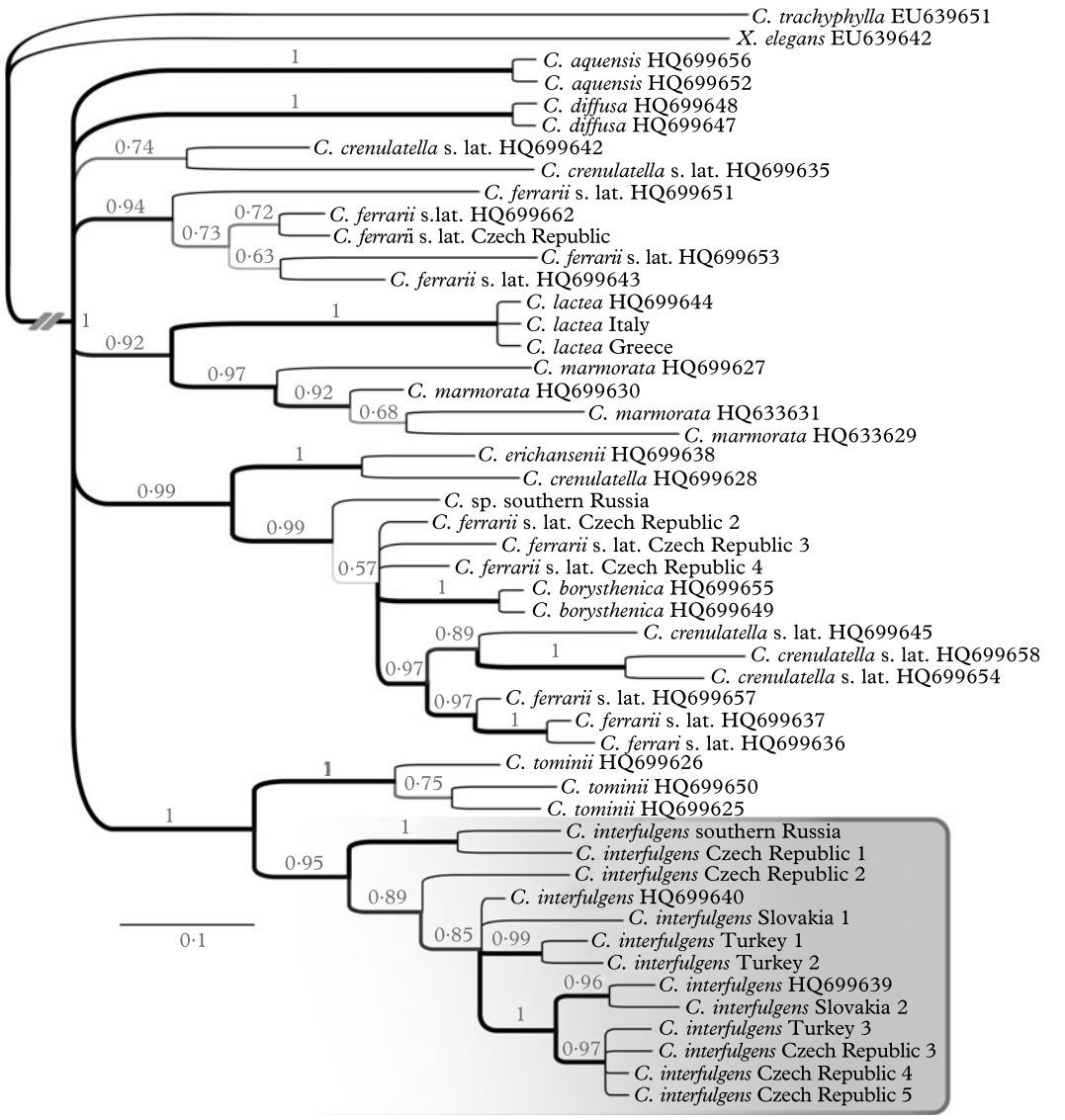

FIG. 2. Bayesian ITS phylogeny of the *Caloplaca crenulatella* group; *C. interfulgens* clade delimited by the grey square.

C. interfulgens (e.g. '*Caloplaca* sp., southern Russia' in Fig. 2) and their delimitation requires further study.

New records. **Austria:** *Niederösterreich*: Wien, Hainburg an der Donau, rocks on SW slopes of hill Braunberg NE of town, 48°09′10″N, 16°57′12″E, 280 m, 2012, *J. Vondrák* 9550 (CBFS).—**Czech Republic:** *Central Bohemia*: Bohemian karst, Beroun, Tmáň, protected area Kotýz, 1·5 km NE of village, 49°54′56″N, 14°2′55″E, 350 m, 2011, *J. Vondrák* 9153, 9155 & 9156 (CBFS); Praha, Dobřichovice, Karlík, limestone outcrops 1 km NW of ruin of Karlík, 49°56′56″N, 14°14′49″E, 300 m, 2011, *I. Frolov & J. Vondrák* 9399 (CBFS); Praha, Radotín, Kosoř, protected area Černá rokle, E of village, 49°59′21″N, 14°20′8″E, 250–300 m, 2011, *Z. Palice & J. Vondrák* 9144 (CBFS). *Southern Moravia*: Pavlovské vrchy hills, Mikulov, Klentnice, SE slope of hill Pálava, 48°51′22″N, 16°38′33″E, 350–400 m, 2012, *J. Vondrák* 9577 (CBFS).—**Germany:** *Baden-Württemberg*: Schwäbishe Alb Mts, Langenau, Albeck, shallow valley W of Kornberghöfe, 520–550 m, 1984, *V. Wirth* 29418 (STU; hb. Wirth). *Rheinland-Pfalz*: Eifel Mts, Uxheim, Dreimühlen, limestone outcrops in dry

grassland, 1992, *V. Wirth* 23937 & *R. Düll* (STU; hb. Wirth).—**Russia:** *Orenburgskaya Oblast'*: surroundings of water reservoir "Iriklinskoe vodokhranilishche", vill. Chapaevka, limestone rocks on opposite slope of lake, NE of village, 52°05′12″N, 58°48′1″E, 270–290 m, 2011, *I. Frolov & J. Vondrák* 9396 (CBFS).—**Slovakia:** *Cerová vrchovina upland*: Filakovo, Hajnáčka, hill Ragač, lime-rich outcrop of volcanic pyroclastics in open beech-oak forest, 48°13′25″N, 19°59′6″E, 500 m, 2012, *J. Vondrák* 10137 (CBFS). *Muranská Planina Mts*: Brezno, Tisovec, hill Okruhla skala, *c.* 2 km W of town, 48°40′42″N, 19°54′57″E, *c.* 800 m, 2011, *J. Vondrák* 9260 (CBFS). *Strážovské vrchy Mts*: Ilava, Zliechov, on S-slope of Mt Strážov, 48°56′59″N, 18°27′16″E, 1000 m, 2012, *J. Vondrák* 10198 (CBFS). *Vihorlat Mts*: Sobrance, Podhorod [Podhradí], 1930, *J. Bučck* (BRA, sub *Caloplaca zimmermannii*, Servít, nomen ined.).

Caloplaca scabrosa Søchting, Lorentsen & Arup

Nova Hedwigia **87: 89** (2008).

Images of European samples and the isotype are available on the lichenological web at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5.

Observation of the type specimen. Isotype (CBFS JV9402, ex C; *Søchting* 5513) examined in detail.

Thallus rough and scabrous by blastidia, densely covering the thallus surface. *Blastidia* (40–)*71*(–130) μm diam. [*10*; 1; 29]. Thallus surface pale grey to sordid white, but tips of blastidia often dark grey. Grey thallus parts containing Cinereorufa-green (green-grey in water, K–, N+ red) in the uppermost thallus cells. Thallus divided into thin and more or less flat angular areoles, *c.* 0·2–1·3 mm diam. The real cortex absent, but indistinct alveolate cortex present in spots, of spherical, thick-walled cells (wall *c.* 1 μm thick). Thallus without anthraquinones, but with atranorin.

Apothecia biatorine, deep red (old apothecia somewhat blackened), with anthraquinones; major: parietin and 7-Cl-emodin; traces of emodin, 7-Cl-citreorosein, 7-Cl-emodinal and parietinic acid (C+ purple owing to chlorinated compounds). *True exciple* of palisade prosoplectenchyma, of cells with glutinized, *c.* 1 μm thick walls. Lower exciple and lower hypothecium brown-red (possibly due to small amount of anthraquinones; with weak K+ purple reaction). *Ascospores* polarilocular, (12·0–)*14·0*(–17·0) × (5·5–)*6·5*(–8·0) μm [*10*; 1; 1·3 & 0·7], with septa (4·0–)*5·0*(–5·5) μm [*10*; 1; 0·5].

Pycnidia not present on the available isotype material. The type material is also described in Søchting *et al.* (2008).

Observations of the Central European specimens. (Fig. 7A).

Thallus rough and scabrous by blastidia, densely covering the thallus surface. *Blastidia* (30–)58–67–72(–130) μm diam. [*30*; 3; 28]. Thallus surface pale grey to white, but tips of blastidia often dark grey. Grey pigmented thallus parts containing Cinereorufa-green (green-grey in water, K–, N+ red) in the uppermost thallus cells. Thallus divided into thin and flat angular areoles, *c.* 0·2–1·0 mm diam. The real cortex absent, but indistinct alveolate cortex present in spots, of spherical, thick-walled cells (walls *c.* 1 μm thick). Thallus without anthraquinones, but with atranorin.

