

The extensive geographical range of several species of *Teloschistaceae*: evidence from Russia

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Abstract: The current view of the geographical ranges of lichens is often distorted by overly narrow or overly broad applications of names and by insufficient survey of most regions of the world. Here we present several cases where species of *Teloschistaceae* formerly thought to be limited to rather small territories in the western or eastern parts of Eurasia are in fact widespread in northern Eurasia. We support our findings with ITS nrDNA data in several new trees showing relationships in the genera *Athallia*, *Calogaya*, *Caloplaca*, *Flavoplaca* and *Gyalolechia*. The widespread species have little in common, except that most of them reproduce both sexually and asexually, and we discuss the possible influence of the combined reproduction on geographical range. *Calogaya bryochryson*, *Calogaya saxicola*, *Gyalolechia epiphyta* and *Gyalolechia ussuriensis* are new combinations. *Calogaya alaskensis* is a younger synonym for *C. bryochryson*. The generally arctic-alpine *Calogaya bryochryson* also occurs on the bark of solitary trees in dry parts of the Altai Mountains. The Australian *Flavoplaca cranfieldii* is a younger synonym of *F. flavocitrina*. *Gyalolechia epiphyta* has been described numerous times, from different regions and substrata, as *Caloplaca juniperi*, *C. laricina*, *C. tarani*, *Gyalolechia arizonica* and *G. juniperina*. The name *Gyalolechia xanthostigmoidea* has recently been used for *G. epiphyta*, but it represents a distinct taxon. *Gyalolechia ussuriensis* is closely related to and morphologically indistinguishable from *G. persimilis*, but they have a different ecology and distribution and we regard them as distinct species. *Caloplaca juniperina* Tomin is lectotypified.

Key words: *Athallia*, biogeography, *Calogaya*, *Caloplaca*, circumpolar distribution, *Flavoplaca*, *Gyalolechia*, lichens, reproductive mode

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Introduction

Geographical ranges of lichen species are often underestimated, mainly because of the very unbalanced intensity of lichen diversity

research in various regions of the world (Arcadia 2013). Some species of microlichen (lichen crusts) have a distribution that is

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probably known reliably, often because of special circumstances, such as species of *Dirina* (Tehler *et al.* 2013), most of which are restricted to coastal sites, a habitat that can be sampled fairly effectively because of its limited area. However, for most species distributional data are scarce, which might result in seemingly implausible disjunctions in known distributions, such as in *Rinodina capensis* (Mayrhofer *et al.* 2014), *Sclerophora amabilis* (Tibell 1999) and many others. Another reason for underestimated geographical ranges is the poor, but all too common, taxonomic practice of redescribing a lichen when it is found in different geographical regions, without adequately considering previous work. For instance, Sheard (2010) provided some cases of crustose species that have been described and redescribed even in recent times.

The opposite problem, too extensive a reported geographical range, can be caused by insufficient taxonomic knowledge. According to the world biodiversity database GBIF (<http://www.gbif.org/>), some 'prominent' lichen names (e.g. *Caloplaca citrina* and *C. holocarpa*) are mapped throughout the world, but these species have not been confirmed outside temperate regions of the Northern Hemisphere (Vondrák *et al.* 2009, 2016). The use of mainly European literature to determine lichens from other parts of the world has led to error in these cases and probably many others.

Russia includes most of northern Eurasia between 28°E and 169°W longitude and investigations of lichen diversity within its territory are essential to discover the real distributions of lichen taxa, especially those previously known only from Europe or North America (Davydov & Printzen 2012). Although the lichen biota of Russia has been quite well studied, it is less known than that of western Eurasia, mainly because the territory is very large and some regions are difficult to access. Here we report on selected examples, supported with molecular data, where our Russian records have changed the previous understanding of a species' range.

Materials and Methods

Specimens

Assessed specimens belong to nine species of *Athallia*, *Calogaya*, *Caloplaca*, *Flavoplaca* and *Gyalolechia* (*Teloschistaceae*). Specimens were collected by the authors from various regions of Russia. Acronyms of the author followed by the author's herbarium numbers are used to identify specimens in the figures and in Table 1. Most specimens are precisely localized by WGS 84 coordinates. Vouchers collected by IU, IZ, JV, GU (Genadii Urbanavichus) and EM are deposited in PRA, those collected by LK and SC in LE, by ED and L. Yakovchenko in ALTB, by DH in LECB, by TS (Toby Spribille) in GZU and by IF in the private herbarium of the author. All specimens were examined and identified by the first author. For the molecular analyses we sequenced the ITS of selected samples from Russia, and also from other countries if GenBank data were scarce, to produce more comprehensive phylogenetic trees (Table 1).

Sequences and phylogenetic reconstructions

DNA was extracted with a CTAB-based protocol (Araş & Cansaran 2006). Primers for PCR amplification of ITS were ITS1F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990). The PCR parameters included an initial hold at 94 °C for 5 min, and then 45 cycles with denaturing at 94 °C (30 s), annealing at 62 °C with the touchdown to 56 °C during the first 7 cycles (30 s), and an extension at 72 °C (60 s).

ITS nrDNA sequence data were used in our study for practical reasons: they are easily generated; the NCBI database (GenBank) includes a number of ITS sequences for reasonable fingerprinting; ITS single-locus genealogies are usually consistent with phenotypic data (seen in numerous ITS-based studies on *Teloschistaceae*) and are generally congruent with the loci nrLSU and mtSSU (e.g. Arup *et al.* 2013). New sequences were submitted to NCBI's BLAST website (Johnson *et al.* 2008; <http://blast.ncbi.nlm.nih.gov/Blast.cgi>) to confirm taxonomic identity.

The 69 sequences from this study (Table 1) were arranged into five alignments for five genera together with close GenBank sequences (Table 2). Alignments were done in BioEdit 7.2.5 free software (Hall 1999) with the use of ClustalW application (Thompson *et al.* 1997) and corrected by hand. Most of the GenBank data used are from Arup (2006), Arup & Grube (1999), Arup *et al.* (2013), Gaya *et al.* (2011), Himelbrant *et al.* (2015), Joshi *et al.* (2011), Kasalický *et al.* (2000), Maliček *et al.* (2014), Powell & Vondrák (2011), Redchenko *et al.* (2012), Šoun *et al.* (2011), Vondrák *et al.* (2008, 2009, 2012a, b) and Wedin *et al.* (2002). Maximum likelihood (ML) phylogenetic analyses were run in the application Phylogeny.fr (Dereeper *et al.* 2008) without Gblocks, with 250 bootstrap replicates and the GTR+I+G nucleotide substitution model. Outgroup sequences were selected from closely related genera on the basis of analyses by Arup *et al.* (2013) and our broader unpublished analyses.