Apothecia deep red (old blackened apothecia not observed), with anthraquinones; major: parietin and 7-Cl emodin; traces of emodin, fragilin and parietinic acid (C+ purple owing to chlorinated compounds); biatorine or zeorine; thalline exciple sometimes strongly expanded in old apothecia. *True exciple* of palisade prosoplectenchyma, of cells with glutinized, 1–2 μm thick walls. Inner exciple and lower hypothecium brown-red (perhaps by anthraquinones). *Ascospores* polarilocular, (11·5–)*13·0*(–15·0) × (6·5–)*7·5* (–9·0) μm [*10*; 1; 1·4 & 0·8], with septa (3·0–)*4·0*(–5·0) μm [*10*; 1; 0·5].

Pycnidia with red tops, containing chlorinated anthraquinones (C+ purple). *Conidia* more or less bacilliform, *c.* 3–4 × 1 μm.

Importance of particular characters. *Caloplaca scabrosa* shares many characters with other related taxa from the *C. crenularia* group (as defined in Fig. 3), so their diagnostic power is rather low. They include: 1) presence of Cinereorufa-green in the thallus; 2) apothecia with chlorinated anthraquinones (C+ purple); 3) structure of the true exciple; 4) brownish pigment in lower hypothecium and inner true exciple; 5) pycnidia with red caps.

Some characters are specific for *C. scabrosa*: 1) presence and size of blastidia; 2) presence of atranorin in the thallus. We have tested the diagnostic power of the presence

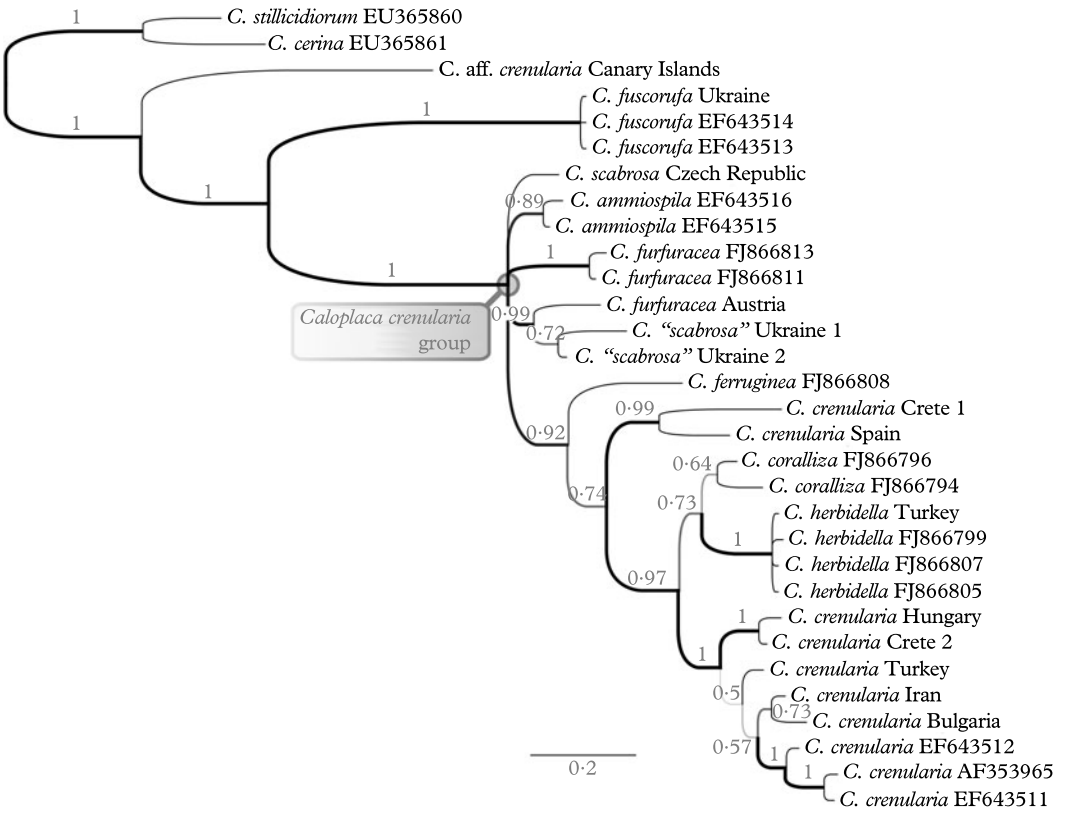

FIG. 3. Bayesian ITS phylogeny of the *Caloplaca crenularia* group including the Central European sample of *C. scabrosa* and *C.* "*scabrosa*" from the Eastern Carpathians.

of atranorin. We analyzed thalli of various species of the *C. crenularia* group: *Caloplaca ammiospila* (Ach.) H. Olivier (CBFS JV10223), *C. crenularia* (With.) J. R. Laundon (CBFS JV4596; 5608; hb. Z. Palice 7837; Poland, *Nowak's exsiccate* 203 in GZU; Sardinia, 1986, Poelt in GZU), *C. ferruginea* (Huds.) Th. Fr. (CBFS JV7224; 7256), *C. furfuracea* H. Magn. (Ural, hb. I. Frolov), and *C. hungarica* H. Magn. (CBFS JV3081). Atranorin was detected in only one sample of *C. crenularia* from the basalt outcrops in the Karkonosze Mountains, W Sudetes (Nowak, *Lich. Polon. Exs*. n. 203), indicating that this *C. crenularia* specimen does not belong in the main *C. crenularia* clade.

The type specimen of *Caloplaca scabrosa* differs from the Central European material in the following characters: 1) size of areoles; 2) thallus thickness; 3) extent of the thalline exciple. Based on our observations of numerous samples of the *C. crenularia* group, these characters were very variable both within and between specimens of a single species, so the differences are of little taxonomic importance. Ascospore size and septum width also differ between the type and the Central European collections, but this difference may be merely a consequence of the low number of available specimens and measurements.

Phylogeny. The ITS sequence of the Central European specimen of *Caloplaca scabrosa* is placed in the basal polytomy of the ITS phylogeny of the *C. crenularia* group (Fig. 3). It is perhaps closely related to the arctic-alpine *C. ammiospila* or boreo-montane *C. furfuracea*.

Taxonomic notes. The epixylic taxon *Caloplaca furfuracea* is very similar to *C. scabrosa*. It likewise produces blastidia (isidia according to Arup & Åkelius 2009) of the same size; tips of blastidia are also usually dark grey due to the Cinereorufa-green content in the alveolate cortex. With the exception of the ecology, the only reliable character distinguishing *C. furfuracea* from *C. scabrosa* is the absence of atranorin.

We have collected samples of a granular to blastidiate lichen in the subalpine belt of the Eastern Carpathians ("*Caloplaca scabrosa*" in Fig. 3). These saxicolous specimens are very similar to both *C. furfuracea* and *C. scabrosa*. They appear to be closer to *C. furfuracea* in the ITS phylogeny but they share chemistry and ecology with *C. scabrosa*.

New records. **Czech Republic:** *Northern Moravia*: Rýmařov, Karlov, central part of Velký kotel corrie, on phyllitic overhanging rock, 1330–1340 m, 2002, *Z. Palice* 7024 (PRA); *ibid.*, 50°03′20″N, 17°14′E, 1250–1300 m, 2004, *J. Vondrák* 1907, 1908 & 1909 (CBFS).

C. "*scabrosa*". **Ukraine:** *Eastern Carpathians*: Svidovets Mts, at glacial lake at bottom of glacial cirque in N slope, 48°15′41″N, 24°13′22″E, on sun-exposed base-rich sandstone boulders close to water, *c.* 1300 m, 2007, *J. Vondrák* 6199 (CBFS).

New species

Caloplaca emilii Vondrák, Khodos., Cl. Roux & V. Wirth sp. nov.

MycoBank No: MB 803332

Thallus grey or brown-grey, non-pruinose, of more or less flat areoles, with Sedifolia-grey and without anthraquinones. Dark grey blastidia always present at margins of thallus units. Mature apothecia zeorine, usually with brown disc and more or less yellow true exciple, C± purple (with chlorinated anthraquinones). Ascospores broadly ellipsoid, less than 15 µm long, with thick septa. Pycnidial tops dark grey. Conidia ellipsoid, not bacilliform.

Type: Bulgaria, Black Sea coast, Kavarna, limestone cliffs on seashore 1·5 km NE of Kamen Brjag, 43°27′58·76″N, 28°33′55·02″E, on coastal limestone outcrop above supralittoral zone, 6 April 2007, *J. Vondrák* 6600 (CBFS—holotype; KHER—isotype). ITS sequence of the holotype: KC416101.

Images of the German sample are available on the lichenological web page at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5.

(Figs 1B, 4, 7B)

Thallus forming irregular spots, brown-grey or pale to dark grey, to several cm wide; often starting on other crustose lichens; of tightly arranged, angular to rounded, flat to slightly convex, areoles or squamules, (0·3–)0·6–*0·9*–1·1(–2·6) mm diam. [*70*; 7; 0·4]. Thickness of thallus 100–500 µm. *Medulla* well-developed only in thick thalli, but up to 400 µm thick; medullary tissue formed of loose prosoplectenchyma; medullary hyphae *c.* 2–3 µm wide with walls thickened up to 1 µm. *Algal layer* 50–140 µm thick; algal cells globose, *c.* 5–20 µm diam. *Cortex* developed in patches, up to 30 µm thick, not gelatinous; sometimes only alveolate cortex present. *Epinecral layer* often present, up to about 10 µm thick. Cortex cells or alveolate cortex cells spherical, thin-walled, about 4–6 µm diam. *Blastidia* simple, globose, dark grey, always present, produced at margins of areoles or squamules, rarely also on their upper surface, (20–)53–*65*–95(–210) µm diam. [*60*; 6; 36]. Extracellular crystals of calcium salts not observed in any thallus part. Pruina absent. *Prothallus* indistinct or absent. Thallus frequently affected by brown hyphomycetes resembling species of *Intralichen*.

Apothecia present in *c.* 50% of samples collected; rare in northern populations; (0·3–)0·5–*0·7*–0·9(–1·4) mm diam. [*40*; 4; 0·2]; zeorine. *Disc* in shades of brown (orange in young apothecia); true exciple usually yellow (contrasting with disc); thalline exciple in shades of grey; pruina absent. *Hymenium* colourless, without distinct gelatinous matrix and without extracellular oil drops, *c.* 70–110 µm high; *epihymenium* ochre to green-yellow. *Hypothecium* colourless, rarely with extracellular oil drops, more or less flat, *c.* 100–300 µm high, formed of cells variable in shape; subhypothecial algal layer present (algal cells underlying entire hypothecium). *Exciple c.* 70–110 µm wide, formed of true exciple, *c.* 30–60 µm wide, and thalline exciple, *c.* 10–70 µm wide. Upper part of true exciple of thin-walled spherical cells *c.* 4–6 × 3–4 µm. Lower part of palisade prosoplectenchyma of thin-walled cells *c.* 5–12 × 1·5–2·0 µm. Thalline exciple without cortex or with indistinct alveolate cortex.

Paraphyses 2·0–2·5 μm wide in lower part, but widening gradually to (2·5–)3·0–*3·5*–4·0(–5·0) μm [*30*; 3; 0·5] in upper part; rarely branched and anastomosed. *Asci* clavate, *c.* 50–70 × 15–20 μm. *Ascospores* polarilocular, (8·0–)12·0–*12·5*–13·5(–15·0) × (5·0–)7·0–*7·5*–8·0(–9·5) μm [*50*; 5; 1·5 & 0·9], septa (4·0–)5·0–*5·5*–6·0(–7·5) μm [*50*; 5; 0·9]. Ascospore length/breadth ratio: (1·0–)1·5–*1·7*–1·8(–2·2) [*50*; 5; 0·3]; septum width/ascospore length ratio: (0·30–)0·40–*0·45*–0·47(–0·60) [*50*; 5; 0·1]. Extracellular crystals of calcium salts absent from all apothecial parts.

Pycnidia not common (observed in only three samples), *c.* 150–200 μm wide, with several partly separated chambers (*Xanthoria*-type), distinguished by their darker grey tops on the thallus surface. *Conidiophores* formed of isodiametric cells, *c.* 2–4 μm diam. *Conidia* ellipsoid, broadly ellipsoid or tear-shaped, rather uniform in size, 2·0–2·5 × 1·5 μm.

Chemistry. True exciple, medulla and lower cortex non-amyloid (I−); hymenium and hypothecium amyloid (I+). Uppermost cells in cortical tissue of thallus and thalline exciple contain Sedifolia-grey (grey in water, K+ violet, N+ red, H_2SO_4+ red, I+ blue). Content of Sedifolia-grey is higher in pycnidial tops. Epihymenium and outer cells in the true exciple contain anthraquinones: fragilin (major) and 7-Cl-emodin (HPLC done in sample JV6597).

Etymology. The epithet is derived from the name of our great friend Emil Červenka, who supported the first author during difficult times.

Similar taxa. Caloplaca areolata (Zahlbr.) Clauzade (without blastidia), *C. chlorina* (Flot.) Sandst. and *C. isidiigera* Vězda (with blastidia but with lecanorine apothecia and bacilliform conidia), *C. concreticola* Vondrák & Khodos. (with blastidia but without anthraquinones in apothecia), *C. soralifera* Vondrák & Hrouzek (with soredia, often pruinose) and *C. xerica* Poelt & Vězda (usually with isidia, without flat areoles, with larger ascospores). A little-known blastidiate morphotype of *Caloplaca atroflava* (Turner) Mong. is a similar lichen; it is very common in Central Europe, but occurs mainly on non-calcareous rocks (orange, C− apothecia, without chlorinated anthraquinones, blastidia usually overgrowing most of thallus surface).

Phylogeny. In the ITS phylogeny (Fig. 4), *Caloplaca emilii* is definitely placed in the *C. xerica* group (*sensu* Vondrák *et al.* 2012*b*). It forms a well-circumscribed clade (PP = 1·0), sister to *C. areolata*. Both taxa form a well-supported monophyletic group (PP = 0·99).

Ecology and distribution. Caloplaca emilii occurs on sun-exposed, usually horizontal, faces of limestone outcrops in fast-drying places in steppes, forest-steppes or in open Mediterranean shrub vegetation, mainly in the *Placocarpetum schaereri* (Roux 1978: 120–130). Co-occurring lichens are *Acarospora cervina*, *Aspicilia calcarea*, *A. contorta*, *Bagliettoa calciseda*, *Caloplaca aurantia*, *C. chalybaea*, *C. coronata*, *C. crenulatella* s. lat., *C. inconnexa*, *C. lactea*, *C. teicholyta*, *C. variabilis*, *Candelariella aurella*, *Diplotomma hedinii*, *D. venustum* s. str., *Heteroplacidium fusculum*, *Lecanora muralis* s. lat., *Lobothallia cheresina* s. lat., *L. radiosa*, *Placocarpus schaereri*, *Placopyrenium canellum*, *Rinodina calcarea*, *R. ocellata*, *R. bischoffii*, *Verrucaria lecideoides*, *V. macrostoma* f. *furfuracea*, and *V. nigrescens* s. lat.

The species is already known from Germany (as the blastidiate variant of *Caloplaca areolata* in Wirth *et al.* 2011). Nevertheless, this lichen has a rather southern distribution in Europe; it is probably most common in the Mediterranean basin and adjacent areas, such as France, Italy, Spain, mainly in the supramediterranean and montane belts (Roux 1978: 124, as *C. areolata*). Although it is common in continental areas around the Black Sea, we do not know it from continental areas east of the Mediterranean basin. In southern areas, it sometimes grows with its close relative *C. areolata* (for example in southern France and Greece). Both taxa have similar ecology, but *C. areolata* without vegetative diaspores appears to be restricted to the Mediterranean region, whereas the blastidiate *C. emilii* also occurs in isolated localities far to the north (Fig. 1B). The

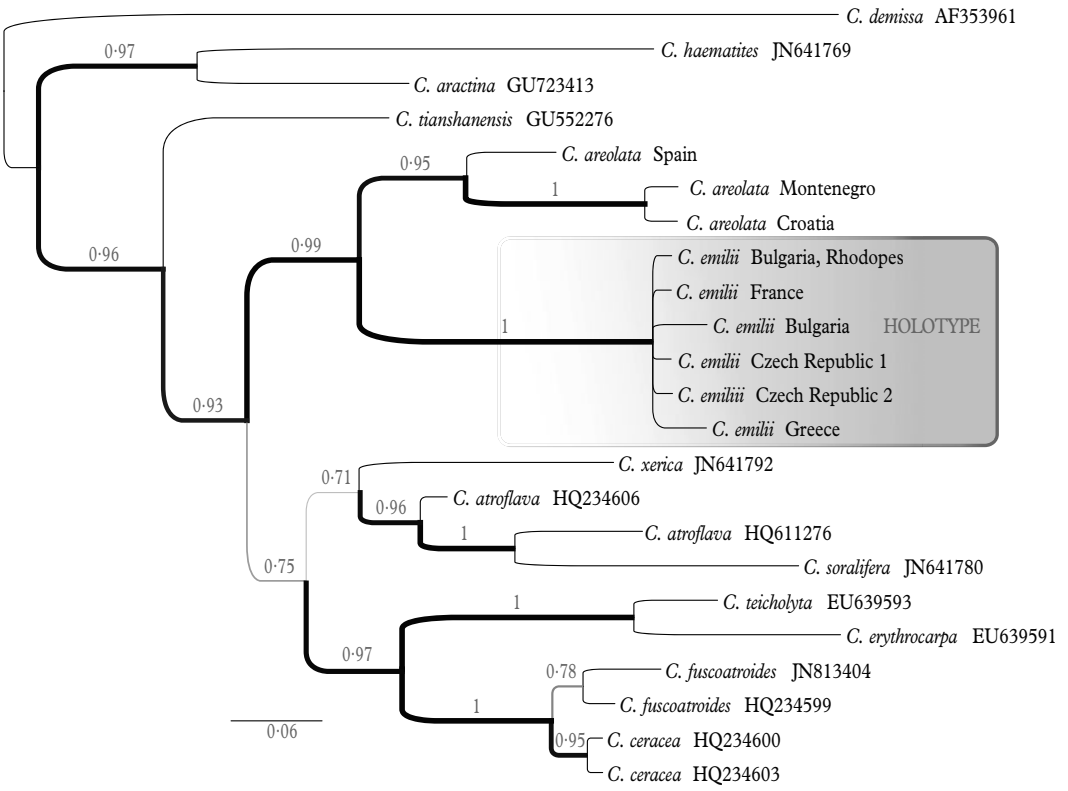

FIG. 4. Bayesian ITS phylogeny of the *Caloplaca xerica* group including *C. emilii* (in the grey square) and *C. areolata*.

ability to reproduce vegetatively may have facilitated the northward extension of its distribution. A similar situation is observed in other Mediterranean lichens from the *C. xerica* group; sorediate/blastidiate *C. albolutescens* (Nyl.) H. Olivier and *C. teicholyta* (Ach.) J. Steiner are known from much more northern territories than the closely related *C. erythrocarpa* (Pers.) Zwackh, which is without vegetative diaspores.