TABLE 1. *New ITS nrDNA sequences for Teloschistaceae used in this study together with locations, substrata and herbarium (hb) information.*

Taxon	Sample / hb. acronym	Locality / altitude (m) / substratum	Latitude(°)	Longitude(°)	GenBank accession numbers
<i>Athallia alnetorum</i>	JV8316 / PRA	Greece, Peloponnese / 300 / <i>Pistacia lentiscus</i>	37-55	23-25	KT804927
<i>A. alnetorum</i>	IU (UT-014) / PRA	Russia, Krasnodar Region, Utrish Reserve / 430 / <i>Quercus</i> twigs	44-7212	37-4684	KT804928
<i>Calogaya arnoldii</i>	JV12552 / PRA	Russia, Yekaterinburg, Rezh / 180 / calcareous schist	57-4858	61-4941	KT804929
<i>C. arnoldii</i>	ED6934 / ALTB	Russia, Altai Mts, Soloneshnoye / 1035 / calcareous schist	51-3545	84-5676	KT804930
<i>C. arnoldii</i>	SC205 / LE	Russia, Trans-Baikal region, Kodar Ridge / 940 / base-rich rock	56-9196	118-0291	KT804931
<i>C. arnoldii</i>	GU (s.n.) / PRA	Russia, Adygea, Caucasus Reserve / 2000 / limestone	44-0164	39-9789	KT804932
<i>C. arnoldii</i>	GU (L-022) / PRA	Russia, Bashkortostan, Shulgan-Tash Reserve / 300 / <i>Betula</i>	53-0419	57-0672	KT804933
<i>C. biatorina</i>	JV10514 / PRA	Czech R., Praha, Radotin / 300 / limestone	49-989498	14-334760	KT804934
<i>C. bryochrysiion</i>	JV10372 / PRA	Russia, Altai Mts, Kosh-Agach / 2000 / <i>Populus laurifolia</i>	50-052	88-709	KT804935
<i>C. bryochrysiion</i>	ED11498 / ALTB	Russia, Altai Mts, Kosh-Agach / 2200 / <i>Salix pentandra</i>	49-7969	89-3619	KT804936
<i>C. bryochrysiion</i>	ED11499 / ALTB	Russia, Altai Mts, Kuray, Kuraika basin / 1670 / <i>Populus laurifolia</i>	50-2669	87-9513	KT804937
<i>C. bryochrysiion</i>	IZ (s.n.) / PRA	Russia, Novaya Zemlya / 0-5 / lime-rich pebbles	76-999722	67-780000	KT804938
<i>C. bryochrysiion</i>	JV9529 / PRA	Svalbard / coastal / calcareous cliff	78-38	16-49	KT804939
<i>C. bryochrysiion</i>	JV7262 / PRA	Austria, Schladming / 2750 / bryophytes on limestone	47-469151	13-625209	KT804940
<i>C. bryochrysiion</i>	JV11086 / PRA	Russia, W Sayan Mts / 2150 / base-rich schist	51-7000	89-8872	KT804941
<i>C. aff. ferrugineoides</i>	JV12708 / PRA	Russia, Altai Mts, Kosh-Agach / 1550 / wood of <i>Juniperus</i>	50-240337	87-876771	KT804942
<i>C. ferrugineoides</i>	JV8534 / PRA	Turkey, Tuzluca / 1300 / shrubs	40-174084	43-674208	KT804943
<i>C. ferrugineoides</i>	ED11221 / ALTB	China, Xinjiang, Dzhungar basin / 940 / shrubs	46-605768	89-585706	KT804944
<i>C. persica</i>	JV8515 / PRA	Turkey, Lake Van / 1750 / <i>Juniperus</i>	38-466427	42-502325	KT804945
<i>C. polycarpoides</i>	JV5541 / PRA	NW Iran, Khalkhal / 1680 / <i>Populus</i>	37-679664	48-491388	KT804946
<i>C. saxicola</i> s. lat.	JV12558 / PRA	Russia, W Sayan Mts / 2150 / base-rich schist	51-700754	89-885716	KT804947
<i>Calogaya</i> sp.	JV12707 / PRA	Russia, Altai Mts, Kosh-Agach / 2700 / limestone	50-145324	88-465936	KT804948
<i>Caloplaca conversa</i> s. lat.	JV10289 / PRA	Russia, Altai Mts, Chermal / 500 / volcanic rock	51-632759	85-782572	KT804949
<i>C. conversa</i> s. lat.	JV10265 / PRA	Russia, Altai Mts, Ulagan / 500 / gneiss	50-92	88-19	KT804950
<i>C. conversa</i> s. str.	JV744 / PRA	Bulgaria, Madzharovo / c. 400 / siliceous rock	41-66	25-66	KT804951
<i>C. conversa</i> s. str.	IF1048 / hb. Frolov	Russia, Bashkortostan, Sargaya / 700 / xerothermic serpentinite	53-35	57-74	KT804952
<i>C. conversa</i> s. str.	JV5538	NW Iran, Taleh / 1640 / siliceous stone	37-623664	48-800237	KT804953
<i>C. conversa</i> s. str.	JV6461	Turkey, Artvin / 550 / siliceous rock	41-189884	41-857240	KT804954
<i>C. egeana</i>	JV6262 / PRA	Great Britain, Gibraltar rock / c. 100 / limestone	36-145139	-5-345071	KT804955
<i>C. isidiigera</i>	GU (L-017) / PRA	Russia, Adygea, Caucasus Reserve / 2030 / limestone	44-0304	40-0251	KT804956
<i>C. stillicidiorum</i> s. lat.	JV11104 / PRA	Russia, Rep. of Tuva, Ak-Sug / 1490 / siliceous stone in river	51-618879	90-076022	KT804957
<i>C. subalpina</i>	GU, L-022 / PRA	Russia, Rep. of Bashkortostan, Shulgan-Tash Reserve / 300 / <i>Betula</i>	53-0419	57-0672	KT804958
<i>C. subalpina</i>	JV9397 / PRA	Russia, Rep. of Bashkortostan, Sibay / 700 / schist	52-7572	58-3761	KT804959
<i>C. subflavorubescens</i>	Joshi (s.n.) / PRA	South Korea (coll. Y. Joshi) ? / bark	?	?	KT804960
<i>Flavoplaca</i> aff. <i>austroclitina</i>	JV8603 / PRA	Greece, Peloponnese, Methana / 240 / volcanic rock	37-614744	23-333514	JN813411
<i>F. austroclitina</i>	JV8712 / PRA	Greece, Nafpaktos, Monastiraki / 10 / limestone	38-400524	21-931378	JN813423
<i>F. flavocitrina</i>	JV8605 / PRA	Greece, Nafpaktos, Monastiraki / 10 / limestone	38-400524	21-931378	JN813420
<i>F. flavocitrina</i>	JV12679 / PRA	Russia, Rep. of Altai, Artibash / 620 / siliceous rock	51-813403	87-192289	KT804961
<i>F. flavocitrina</i>	SC197 / LE	Russia, Trans-Baikal region, Kodar Ridge / 940 / base-rich rock	56-9196	118-0291	KT804962