Taxonomic notes. Caloplaca emilii is well known from the Mediterranean regions of France, where it has been named *C. areolata* (Clauzade 1963, 1965, 1969; Roux 1978) or later *C. isidiigera* (Roux 1982, 1984; Boissière *et al.* 1989; Houmeau & Roux 1991; Roux & Gueidan 2002; Bricaud 2007). However, these names belong to other taxa; *C. areolata* lacks vegetative diaspores (see also under ecology) and *C. isidiigera* is an unrelated species with lecanorine apothecia and a (sub-)alpine distribution (Vězda 1978; Šoun *et al.* 2011).

Caloplaca areolata has recently been considered a synonym of *C. spalatensis* Zahlbr. (e.g. Nimis & Martellos 2008). This synonymization is incorrect, because *C. spalatensis* is a very different lichen which belongs to the *C. crenularia* group (images of both holotypes, deposited in the herbarium W, are available on the lichenological web page at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5).

Paratypes. **Austria:** *Niederösterreich*: Wien, Hainburg an der Donau, rocks on SW slopes of hill Braunberg NE of town, 48°09′10″N, 16°57′12″E, 280 m, 2012, *J. Vondrák* 9570 (CBFS).—**Bulgaria:** *Black Sea coast*: Kavarna, Kamen Brjag, 43°27′59″N, 28°33′55″E, 2007, *J. Vondrák* 6600 (CBFS). *The Rhodopes*: Madzharovo, Silen, Byal Kladenets, in valley below village,

41°37′N, 25°40′E, 350 m, 2004, *J. Vondrák* 2223 (CBFS).—**Czech Republic:** *Southern Moravia*: Mikulov, in town, ruin of castle Kozí Hrádek, 48°48′34″N, 16°38′17″E, 2011, *J. Vondrák* 9358 *& O. Vondráková* (CBFS); Mikulov, Klentnice, SE slope of hill Pálava, 48°51′22″N, 16°38′33″E, 350–400 m, 2012, *J. Vondrák* 9581 (CBFS); Mikulov, Klentnice, at ruin of Sirotčí hrádek, 48°50′43″N, 16°38′25″E, *c.* 410 m, 2011, *J. Vondrák* 9357 *& O. Vondráková* (CBFS).—**France:** *Provence*: Vaucluse, Gordes, entre les Devens et Lancie, sur dalle de molasse miocène au ras su sol, 43·9026°N, 5·1931°E, 275 m, 1975, *G. Clauzade* (MARSSJ 189); Vaucluse, Mirabeau, 520 m, 2005, *C. Roux* 23475 (hb. Roux).—**Germany:** *Bayern*: Oberfranken, Fränkische Alb: Kleinziegenfelder Tal, Grenzstein, 1976, *V. Wirth* 6101 (STU).—**Greece:** *Attica*: Poros, limestone outcrops in N-part of island, 37°31′28″N, 23°29′10″E, *c.* 200 m, 2010, *J. Vondrák* 8726, 8832 *& O. Vondráková* (CBFS).—**Romania:** *Dobrogea*: Târguşor, 44°27′46·26″N, 28°28′07·59″E, 2007, *J. Vondrák* 6599 (CBFS); Tulcea, Enisala, 44°52′42·09″N, 28°51′01·27″E, 2007, *J. Vondrák* 6604 (CBFS); Tulcea, Popina Island, 44°58′03″N, 28°58′57″E, 2007, *J. Vondrák* 6596, 6597, 6598 & 7149 (CBFS).—**Ukraine:** *Kherson region*: Berislav, Burgunka, 2008, *A. Khodosovtsev & G. Naumovich* (KHER, dupl. in CBFS).

Caloplaca molariformis Frolov, Vondrák, Nadyeina & Khodos. sp. nov.

MycoBank No: MB 803333

Anthraquinones entirely absent. Thallus epilithic, thick, ochre or dark grey, pruinose in spots, with Sedifolia-grey in superficial fungal cells. Blastidia and/or soralia always present. Thallus formed by high algal and fungal stacks (*sensu* Vondrák & Kubásek 2013). Fungal stacks of colourless palisade prosoplectenchyma, of cells elongated vertically. The upper thallus surface with ridges derived from the epinecral layer, above fungal stacks (similar structure is described in South African "Fensterflechten" by Vogel 1955). Epihymenium and outer part of true exciple brown to grey, with Sedifolia-grey, K+ (slightly) violet to violet-brown. Ascospores *c.* 14–18 µm long with rather thin septa, *c.* 3 µm wide.

Type: Slovakia, Cerová vrchovina upland, Filakovo, Hajnáčka, Šurice, SW-slope of the hill Soví hrad, 48°13′34″N, 19°54′45″E, on lime-rich outcrop of volcanic pyroclastics in sun-exposed abandoned quarry, *c.* 250 m, 8 November 2012, *J. Vondrák* 10192 (CBFS—holotype; isotypes to be distributed in Exsiccates of *Caloplaca*, fasc. 4). ITS sequence of the holotype: KC416142.

More images available on the lichenological web page at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5.

(Figs 5, 7C; fig. 2 in Vondrák & Kubásek 2013)

Thallus epilithic, ochre, white-grey to dark grey, usually with white pruinose spots, forming irregular spots to several cm wide; of tightly arranged, angular to rounded, more or less flat areoles or somewhat umbilicate squamules, (0·44–)0·70–*0·95*–1·26 (–2·05) mm diam. [*100*; 10; 0·35]. Marginal areoles sometimes bigger than areoles in the centre. Several small, tightly arranged areoles may merge to form larger units, but on the contrary, large areoles are sometimes divided into smaller subareoles due to secondary crevices. Thickness of the thallus, together with brown (probably necrotic) lower medulla (0·2–)0·6–*1·2*–2·2(–5·0) mm [*30*; *3*; 1·0]; thickness of the thallus without lowermost brown part (0·1–)0·3–*0·4*–0·5(–0·9) mm [*30*; 3; 0·2]. The brown lower medulla usually distinct, up to 12·5 times thicker than the rest of the thallus. Colourless medulla also present, (50–)140–*235*–330(–550) µm thick [*26*; 3; 145]; cells hardly observable due to presence of extracellular crystals insoluble in KOH and only partly dissolved and recrystallized into needles in H_2SO_4. *Algal cells* arranged in vertical stacks, (30–)67–*91*–129(–250) wide [*47*; 6; 44], and (100–)223–*263*–334(–550) µm high [*47*; 6; 112]. Algal cells globose, (8·0–)12·6–*13·7*–14·5(–22·0) µm diam. [*30*; 3; 3·2]. *Cortex* above the algal stacks absent or indistinct, alveolate cortex present, up to *c.* 15–30 µm thick; upper fungal cells in algal stacks grey, containing Sedifolia-grey. Fungal stacks (measured with epinecral layer) (13–)45–*86*–120(–270) wide [*46*; 6; 55] and (75–)180–*322*–505(–750) µm high [*46*; 6; 165]; formed by vertically oriented palisade prosoplectenchyma; size of cells in the middle part of stacks (4·5–)9·4–*11·9*–13·3(–18·0) × (3·0–)3·7–*4·3*–4·8(6·5) µm [*30*; 3; 3·9 & 0·9]. In lower part of stacks, cells longer and narrower; in uppermost part, cells almost isodiametric, *c.* 4–7 µm diam. *Epinecral layer* above fungal stacks usually well-developed, (5–)20–*95*–200(–350) µm thick [*81*; 9; 72]; dead cells (colourless in cotton blue) recognizable in the lower part. Boundary between epinecral layer and upper cells of the fungal stack sometimes indistinct, but recognizable after KOH treatment as a sordid grey-violet

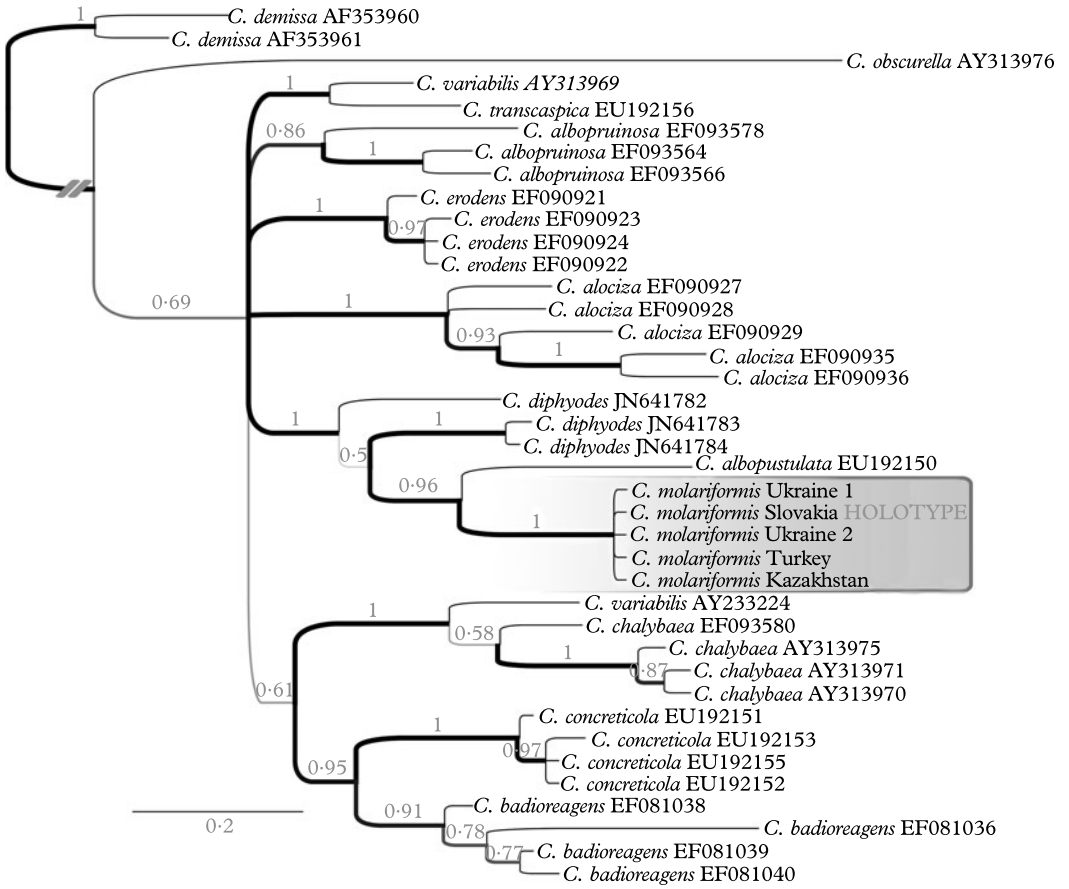

FIG. 5. Bayesian ITS phylogeny of the *Pyrenodesmia* subgroup of *Caloplaca*, including *C. molariformis* clade delimited by the grey square.

line caused by traces of the Sedifolia-grey in uppermost fungal stack cells. Epinecral layer often forms distinct ridges on thallus surface above fungal stacks, because it is absent from surface of algal stacks (Fig. 7C). Epinecral ridges best developed in samples from deserts of Western Kazakhstan, but less distinct in samples from Slovakia and Ukraine. Fungal stacks sometimes reaching medulla at the bottom and the boundary between the stacks and medulla recognized by the crystals abundant in medulla but absent from stacks. Margins of areoles and squamules and the lower surface of squamules usually with cortex, up to *c.* 20 µm thick, of isodiametric cells, *c.* 4–7 µm diam. Vegetative diaspores are blastidia (always present) or rarely soredia; sometimes diaspores poorly developed, present only on few areoles. *Blastidia* simple, more or less globose, (30–)54–*67*–89(–150) µm diam. [*52*; 6; 25], dark grey, present on the margin and upper surface of areoles and squamules; detached blastidia occasionally cover the whole surface. Blastidia sometimes with appearance of consoredia, with internal soredia-like structures. Extracellular crystals soluble in KOH and Sedifolia-grey pigment present in outer fungal cells of blastidia. *Soralia* rarely observed, on the upper surface between epinecral ridges; *soredia c.* 25–40 µm diam. White pruina always present, better developed between epinecral ridges.

Prothallus indistinct or absent. Thallus frequently affected by brown hyphomycetes resembling species of *Intralichen*.

Apothecia (0·33–)0·42–*0·55*–0·72(–1·32) mm diam. [*100*; 10; 0·15], zeorine or rarely almost lecanorine; mature apothecia sessile, usually not abundant on thallus, sometimes absent. Richly fertile populations known only from Slovakia and Ukraine. *Disc* brown to black, not pruinose, sometimes cracked; true exciple concolourous with the disc, occasionally white pruinose; thalline exciple concolourous with the thallus, with white pruina. *Hymenium* (63–)91–*102*–109(–175) µm high [*30*; 3; 23], colourless, often with very small (<1 µm) extracellular oil drops, sometimes strongly inspersed with extracellular oil drops up to *c.* 2 µm diam., sometimes not inspersed; without crystals. *Epihymenium* brown, grey or grey-brown. *Hypothecium* colourless, underlain by the algal layer, usually with extracellular oil drops, without extracellular crystals; with a central conical extension downward, (75–)153–*174*–185 (–275) µm high [*30*; 3; 48]; formed of thin-walled cells variable in shape. *Exciple c.* 10–160 µm wide. *True exciple* (10–)18–*35*–54(–93) µm wide [*30*; 3; 22], and thalline exciple (0–)18–*24*–27(–68) µm wide [*30*; 3; 20]. Upper part of the true exciple grey-brown, brown-grey or grey, of thin-walled cells (4·0–)6·2–*6·6*–7·3(–10·0) × (2·0–)3·4–*4·5*–5·2(–8·0) µm [*100*; 10; 1·1 & 1·1]. Lower part colourless, of palisade prosoplectenchyma of thin-walled cells (6·0–)7·7–*8·2*–8·7(–11·5) × (2·0–)2·4–*2·8*–3·3 (–5·0) µm [*30*; 3; 1·3 & 0·8]. *Thalline exciple* sometimes with cortex in its upper part, *c.* 8–20 µm thick; cortex changing into alveolate cortex in the lower part of thalline exciple. Cells of the cortex spherical, *c.* 3·5–7·0 µm diam., often hardly observed due to extracellular crystals insoluble in KOH. *Paraphyses* (1·5–)2·1–*2·3*–2·8(–3·5) µm wide [*100*; 10; 0·4] in lower part, but widening gradually to (3·0–)3·5–*4·4*–5·5(–6·5) µm [*100*; 10; 0·8] in upper part; rarely branched and anastomosed; the uppermost cell of paraphyses usually dead and deformed. *Asci* clavate, (40–)58–*64*–69(–85) × (12–)17–*20*–21(–28) µm [*30*; 3; 1 & 10]. *Ascospores* polarilocular, (12·0–)14·3–*16·2*–18·3(–23·0) × (5·0–)6·4–*7·7*–9·1(10·5) µm [*70*; 8; 2·3 & 1·3]; septa (2·0–)2·6–*3·0*–3·3(–4·0) µm wide [*70*; 8; 0·5]. Ascospore length/breadth ratio: (1·40–)1·98–*2·12*–2·27(–2·86) [*70*; 8; 0·32]; septum width/ascospore length ratio: (0·11–)0·17–*0·19*–0·22(–0·30) [*70*; 8; 0·04]. Ascospores with well-developed septa often absent.

Pycnidia rare, *c.* 140–190 µm wide, mainly with a single chamber, present on the upper thallus surface, but also on the lower surface of squamules; superficially hardly distinguishable. Old pycnidial chambers sometimes filled by crystals insoluble in KOH. *Conidiophores* of spherical or triangular, more or less isodiametric cells. *Conidia* narrowly to broadly ellipsoid, 2·5–4·5 × 1·5–2·0 µm [*14*; 2; 0·2 & 0·5].

Chemistry. Spot tests: thallus K± violet (sometimes not observable or observable only in spots with blastidia and soredia), apothecia K−, thallus and apothecia C−, P−, UV−. Epihymenium, uppermost true exciple, uppermost fungal cells in thallus and vegetative diaspores contain Sedifolia-grey (grey or invisible in water, K+ sordid violet). The reaction above fungal stacks usually weaker than above algal stacks. Strongest reaction in superficial hyphae of vegetative diaspores. True exciple non-amyloid (I−); hymenium and hypothecium amyloid (I+). No substances revealed by HPLC (apothecia and thallus of an isotype were investigated).

Etymology. Areoles and squamules of the lichen thallus often resemble molars of herbivores.

Similar taxa. The thallus anatomy, with tissues in stacks, is very rare within the *Pyrenodesmia* subgroup of *Caloplaca*. It is present in one known species only, *Caloplaca albovariegata* (B. de Lesd.) Wetmore, which is very similar to *C. molariformis* but has no vegetative diaspores (Wetmore 1994; lectotype in UPS seen). This species was described from North America, but similar morphotypes are known in continental Eurasia (our observations). Zhou *et al.* (2012) reported a taxon with tissues in stacks from China and named

it *C. albovariegata*, but it has a thallus surface without ridges derived from the epinecral layer and it does not resemble *C. molariformis*. Other similar taxa are *Caloplaca albopustulata* Khodos. & S.Y. Kondr. (with pustules and schisidia), *C. bullata* (Müll. Arg.) Zahlbr. (bullate thallus without vegetative diaspores), *C. concreticola* (with soralia) and *C. transcaspica* (Nyl.) Zahlbr. (without vegetative diaspores), but all these taxa have thallus tissues arranged in horizontal layers, not in stacks. They also do not have specific ridges derived from the epinecral layer. (Type specimens and other comparative material studied by the authors.)