TABLE 1. *Continued*

Taxon	Sample / hb. acronym	Locality / altitude (m) / substratum	Latitude(°)	Longitude(°)	GenBank accession numbers
<i>F. flavocitrina</i>	SC244 / LE	Russia, Trans-Baikal region, Kodar Ridge / 1590 / siliceous rock	56-9194	118-0011	KT804963
<i>F. flavocitrina</i>	SC246 / LE	Russia, Trans-Baikal region, Kodar Ridge / 1590 / siliceous rock	56-9194	118-0011	KT804964
<i>F. flavocitrina</i>	JV10226 / PRA	Slovakia, Revúca, Muráň / 700 / <i>Quercus</i>	48-770250	20-079807	KT804965
<i>F. flavocitrina</i>	Muchnik (s.n.) / PRA	Russia, Oryol Region, Khomutovo / 180 / limestone	52-8406	37-5663	KT804966
<i>F. flavocitrina</i>	JV9178 / PRA	Slovakia, Revúca, Muráň / 700 / limestone	48-770250	20-079807	KT804967
<i>F. geleverjiae</i>	JV8887 / PRA	Greece, Nafpaktos, Monastiraki / 10 / limestone	38-400524	21-931378	JN813406
<i>Gyalolechia</i> aff. <i>ussuriensis</i>	TS38925 / GZU	USA, Alaska, Glacier Bay NP / 70 / <i>Cupressus nootkatensis</i>	58-35637	-136-38144	KT804988
<i>G. allochroa</i>	TS39368 / GZU	USA, Alaska, Glacier Bay NP / 810 / vertical siliceous rock	58-46046	-135-56179	KT804968
<i>G. epiphyta</i>	JV5696 / PRA	NW Iran, Lake Urmia / 1280 / soil bryophytes	37-883040	45-571059	KT804973
<i>G. epiphyta</i>	JV5585 / PRA	NW Iran, Lake Urmia / 1370 / soil bryophytes	37-787453	45-454082	KT804974
<i>G. epiphyta</i>	JV12710 / PRA	Russia, Altai Mts, Kosh-Agach / 1550 / <i>Juniperus sabina</i>	50-240337	87-876771	KT804975
<i>G. epiphyta</i>	JV5582 / PRA	NW Iran, Lake Urmia / 1280 / soil bryophytes	37-883040	45-571059	KT804976
<i>G. epiphyta</i>	JV12411 / PRA	China, Xinjiang, Tianshan Grand Canyon / 2400 / <i>Picea schrenkiana</i> wood	43-326478	87-362703	KU360123
<i>G. epiphyta</i>	JV12412 / PRA	China, Xinjiang, Tianshan Grand Canyon / 2400 / <i>Picea schrenkiana</i> bark	43-326478	87-362703	KU360122
<i>G. epiphyta</i>	JV13626 / PRA	Iran (coll. V. Tahereh) ? / soil bryophytes	?	?	KT804977
<i>G. flavorubescens</i>	JV5575 / PRA	NW Iran, Talesh / 1640 / <i>Fagus orientalis</i>	37-623664	48-800237	KT804969
<i>G. flavorubescens</i>	JV418 / PRA	Italy, Sicily, NP Nebrodi / c 1000 / <i>Quercus</i>	37-92	14-67	KT804970
<i>G. flavorubescens</i>	JV5599 / PRA	NW Iran, Talesh / 170 / <i>Swida</i>	37-705114	48-887425	KT804980
<i>G. flavorubescens</i>	JV5691/1 / PRA	NW Iran, Talesh / 1150 / <i>Acer</i>	37-656739	48-819694	KT804981
<i>G. flavorubescens</i>	JV5691/2 / PRA	NW Iran, Talesh / 1150 / <i>Acer</i>	37-656739	48-819694	KU360124
<i>G. flavorubescens</i>	JV5700/1 / PRA	NW Iran, Talesh / 500 / <i>Fagus orientalis</i>	37-681581	48-819696	KT804982
<i>G. flavorubescens</i>	JV5700/2 / PRA	NW Iran, Talesh / 500 / <i>Fagus orientalis</i>	37-681581	48-819696	KT804983
<i>G. flavorubescens</i>	JV5718 / PRA	NW Iran, Talesh / 500 / <i>Ferula</i>	37-681581	48-819696	KT804984
<i>G. flavorubescens</i>	JV5723 / PRA	NW Iran, Talesh / 40 / <i>Cerasus</i>	37-717774	48-960760	KT804985
<i>G. flavorubescens</i>	JV5738 / PRA	NW Iran, Talesh / 1150 / <i>Acer</i>	37-656739	48-819694	KT804986
<i>G. flavorubescens</i>	JV5844 / PRA	NW Iran, Talesh / 500 / <i>Acer</i>	37-681581	48-819696	KT804987
<i>G. flavorubescens</i>	JV14390 / PRA	Russia, Caucasus, Kavkazskii Zapovednik / 1600 / <i>Populus tremula</i>	44-068597	40-001542	KU360121
<i>G. flavovirescens</i>	JV5537 / PRA	NW Iran, Namin / 1350 / base-rich siliceous rock	38-426759	48-581384	KT804971
<i>G. flavovirescens</i>	JV5615 / PRA	NW Iran, Khalkhal / 1900 / base-rich siliceous rock	37-611880	48-740579	KT804972
<i>G. persimilis</i>	JV7486 / PRA	USA, Davis, Winters / 900 / <i>Quercus</i>	38-500055	-122-118556	KT804978
<i>G. persimilis</i>	GZU, Wetm.: Tel. Exs. 33 / GZU	Mexico, Baja California / 1700 / <i>Quercus tuberculata</i>	23-601700	-109-931902	KT804979
<i>G. ussuriensis</i>	JV13417 / PRA	Russia, Krasnoyarsk Region, Minusinsk / 440 / <i>Salix</i>	53-0830	93-0944	KT804989
<i>G. ussuriensis</i>	ED11500 / ALTB	Russia, Primorsky krai Area, Terney / 570 / <i>Populus</i>	45-8963	137-3130	KT804991
<i>G. ussuriensis</i>	ED11220 / ALTB	Russia, Altai Mts, Zalesovsk / 430 / <i>Populus tremula</i>	54-4166	85-1166	KT804990
<i>G. xanthostigmoidea</i>	TS32410 / GZU	Canada, Québec, Côte-Nord, Lac Gobeil / 110 / <i>Thuja occidentalis</i>	48-232099	-69-658427	KT804992

TABLE 2. Alignment of the 69 sequences from this study for five genera of *Teloschistaceae*.

Alignment	All sequences / new sequences	Outgroup	Alignment length	Variable positions / variable in ingroup
part of <i>Athallia</i> (Supplementary Material Fig. S1)	17/2	<i>Athallia pyracea</i>	530	60/40
<i>Calogaya</i> (Fig. 1)	54/19	<i>Rusavskia</i>	544	214/200
<i>Caloplaca</i> (Supplementary Material Fig. S2)	52/12	<i>Rufoplaca</i> and <i>Caloplaca</i> <i>conversa</i>	551	292/133
part of <i>Flavoplaca</i> (Fig. 3)	36/13	<i>Flavoplaca limonia</i> and <i>F. austrocirina</i>	596	67/48
<i>Gyalolechia</i> (Fig. 4)	57/28	<i>Blastenia</i>	560*	289/273

* without 21 BP insertion in one sequence

Results

Athallia alnetorum (Giralt et al.) Arup et al.

See Arup et al. (2013) for nomenclatural details.