Phylogeny. In the ITS phylogeny (Fig. 5), *Caloplaca molariformis* is placed in the *C. variabilis* group, closely related to *C. albopustulata*.

Distribution and ecology. Caloplaca molariformis is mainly distributed in steppes and deserts of Iran, Kazakhstan, continental Turkey and southern Russia, at altitudes of 50–2100 m. Two isolated localities are also known from the steppe or forest-steppe, in eastern Ukraine and southern Slovakia. The species occurs in sunny habitats on soft limestone, chalk, calcareous sandstone or tuffs with evident content of lime (always reacting with HCl). Co-occurring lichen taxa include *Acarospora* spp., *Aspicilia* spp., *Caloplaca concreticola*, *C. crenulatella* s. lat., *C. decipiens*, *C. flavocitrina*, *C. soralifera*, *C. sororicida*, *C. teicholyta*, *C. tominii*, *C. transcaspica* s. lat., *C. xerica*, *Candelariella aurella*, *Lecanora muralis* s. lat., *Lemmopsis arnoldiana*, *Lichinella* sp., *Verrucariaceae* spp. (e.g. *Staurothele frustulenta*, *Verrucaria macrostoma*, *V. nigrescens* agg.).

Paratypes. **Iran:** *West Azerbaijan*: Lake Urmia, rocks at road *c.* 2 km N of Saraydeh, 37°52′59″N, 45°34′26″E, 1280 m, 2007, *J. Vondrák* 5556 (CBFS); Khoy, airport, 38°25′16·17″N, 44°54′24·05″E, 1180 m, 2007, *J. Vondrák* 5801 (CBFS); Lake Urmia, rocky outcrops near coast N of Aq Gonbad, 37°49′12·02″N, 45°25′09·61″E, *c.* 1290 m, 2007, *J. Vondrák* 5846 (CBFS).—**Kazakhstan:** *Mangistau province*: Mangistau district, village Shetpe, West Karatau ridge, *c.* 15 km N of village, 44°14′35″N, 52°03′19″E, 100 m, 2009, *A. Khodosovtsev* 7775–7781 *& J. Vondrák* 8262, 8247, 9477 & 9487 (CBFS, KHER); Beyneu district, village Beyneu, *c.* 50 km SW of town at road to Aktau, valley of salt river Manashi, 45°01′26″N, 54°59′56″E, 50 m, 2009, *A. Khodosovtsev & J. Vondrák* 9483 (CBFS); Mangistau district, West Aktau ridge, soft valley with rocky outcrops at river Akespe, 44°24′21″N, 51°35′59″E, 100 m, 2009, *A. Khodosovtsev & J. Vondrák* 9486 (CBFS); Mangistau district, at road between village Shetpe and Say-Utes, *c.* 30 km SW of Say-Utes, 44°09′20″N, 52°39′10″E, 260 m, 2009, *A. Khodosovtsev & J. Vondrák* 9506 (CBFS); Mangistau district, East Karatau ridge, rocks at road between Zhatybay and Shetpe, *c.* 30 km SW of Shetpe, 43°57′00″N, 52°05′52″E, 180 m, 2009, *A. Khodosovtsev & J. Vondrák* 9499 (CBFS).—**Russia:** *Orenburgskaya Oblast'*: Orenburg, village Mikhaylovka (*c.* 30 km SES of city), Khanskaya gora hill, S of village, above brook Berd'yanka, 51°25′48″N, 55°26′27″E, *c.* 200 m, 2011, *I. Frolov & J. Vondrák* 9456 (CBFS); Saraktash district, protected area Kamennaya, rock outcrops in S-slope above river Sakmara, 51°56′53″N, 55°58′23″E, 180 m, 2012, *I. Frolov & J. Vondrák* 10225 (CBFS). *Republic of Altay*: Kosh-Agach district, Kosh-Agach, Telengit-Sortogoy, S-slopes of Kuray Ridge (easternmost part), *c.* 6 km N of village, 50°04′24″N, 88°42′30″E, 2000–2100 m, 2012, *I. Frolov & J. Vondrák* 10224 (CBFS).—**Slovakia:** *Cerová vrchovina upland*: Filakovo, Hajnáčka, Šurice, SW-foot of hill Soví hrad, 48°13′34″N, 19°54′45″E, 240–250 m, 2012, *Z. Fakovcová, A. Guttová, J. Liška, Z. Palice* 15905 *& J. Vondrák* 10190 (CBFS, PRA; topotypes).—**Turkey:** *Eastern Anatolia*: Iğdır, shale hills SE of town, 39°51′23″N, 44°05′42″E, 1060 m, 2007, *J. Vondrák* 6463 (CBFS). *Central Anatolia*: Yozgat, Boğazlıyan, Özler village, 39°04′10″N, 35°08′17″E, 1100 m, 2012, *J. Vondrák* 9751 (CBFS); Kayseri, Talas, Derevenk valley, 38°41′23″N, 35°34′52″E, 1230 m, 2012, *J. Vondrák* 9760, 9809 & 9787 (CBFS); Kayseri, south-east of Himmetdede, north-west of Kalkancık village, montane steppe with shrubs, 38°53′43″N, 35°07′01″E, 1170 m, 2012, *J. Vondrák* 9791 (CBFS).—**Ukraine:** *Donetsk Upland*: Luhansk region, Lutugyno district, steppe slopes with marl outcrops near village Rozkishne, in botanical reserve "Balka Ploska", *c.* 150 m, 2007, *O. Nadyeina* 131, 132 & 134 (KW). [Specimens from Ukraine were published as *Caloplaca concreticola* in Nadyeina (2009)].

Caloplaca substerilis Vondrák, Palice & van den Boom sp. nov.

MycoBank No: MB 803334

Similar to *Caloplaca ulcerosa*, but differs in thallus morphology. Thallus endophloeodal, but also forming minute areoles or squamules; sorediate; without any pigments or TLC identifiable compounds. Apothecia up to *c.* 0·5 mm diam., orange-red, not pruinose, without chlorinated anthraquinones, biatorine to zeorine. Ascospores broadly ellipsoid, *c.* 10–15 µm long, with septa *c.* 4–6 µm wide. Pycnidia with yellow caps containing anthraquinones. Conidia bacilliform, *c.* 3–4 × 1·0–1·5 µm.

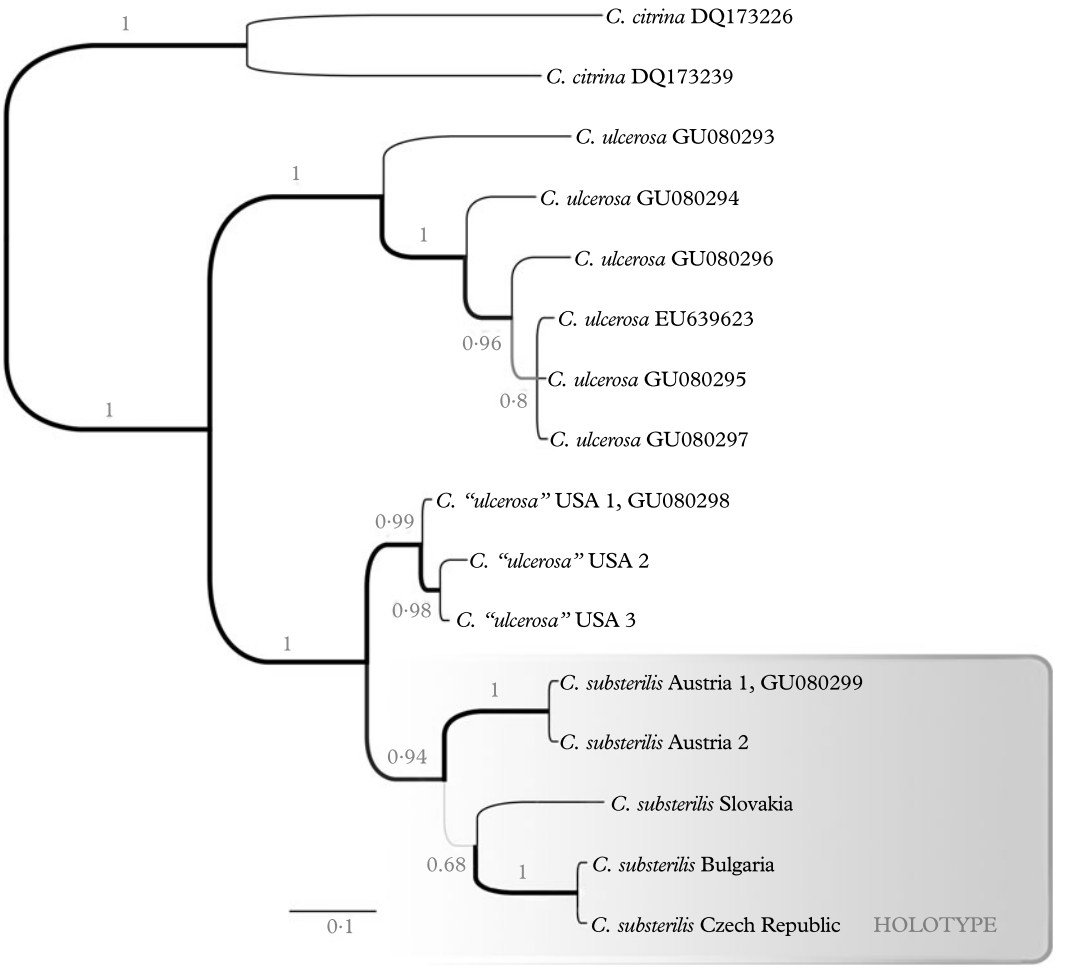

FIG. 6. Bayesian ITS phylogeny of *Caloplaca ulcerosa* and related taxa including *C. substerilis* (delimited by the grey square).