Caloplaca alnetorum Giralt et al. was combined into *Athallia* by Arup et al. (2013). It resembles some morphotypes of *Gyalolechia flavorubescens* s. lat., but according to Giralt et al. (1992) differs in ascospore size and shape of conidia. We confirm that ascospore size is diagnostic, but we observed bacilliform conidia, characteristic of *G. flavorubescens*, in some specimens of *A. alnetorum* (specimens from Latvia; Frolov 663, 664). *Athallia alnetorum* is well known in Mediterranean mountains and the Alps (e.g. Giralt et al. 1992; Vondrák & Wirth 2013). It is new to Russia from the western foothills of the Caucasus Mountains but it is also common on the Baltic Sea coast in Latvia (I. Frolov, unpublished data), thus more northern Russian records are possible. The ITS sequence of the Russian specimen is within the *A. alnetorum* clade (see Supplementary Material Figure S1, available online).

Russian specimen. Russia: Krasnodar Krai: Caucasus Mts, Utrish Reserve, forested mountain c. 20 km SE from Anapa, alt. 430 m, 44.7212°N, 37.4684°E, broad-leaved forest, on branch of *Quercus petraea*, 2014, I. Urbanavichene s. n. (PRA).

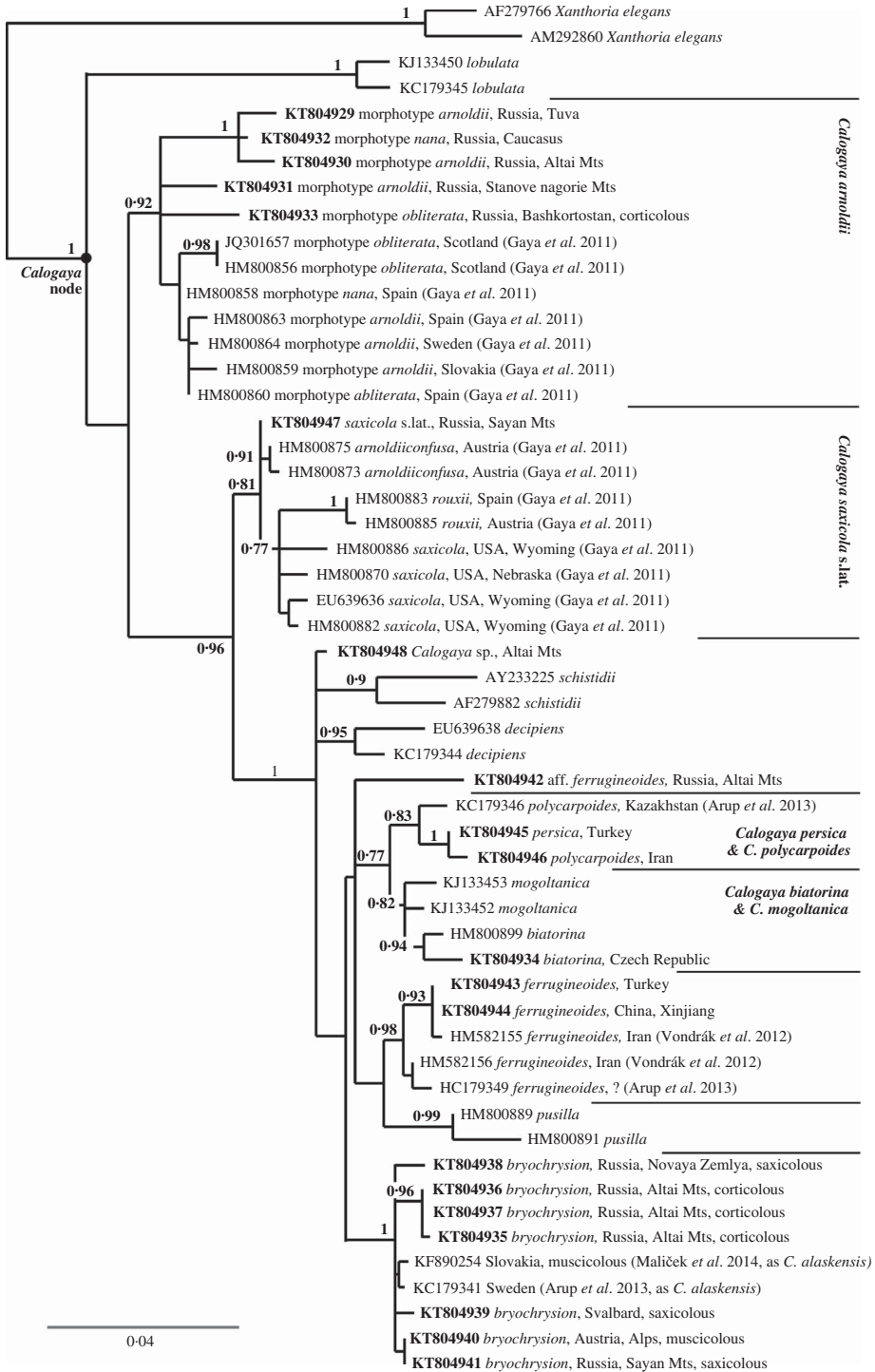
Calogaya arnoldii (Wedd.) Arup et al.

See Arup et al. (2013) for nomenclatural details.

A common lichen which has been called *Caloplaca saxicola* (Hoffm.) Nordin by numerous Russian lichenologists (cf. Urbanavichus 2010) but proved to be *Calogaya arnoldii* (sensu Gaya 2009; Gaya et al. 2011). *Calogaya arnoldii* and *Calogaya saxicola* (the combination proposed below) are closely related and the differences are subtle; they mostly concern shape and size of ascospores. However, both taxa are phenotypically variable, their characters overlap, and they cannot be identified with certainty from their phenotype. The Russian specimens were identified from their ITS sequences (Fig. 1). One Russian specimen from the Western Sayan Mountains (JV12558) has an ITS sequence (KT804947) similar to *Calogaya saxicola sensu Gaya et al.* (2011) and could be considered conspecific with *C. saxicola*.

We consider the subspecies *arnoldii*, *nana*, and *obliterata* proposed by Gaya (2009) to be merely expressions of phenotype plasticity within the species *C. arnoldii*, and our opinion is reflected in the ITS tree (Fig. 1).

Russian specimens. Russia: Republic of Adygea: Caucasus Mts, Caucasus Reserve, Kamennoe More Ridge, the edge of a cliff above Armyanka River, 44.0164°N, 39.9789°E, alt. 2000–2030 m, on limestone, 2011, G. Urbanavichus s. n. (PRA). Republic of Bashkortostan: Southern Ural Mts, Shulgan-Tash Reserve, cliff above Kapova Cave at the banks of Belaya River, 53.0419°N, 57.0672°E, alt. 300 m, on bark of *Betula*, 2007, G. Urbanavichus s. n. (PRA). Altai Krai: Soloneshensk district, Bashchelaksky Range, valley of Shinok River, alt. 1035 m, 51.3545°N, 84.5676°E, on stone, 2003, E. Davydov 6934 (ALTB). Sverdlovsk Region: Yekaterinburg, Rezh, Glinskoe, 0.5 km E of Chepchugovo Village, 57.4858°N, 61.4941°E, on lime-rich schist,



2013, *Ĵ. Vondrák* 12552 (PRA). *Zabaikalsky Krai*: Kodar Ridge, 56.9196°N, 118.0291°E, on lime-enriched siliceous rock, 2013, *L. Konoreva* s. n. (LE).