Type: Czech Republic, Southern Bohemia, Novohradské hory Mts, Benešov nad Černou, Žofín, alt. 745 m, 48°40′29″N, 14°41′38″E, on bark of solitary *Ulmus glabra*, 26 May 2010, *J. Vondrák* 7920, *A. Vondráková & O. Redchenko* (CBFS—holotype). ITS sequence of the holotype: KC416109.

More images available on the lichenological web page at the University of South Bohemia http://botanika.bf.jcu.cz/lichenology/index.php?pg=5.

(Figs 6, 7D)

Thallus endophloeodal or partly of diffuse tiny squamules (somewhat epiphloedal areolate thallus present in samples from the Alps); sorediate; forming irregular pale grey to white spots or extensive crusts, covering large areas of trunks. *Squamules* 100–150 μm thick and (0·10–)0·17–0·18–0·19(–0·30) mm diam. [*30*; 3; 0·05]. *Soralia* small, usually extended in one direction (rarely rounded), usually up to 0·2 mm in length, formed in tiny cracks in the tree bark or on margins and lower surface of squamules, usually not in concave, crater-like depressions (typical for *Caloplaca ulcerosa* Coppins & P. James); soralia in older lichens often tightly arranged and may resemble a continuous sorediate crust. *Soredia* without pigmentation, (15–)23–*24*–26(–30) μm diam. [*40*; 4; 4]; consoredia (30–)37–*41*–46(–65) μm diam. [*40*; 4; 8]. Fungal cells in soredia or consoredia

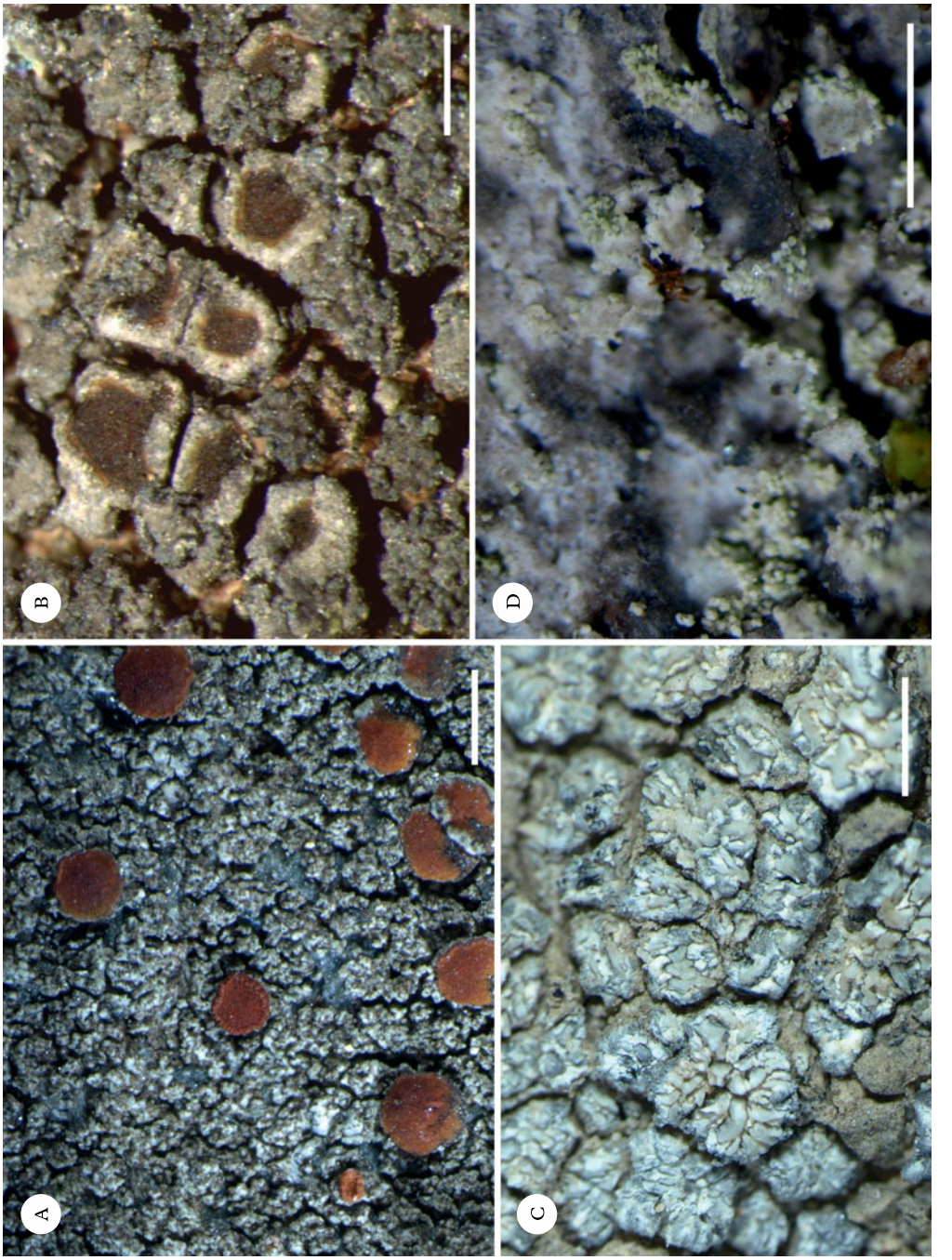

Fig. 7. A, *Caloplaca scabrosa* (CBFS JV1908); B, *C. emilii* (holotypus); C, *C. molariformis*, morphotype with well-developed epinecral ridges above fungal stacks (CBFS JV9486); D, *C. substerilis* (CBFS JV7920, holotypus). Scales: A & C = 1 mm; B & D = 0·5 mm.

(3·5–)5·4–*5·5*–5·7(–7·5) × (2·0–)3·2–3·3–3·4(–4·5) [*20*; 2; 1·1 & 0·8]. Surface of soredia papillate; papillae formed of fungal cell outgrowths, up to 7 µm high. *Medulla* indistinct or absent. *Algal layer* forms majority of thallus, *c.* 100–140 µm thick; algal cells globose, *c.* 5–20 µm diam.; old cells often internally divided into several irregularly spherical autospores (cell division typical for *Trebouxia*; e.g. Peksa & Škaloud 2008). True cortex absent; alveolate cortex developed in patches, up to 20 µm thick, of thin-walled, more or less spherical cells. *Epinecral layer* indistinct. Thallus surface papillate; papillae of the same size and character as those in soredia. Extracellular crystals of calcium salts not observed in any thallus part. *Pruina* absent. *Prothallus* indistinct or absent.

Apothecia present in *c.* 20% of samples collected (indicated by asterisk in the list of paratypes), but fertile specimens usually with scattered apothecia. The sample from the Alps (*van den Boom* 15927) with many apothecia is exceptional. Apothecia mostly up to 0·5 mm diam.; biatorine or zeorine. *Disc* orange to orange-red; true exciple yellow-orange to orange (usually somewhat paler than disc); thalline exciple (when visible) yellow to white; pruina absent or indistinct. *Hymenium* colourless, somewhat gelatinous, without extracellular oil drops, *c.* 60–70 µm high; *epihymenium* ochre. *Hypothecium* colourless, up to 100 µm high, more or less flat, but with downward extension through the subhypothecial algal layer in the centre, of thin-walled cells variable in shape; extracellular oil drops not seen. *Exciple c.* 40–80 µm wide, formed of true exciple, *c.* 30–70 µm wide, and thalline exciple, *c.* 0–30 µm wide. Upper part of true exciple of cells *c.* 4–8 × 3–5 µm, with thin or more than 1 µm thick, glutinized walls. Lower part of palisade prosoplectenchyma of thin-walled cells, 6–11 × 2–4 µm. Thalline exciple sometimes with alveolate cortex in lower part, up to 30 µm thick, of spherical cells; thalline exciple sometimes sorediate. *Paraphyses* 1·5–2·0 µm wide in lower part, but about three upper cells widened; branching and anastomosing not observed; paraphyses tips (3·5–) 4·6–*4·6*–4·6(–5·5) µm [*20*; 2; 0·7] wide. *Asci* clavate, *c.* 50–60 × 10–16 µm. *Ascospores* polariloculare, (10·0–)12·0–*12·0*–12·5(–16·5)×(5·0–)7·5–*8·0*–8·0(–10·5) µm [*20*; 2; 1·4 & 1·3], septa (4·0–)4·5–*5·0*–5·5(–8·5) µm wide [*20*; *2*; 1·3]. Ascospore length/breadth ratio: (1·2–)1·6–*1·6*–1·7(–2·2) [*20*; 2; 0·3]; septum width/ascospore length ratio: (0·26–)0·34–*0·40*–0·42(–0·52) [*20*; 2; 0·1]. Extracellular crystals of calcium salts absent from all apothecial parts.