***Calogaya bryochryson* (Poelt) Vondrák comb. nov.**

MycoBank No.: MB 814538

Caloplaca bryochryson Poelt, *Feddes Repertorium* 58: 175 (1955); type: Germany, Wettersteingebirge, Gipfel der Alpspitze, in feinen Felsspalten an Vogelblöcken, 1954, *Poelt* (M-0024347—holotype seen).

Syn. nov. *Caloplaca alaskensis* Wetmore, *Bryologist* 107: 507 (2004); type: USA, Alaska, valley of Mancha Creek with Firth River, 1958, *Sharp* 6531 (MIN—holotype).—*Calogaya alaskensis* (Wetmore) Arup et al. (2013: 38).

(Fig. 5A)

The name *Caloplaca bryochryson* was synonymized with *C. epiphyta* by Hansen et al. (1987). Söchting & Tønsberg (1997), however, considered *C. epiphyta* synonymous with *C. xanthostigmoidea* (= *Gyalolechia xanthostigmoidea*), but recognized *C. bryochryson* as distinct. *Caloplaca xanthostigmoidea* and related taxa (now the genus *Gyalolechia*) contain fragilin and some chlorinated anthraquinones, but the type of *C. bryochryson* has parietin as the main anthraquinone and lacks substances characteristic of *Gyalolechia* (Söchting & Tønsberg 1997). Those authors therefore suggested that *C. bryochryson* is related to *C. citrina*, a morphologically similar taxon with the same pigments.

We examined *Caloplaca bryochryson* specimens from the Austrian Alps (in GZU, PRA) and also obtained an ITS sequence (JV7262 in Table 1) that groups with two *C. alaskensis* sequences (Fig. 1). We further compared the type of *C. bryochryson* (Poelt 1955) with numerous samples of *Calogaya alaskensis* and consider both names synonymous. The epithet *bryochryson* has priority over *alaskensis*, so a new combination is required.

Wetmore (2004) described *Caloplaca alaskensis* (now *Calogaya*) from only two

localities in Alaska, but within a few years it had been reported from numerous arctic and boreal-alpine localities in North America, Europe, Svalbard and Greenland (Söchting et al. 2008). The latter authors also provided ITS sequence data showing that geographically distant samples called *C. alaskensis* belong to the same species. Recently it was also found in central Europe, in the Carpathians (Malíček et al. 2014).

We obtained five ITS sequences from five Russian samples of *Calogaya bryochryson*. Two are from arctic-alpine habitats and typical substrata (calcareous rock, calciphilous bryophytes), but the other three are from dry continental, semi-desert habitats in the Altai Mountains. They were collected on *Populus laurifolia* and *Salix pentandra* growing along rivers in high mountains mostly covered by dry steppe communities. This corticolous population may eventually prove to be an incipient species that is already distinct from the arctic-alpine population, but that is not evident from the ITS (Fig. 1) and morphological data, and so for the present we include it in *C. bryochryson*.

Russian specimens. Russia: Republic of Altai: Kosh-Agach district, SE part of Kuray Ridge, NE of Chagan-Uzun Village, alt. 2000 m, 50.052°N, 88.709°E, on bark of *Populus laurifolia*, 2012, *I. Frolov & Ĵ. Vondrák* 10372 (PRA); Kosh-Agach district, left bank of Yustyd River, 2 km downstream of junction of Boguty and Naryngol Rivers, alt. 2200 m, 49.7969°N, 89.3619°E, on bark of *Salix pentandra*, 2013, *E. Davydov* 11498 (ALTB); Kosh-Agach district, Kurai, right bank of Kuraika River at 5 km N of Kurai, alt. 1670 m, 50.2669°N, 87.9513°E, on bark of *Populus laurifolia*, 2013, *E. Davydov* 11499 (ALTB). *Republic of Tuva:* West Sayan Mts, Ak-Dovurak, Ak-Sug, Enge-Beldir, glacier cirque in S-slope from pass ‘Sayanskiy’, 2200 m, at road A161, close to Republic of Khakasia border, alt. 2150–2200 m, 51.7000°N, 89.8872°E, on base-rich schist, 2013, *I. Frolov & Ĵ. Vondrák* 11086 (PRA). *Arkhangelsk Region:* Novaya Zemlya Archipelago, NE extremity of Severny Island, Karlsen Cape, alt. 0–5 m, 76.9997°N, 67.7800°E, on lime-rich pebbles at seashore, 2013, *I. Zhdanov* (LE). *Zabaikalsky Krai:* Kodar ridge, Hadytkanda valley, alt. 1230 m, 56.7480°N, 117.2650°E, 2015, *S. Chesnokov* 249 (LE); *ibid.*, valley of Zolotoy brook, alt. 1410 m, 56.8389°N, 117.3064°E, 2015, *S. Chesnokov* 161 (LE).

FIG. 1. Maximum likelihood ITS phylogeny of *Calogaya* showing positions of *C. arnoldii*, *C. bryochryson* and *C. ferrugineoides*. New sequences are in bold; bootstrap supports (BS > 0.7) are shown at nodes.

**Calogaya saxicola (Hoffm.) Vondrák
comb. nov.**

MycoBank No.: MB 815508

Psora saxicola Hoffm., *Descr. Adumb. Pl. Lich.* 1 (3): 82, Tab. 17, Fig. 3 (1790); type: Sweden (H-Ach 1019E "*Lecanora murorum*, *Svecia*")—neotype selected by Nordin (1972).

Caloplaca isidiigera Vězda

See Šoun *et al.* (2011) for nomenclatural details.

(Fig. 2A; distribution map)

Caloplaca isidiigera, described from the Carpathians (Vězda 1978), is known from numerous montane–alpine sites in Europe and North America (Šoun *et al.* 2011). We newly report it from several localities in southern Siberia and suggest that it has a circumpolar distribution. *Caloplaca isidiigera* also occurs at low altitudes in continental Eurasia (e.g. JV9541 from the Chelyabinsk Region). An ITS sequence from the specimen from the Caucasus Mountains falls within the *Caloplaca isidiigera* clade (see Supplementary Material Figure S2, available online).

Russian specimens. Russia: Republic of Adygeya: Caucasus Mts, Caucasus Reserve, Kamennoe More Ridge, c. 0.85 km N of Mt. Nagoi Koshi, on limestone, 44-0304°N, 40-0251°E, alt. 2025 m, 3 vii 2011, *G. Urbanavichus* s. n. (PRA). *Republic of Altai:* Altai Mts, Choya district, Karakoksha, settlement Uymen', Mt. Sagani (2036 m), c. 40 km S of Karakoksha, alt. 1700–2030 m, on vertical face of base-rich rock in subalpine zone, 2012, *I. Frolov & Ĵ. Vondrák* 10315 (PRA). *Republic of Bashkortostan:* Ural Mts, Irendik Range, Sibay, Gadelsha Village (c. 15 km W of Sibay), waterfall Gadelsha in upper stream of brook Khudolaz, alt. 500–800 m, 52-7572°N, 58-3761°E, on shaded base-rich siliceous stone in brook, 2011, *I. Frolov & Ĵ. Vondrák* 10512 (PRA). *Republic of Tuva:* West Sayan Mts, Ak-Dovurak, Ak-Sug, Enge-Beldir, glacier cirque in S-slope from pass 'Sayanskiy pereval', 2200 m, at road A161, close to border with Republic of Khakasia, alt. 2150–2200 m, 51-7000°N, 89-8872°E, on S-exposed schist outcrop, below overhang, in alpine zone, 2013, *I. Frolov & Ĵ. Vondrák* 11099 (PRA). *Chelyabinsk Region:* Magnitogorsk, in steppe c. 10 km S of town, alt. c. 300 m, 53-2613°N, 58-9263°E, on limestone boulders in steppe, 2011, *O. Vondráková & Ĵ. Vondrák* 9541 (PRA). *Krasnoyarsk Krai:* West Sayan Mts, Minusinsk, at road Minusinsk–Kyzyl, 2 km E of pass 'Buybinskiy pereval', E-exposed glacier cirque with mica-schist bedrock, alt.

1550–1600 m, 52-8491°N, 93-2808°E, on vertical mica-schist rock face in subalpine zone, 2013, *I. Frolov & Ĵ. Vondrák* 12653, 12654, 12697 (PRA). *Murmansk Region:* Pechenga, Kandalakskiy Reserve, Bolshoy Aynov Island, alt. 20 m, 69-8355°N, 31-5691°E, on siliceous stone, 2010, *A. V. Melekhin* s. n. (KPABG, det. *I. Frolov*).

Caloplaca subalpina Vondrák *et al.*

See Šoun *et al.* (2011) for nomenclatural details.

(Fig. 2A; distribution map)

Caloplaca subalpina was previously known from subalpine and alpine zones of the Alps, the Carpathians, the Pyrenees and the Sudetes (Vondrák *et al.* 2008), but according to our new data, its range extends much further eastwards, to the Western Sayan Mountains. No previous reports were corticolous, but one of our collections is from birch bark, where it is accompanied by two other generally saxicolous lichens, *Caloplaca arnoldii* and *Xanthoria sorediata*. ITS sequences of two Russian samples are placed in the *Caloplaca subalpina* clade (see Supplementary Material Figure S2, available online).

Russian specimens. Russia: Republic of Bashkortostan: Southern Ural Mts, Irendik Range, Sibay, Gadelsha Village (c. 15 km W of Sibay), waterfall Gadelsha in upper stream of brook Khudolaz, alt. 500–800 m, 52-7572°N, 58-3761°E, on vertical face of base-rich schist, with *Leproplaca obliterans*, 2011, *I. Frolov & Ĵ. Vondrák* 9397 (PRA); Southern Ural Mts, Shulgan-Tash Reserve, cliff above Kapova Cave at the banks of Belaya River, 53-0419°N, 57-0672°E, alt. 300 m, on bark of *Betula*, 2007, *G. Urbanavichus* s. n. (PRA). *Krasnoyarsk Krai:* West Sayan Mts, Minusinsk, at road Minusinsk–Kyzyl, 2 km E of pass 'Buybinskiy pereval', E-exposed glacier cirque with mica-schist bedrock, alt. 1550–1600 m, 52-8491°N, 93-2808°E, on vertical mica-schist rock face in subalpine zone, 2013, *I. Frolov & Ĵ. Vondrák* 12652, 12658, 12667, 12673 (PRA).

**Flavoplaca flavocitrina (Nyl.)
Arup *et al.***

See Arup *et al.* (2013) for nomenclatural details.

Syn. nov. *Caloplaca cranfieldii* S. Y. Kondr. & Kärnefelt in Kondratyuk *et al.*, *Bibl. Lichenol.* 95: 352 (2007); type: Western Australia, Northampton, Lynton, on sandstone, 2004, *Kärnefelt & Cranfield* (Kondratyuk 20423,