Pycnidia more common than apothecia (observed in *c.* 50% of samples), *c.* 50–100 µm wide, with several partly separated chambers (*Xanthoria*-type), distinguished by their yellow tops containing anthraquinones. *Conidiophores* various in height, formed of rectangular, triangular or spherical cells, *c.* 3–5 × 4–8 µm. *Conidia* usually bacilliform, straight or slightly curved, rarely ellipsoid or tear-shaped, (2·5–)3·2–*3·4*–3·5(–5·0) × (1·0–) 1·2–*1·2*–1·3(–1·5) µm [*20*; 2; 0·7 & 0·2].

Chemistry. Spot tests: thallus K–, C–, P–, UV± white; apothecia K+ purple, C–, UV–. True exciple non-amyloid (I–). Hymenium and the upper part of hypothecium (subhymenium) amyloid (I+). The C– reaction of epihymenium and outer cells in the true exciple suggests an absence of chlorinated anthraquinones. No compounds revealed from thallus by TLC.

Etymology. '*Substerilis*' reflects the usually sterile occurrence.

Similar taxa. Apothecial characters in the new species are identical to those of the closely related *Caloplaca ulcerosa*, but they differ in thallus characters. In *C. substerilis*, the thallus is endophloeodal or of diffuse minute squamules, with marginal soralia, while *Caloplaca ulcerosa* forms an epiphloedal non-squamulose thallus with round to irregular soralia formed in crater-like depressions. The latter species further differs in its shorter, ellipsoid conidia (*c.* 2·5–3·0 × 1·5 µm), much higher fertility and in ecology; it is a maritime species (Vondrák *et al.* 2009*b*).

White morphotypes of *C. phlogina* (Ach.) Flagey are similar (see Kondratyuk *et al.* 1998; Vondrák *et al.* 2010*b*); they also have

papillate soredia of similar size without pigmentation, yellow pycnidial caps and an endophloedal thallus, sometimes with minute white squamules. However, *C. phlogina* differs in frequently having apothecia: these are large (mostly >0·5 mm diameter), yellow-orange, with a rough surface caused by yellow anthraquinone pruina. Ascospores are significantly smaller with thinner septa: ascospores (8·5–)10·5–*10·8*–11·2(–13·0) × (4·0–)5·0–*5·4*–5·7(–7·0) µm [*30*; 3; 1·0 & 0·7], and septa (2·5–)3·1–*3·6*–3·8(–4·5) µm wide [*30*; 3; 0·6].

Sterile thalli may resemble a number of taxa, including: *Caloplaca obscurella* (J. Lahm) Th. Fr. (with rounded crater-like soralia, brown apothecia), *C. sterilis* Šoun *et al.* (on steppe shrubs, with lecanorine apothecia), *C. subalpina* Vondrák *et al.* (saxicolous, with lecanorine apothecia and Sedifolia-grey in soredia), *Candelariella subdeflexa* (Nyl.) Lettau (with different apothecia and more conspicuous squamules producing conidia from the underside) and *Rinodina degeliana* Coppins (areolate-squamulose thallus with marginal soralia; presence of atranorin and zeorin).

Phylogeny. In the ITS phylogeny (Fig. 6), *Caloplaca substerilis* forms a well-supported clade, sister to the clade of North American *C.* "*ulcerosa*". Both taxa are sister to the European *C. ulcerosa*. Close relatives of these three taxa are not known.

Ecology and distribution. Caloplaca substerilis occurs on nutrient-rich bark of *Acer campestris*, *A. platanoides*, *Carpinus*, *Juglans*, *Quercus*, *Populus* and *Ulmus* in well-lit conditions, sometimes overgrowing mosses on bark. Specimens from the Alps were collected on the bark of *Sambucus* and on *Picea abies* twigs. Co-occurring lichens are more or less nitrophilous *Caloplaca cerinelloides*, *C. monacensis*, *C. obscurella*, *Lecanora hagenii*, *Macentina dictyospora*, *Phaeophyscia nigricans*, *P. orbicularis*, *Physcia* spp., *Physconia* sp., *Piccolia ochrophora*, *Rinodina pityrea*, *Xanthomendoza fulva* and *Xanthoria parietina*.

Caloplaca substerilis shows continental bias in Europe. It appears to be quite common in the Southern Ural Mountains (most of known localities). It is probably distributed throughout eastern and central Europe in suitable woodland areas with preserved undisturbed solitary elm and poplar trees. So far it is known from Austria, Bulgaria, the Czech Republic, Russia and Slovakia.

Taxonomic notes. The North American taxon called *Caloplaca ulcerosa* (Wetmore 2004) is morphologically more similar to *C. substerilis* than to *C. ulcerosa* s. str. We have examined three samples of the North American taxon (GZU: Iowa, *Teloschistaceae* Exsiccati 95; Iowa, *Wetmore* 93230; South Dakota, *Advaita* 6490), and did not find any diagnostic difference from *C. substerilis*. It corresponds well with the ITS phylogeny, where both taxa form a monophyletic group. The distribution of the North American taxon (Wetmore 2009) and the distribution of *C. substerilis* are similarly continental and different from the maritime distribution pattern of *C. ulcerosa* s. str. (Vondrák *et al.* 2009*b*). Provisionally, we call the North American specimens *C.* "*ulcerosa*" in Fig. 6.

Two ITS sequences of *C. substerilis* from the Alps form a separate lineage from the other *C. substerilis* sequences. The specimens from the Alps also differ slightly in morphology (frequent apothecia, more or less epiphloeodal thallus and absence of minute squamules) and ecology. While most samples were collected from solitary elms, poplars and oak, specimens from the Alps came from *Sambucus* bark and spruce twigs. This suggests that the populations from the Alps might represent a distinct infraspecific taxon.

Paratypes (fertile specimens indicated by asterisk). **Austria:** *Steiermark*: Schladming, Ramsau am Dachstein, in gorge with road from Ramsau to Weissenbach, *c.* 850 m, 2009, *J. Vondrák* 7257 (CBFS). **Kärnten*: Gailtaler Alpen, 10 km WNW of Weissbriach, 0·5 km SE of Felstritz, open pine forest, 550 m, 1994, *P. van den Boom* 15927 (hb. van den Boom).—**Bulgaria:** *The Rhodopes*: Madzharovo district, Silen, Rabovo, valley of small brook N of village, 41°37′N, 25°40′E, 250 m, 2004, *J. Vondrák* (CBFS, in sample "*Caloplaca virescens*, Exs. of *Caloplaca*, Nr 11").—**Czech Republic:** *Southern Bohemia*: Novohradské hory Mts, Benešov nad Černou, Žofín, 48°40′29″N, 14°41′38″E, 745 m, 2009, 2010, *Z. Palice* 12943 & 13676 (PRA, topotypes); Šumava Mts, Borová Lada, Knížecí Pláně, avenue of old trees along

yellow-marked tourist footpath near abandoned cemetery, 48°57·61′N, 013°37·19′E, 1000–1020 m, 2005, *Z. Palice* 8928 (PRA); distr. Jindřichův Hradec, Novobystřická vrchovina, W slope of crest Homolka–Fabián–"Lesovna v Dubovici", 49°02′N, 14°58′50″E, 540 m, 2002, *M. Kukwa & Z. Palice* 6844 (PRA). *Western Bohemia*: Šumava Mts, Zhůří, valley of Pěnivý potok brook, nearby the settlement Bílý Potok, 49°06·3′N, 13°34·1′E, 770 m, 2005, *Z. Palice* 9414 *& J. Palicová* (PRA). *Southern Moravia*: Mikulov, Klentnice, protected area Soutěska, 48°51′48″N, 16°38′40″E, 400 m, 2013, *J. Vondrák* 10668, 10669, *I. Frolov & N. Pirogov* (CBFS).—**Russia:** *Chelyabinskaya Oblast'*: Southern Ural Mts, Ust'-Katav, vill. Orlovka (*c.* 10 km SW of Ust'-Katav), fragments of forest with *Ulmus laevis-Ulmus glabra* in valley of small brook *c.* 2 km SE of village, 54°52′04″N, 58°06′36″E, 500 m, 2012, *J. Vondrák* 9963 (CBFS). *Orenburgskaya Oblast'*: Kuvandik, vill. Maloe Churaevo (25 km N of Kuvandik), camp *c.* 2 km W of village, steppes and *Quercus robur-Tilia cordata-Ulmus laevis* woodland areas around camp, 51°40′9″N, 57°27′14″E, 250–500 m, 2011, *J. Vondrák* 9957, 9968 & 9970 (CBFS); *Saraktash, vill. Andreevka (*c.* 25 km NE of Saraktash), alluvial forest with *Tilia cordata*, *Populus* sp. and *Ulmus laevis*, *c.* 8 km NW of village, in valley of river Bolshoy Ik, 52°00′29″N, 56°33′39″E, 150 m, 2012, *J. Vondrák* 9967 (CBFS). **Republic of Bashkortostan*: Irendik range, Sibay, vill. Gabelsha (*c.* 15 km W of Sibay), waterfall Gadelsha in upper stream of brook Khudolaz, 52°45′26″N, 58°22′34″E, 500–800 m, 2011, *J. Vondrák* 9361 (CBFS).—**Slovakia:** *West Carpathians*: Muránská planina Mts, Mt Cigánka, well-lit oak forest on limestone on S slope, 48°45′18″N, 20°03′22″E, 800 m, 2010, *J. Halda & Z. Palice* 13441 (PRA).

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