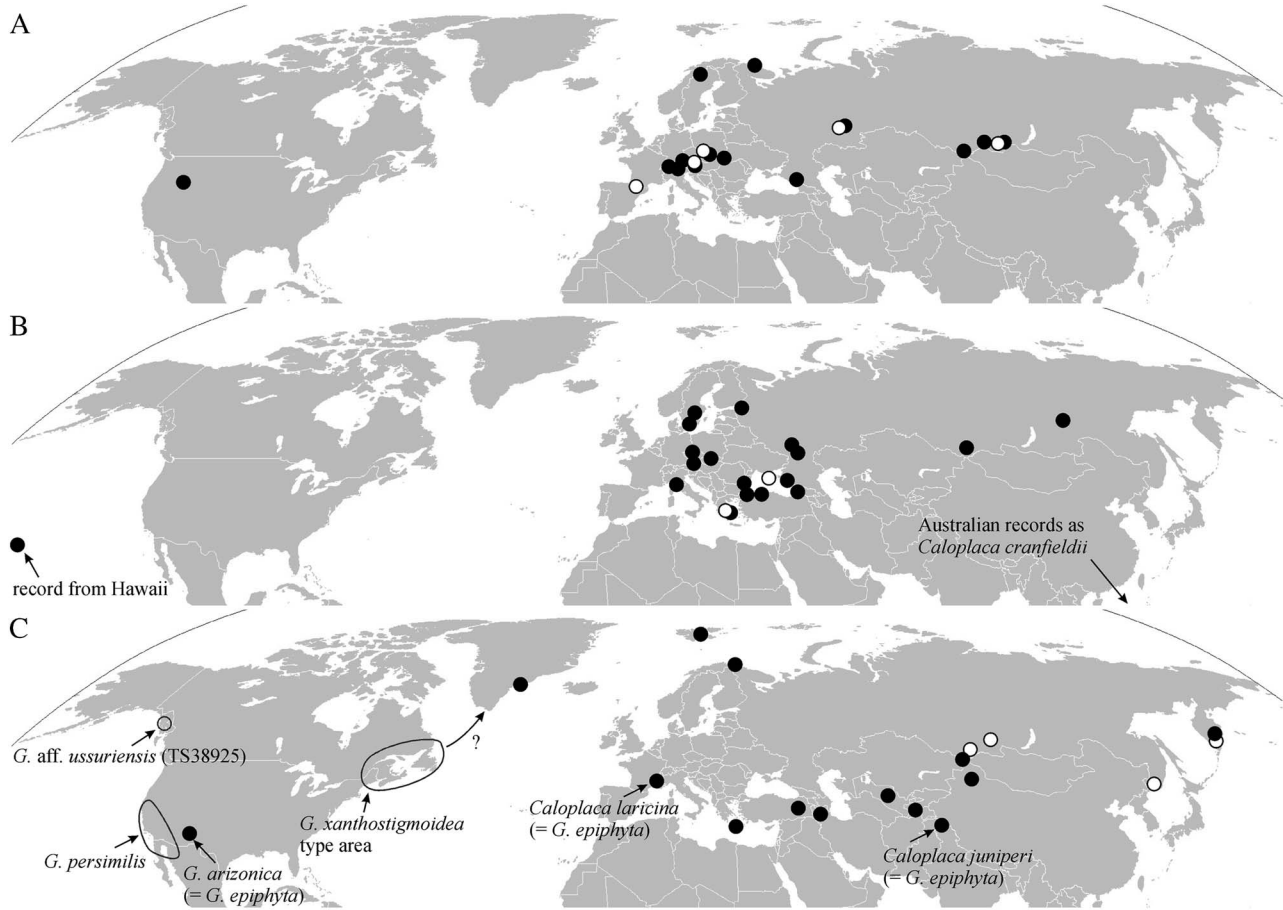


FIG. 2. Locations of specimens sequenced and confirmed in this study. A, *Caloplaca isidiigera* (black dots) and *C. subalpina* (white dots); B, *Flavoplaca flavocitrina* (black dots) and the closely related *F. geleverjæ* (white dots); C, *Gyalolechia epiphyta* (black dots) and *G. ussuriensis* (white dots), with approximate ranges of other soorediate *Gyalolechia* (outlined).

PERTH—holotype; GZU—isotype seen).—*Flavoplaca cranfieldii* (S. Y. Kondr. & Kärnefelt) Arup *et al.*, *Nord. J. Bot.* **31**: 45 (2013).

(Fig. 2B; distribution map)

Caloplaca flavocitrina (Nyl.) H. Olivier was synonymized with *C. citrina* by Laundon (1965) and this view was accepted by many, including Russian authors (e.g. Stepanchikova *et al.* 2014). However, some recent authors have regarded *C. flavocitrina* as distinct from other yellow sorediate crusts of *C. citrina* s. lat. (cf. Vondrák *et al.* 2007). ITS sequence data have confirmed that it is distinct (Arup 2006; Vondrák *et al.* 2009). It is now placed in the genus *Flavoplaca*, which includes both sorediate and non-sorediate crusts (Arup *et al.* 2013).

Flavoplaca flavocitrina s. lat. (including *F. geleverjae*) forms a well-supported clade (BS = 1, Fig. 3), sister to a clade composed of *F. austrocitrina* and *F. limonia* that acts as outgroup. *Flavoplaca flavocitrina* differs from this outgroup in 13 nucleotide substitutions in our ITS alignment. *Flavoplaca citrina*, *F. confusa* and *F. nigromarina*, three morphologically similar taxa, are less closely related to *F. flavocitrina* in ITS. *Flavoplaca geleverjae* differs from *F. flavocitrina* in five nucleotide substitutions (two of them shared with the outgroup) and it may be a distinct species (Khodosovtsev *et al.* 2003; Vondrák *et al.* 2009). The sequence EU563389 (*F.* aff. *flavocitrina*, Bulgaria) is also included in the *Flavoplaca flavocitrina* s. lat. clade, but differs from *F. flavocitrina* in five substitutions (four of them shared with the outgroup). The corresponding specimen has *F. flavocitrina* morphology.

Flavoplaca flavocitrina is exceptional among taxa of this genus owing to its very broad ecological range. It can grow on mineral-rich siliceous and calcareous rocks, numerous artificial substrata (e.g. tarmac, concrete), dust-impregnated wood and on base-rich bark (e.g. *Acer platanoides*, *Ulmus glabra*). No other species of *Flavoplaca* is so indifferent to substratum, and very few species anywhere in *Teloschistaceae* are so indifferent. It may be almost cosmopolitan in the Northern

Hemisphere, which is also exceptional in *Flavoplaca*: as well as numerous European and Mediterranean records, it is known from North America (Brodo *et al.* 2013), Hawaii (Vondrák *et al.* 2009) and Siberia (this paper).

Flavoplaca flavocitrina also occurs in the Southern Hemisphere (Australia), where it has been known as *Caloplaca cranfieldii* (Kondratyuk *et al.* 2007; \equiv *Flavoplaca cranfieldii*). The isotype of *C. cranfieldii* in GZU matches *F. flavocitrina* morphologically, and the ITS sequence from the type (published by Arup *et al.* 2013) falls into the *F. flavocitrina* clade in our phylogenetic reconstruction (Fig. 3). We consider *C. cranfieldii* to be a synonym of *Flavoplaca flavocitrina*.

There are several reports of *Flavoplaca flavocitrina* from European Russia (Vondrák *et al.* 2009; Muchnik *et al.* 2014; Himelbrant *et al.* 2015). We can now add records from two Siberian localities, from siliceous rocks in natural habitats. It is definitely the most widely distributed species of *Flavoplaca* in Russia; most others are restricted to the Black Sea coast, such as *F. arcisproxima*, *F. austrocitrina* and *F. communis* (Vondrák *et al.* 2009), or to European Russia, such as *F. dichroa* (e.g. Vondrák *et al.* 2010). Identification of *Flavoplaca flavocitrina* should be confirmed by molecular barcoding (ITS sequences), because some taxa, including *F. citrina* (not confirmed from Russia), are very similar.

Russian specimens. **Russia:** Republic of Altai: Altai Mts, Turochak district, Artibash, c. 5 km NW of village, SW-exposed gneiss rocks above right bank of Biya River, alt. 450 m, on vertical face of siliceous rock, 2012, I. Frolov & J. Vondrák 12679 (PRA). Oryol Region: Krasnaya Zarya district, Khomutovo, alt. 180 m, 52-8406°N, 37-5663°E, on limestone, 2014, Muchnik s. n. (PRA). Zabaikalsky Krai: Kodar Ridge, alt. 940 m, 56-9196°N, 118-0291°E, 2013, L. Konoreva s. n. (LE, Chesnokov197); *ibid.*, alt. 1590 m, 56-9194°N, 118-0011°E, on siliceous rock, 2013, L. Konoreva s. n. (LE, Chesnokov244, 246).

Gyalolechia epiphyta (Lyngé) Vondrák comb. nov.

MycoBank No.: MB 815509

Caloplaca epiphyta Lyngé, *Skrifter om Svalbard og Ishavet* **81**: 119 (1940); type: [Greenland], Østgrønland, Jackson, Ø, 1929, Lyngé (O-L-1279—holotype, seen in <http://nhm2.uio.no/lav/web/index.html>).

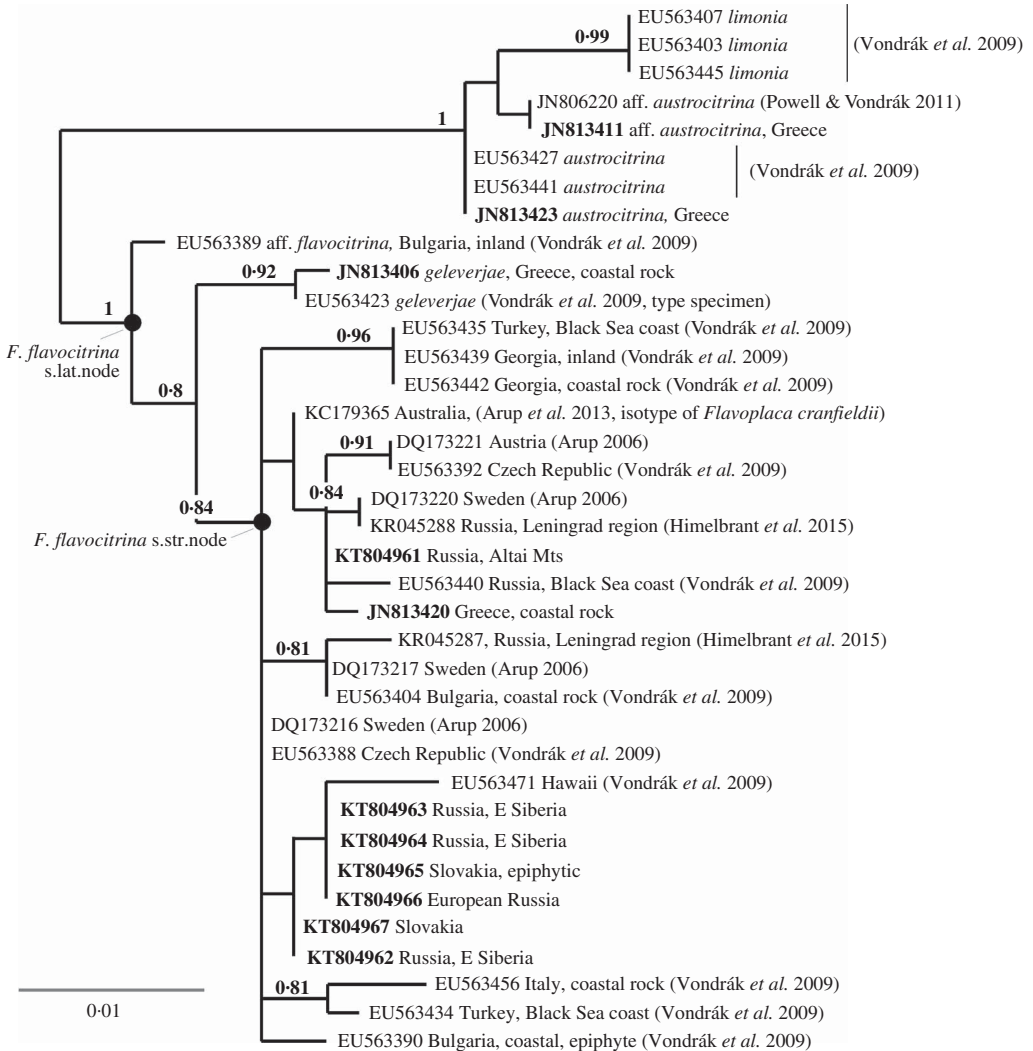


FIG. 3. Maximum likelihood ITS phylogeny of a section within *Flavoplaca* including *F. flavocitrina*. New sequences are in bold; bootstrap supports (BS > 0.7) are shown at nodes.

Syn. nov. *Caloplaca arizonica* H. Magn., *Bot. Not.* 1944: 69–70 (1944); type: USA, Arizona, Grand Canyon NP, Coconino Plateau, on *Juniperus monosperma*, 1926, E. & G. DuRoi 182/1 (UPS—holotype, not seen).—*Gyalolechia arizonica* (H. Magn.) Sochting et al. in Arup et al. (2013: 70).

Syn. nov. *Caloplaca juniperi* Poelt & Hinteregger, *Bibl. Lichenol.* 50: 150–152 (1993); type: Pakistan, Karakorum Mountains, Gilgit, Rakaposhi Range, Baghrot, N-facing flank opposite Sat, alt. 2600–2700 m (36°03'N, 74°35'E), on old *Juniperus*, 1991, J. Poelt (GZU—holotype, seen).

Syn. nov. *Caloplaca juniperina* Tomin, *Bot. Materialy, Notulae System. e Sect. Cryptog. Inst. Bot. Nomine V. L. Komarovii Acad. Sci. URSS* 9: 11–12 (1953); syntypes—Uzbekistan (Uzbecksaya SSR), northern slopes of Alay ridge, 1) Dzhaylayau Shayd, 26 vii 1948; 2) Dzhaylayau Mashelan', 10 vii 1950; 3) *ibid.*, 15 vi 1951; all syntypes collected by F. Shafeev (syntype 2 in LE seen and selected here as lectotype).—*Gyalolechia juniperina* (Tomin) Sochting et al. in Arup et al., *Nord. J. Bot.* 31: 71 (2013).

Syn. nov. *Caloplaca larcina* Rondon, *Rev. Bryol. Lich.* 32: 260 (1963); type: France, Hautes-Alpes, Ville-Vieille

en Queyras, alt. 1400 m, [44°41'36"N, 6°24'98"E], on wood of *Larix decidua*, 1957, Y. Rondon (G00288634—type not seen).

Syn. nov. *Caloplaca tarani* S. Y. Kondr. *et al.* in Kondratyuk *et al.*, *Acta Bot. Hungarica* 55: 48–52 (2013); type: Russia, Sakhalin Island, Smirnykhovskiy district, at the base of Mt Pogranichnaya, mixed deciduous and coniferous forest, on bark of *Ulmus laciniata*. 30.05.1997, A. A. Taran (SAKH—holotype, Fig. 4 in Kondratyuk *et al.* 2013).

(Fig. 2C, distribution map; Fig. 5B)

Gyalolechia epiphyta is diagnosed by its blastidiate/granulose thallus and absence of true soralia (Fig. 5B), but it is quite similar to the sorediate taxa *Gyalolechia persimilis*, *G. ussuriensis* and *G. xanthostigmoidea*. *Gyalolechia epiphyta* forms a supported clade in the ITS tree (Fig. 4). Variability among 12 sequences included in the ITS tree was detected in 19 positions, but this variability is rather randomly distributed; each sequence pair within the clade is more than 98.5% identical. The exception is KC179447 (from Greenland) which contains an indel of 21 bp length that is absent in other *Gyalolechia* species. The closest relative is *G. flavorubescens* s. lat. (including *G. xanthostigmoidea* and “*Caloplaca*” *subflavorubescens*) which forms a supported ITS clade with considerable internal variability (Fig. 4).

Gyalolechia epiphyta is widely distributed in the Arctic and temperate zones of the Northern Hemisphere. In continental regions it prefers steppes and dry forests. It is usually epiphytic or epixylic (often on *Juniperus*), but also epigeic or epibryic in rock crevices in arctic-alpine habitats or in steppes. Its epilithic occurrences are common in the Arctic. It is variable in thallus morphology; in particular, the size of vegetative diaspores (blastidia, granules) varies considerably, often within a single thallus. When it grows on bark, it is commonly fertile, but specimens from soil or bryophytes are usually sterile.

The wide geographical range of *G. epiphyta* and its occurrence in different climatic zones and on different substrata has resulted in it being described as new several times under different names. We consider

Gyalolechia arizonica synonymous with *G. epiphyta*. We have not seen its type specimen, but the ITS sequence of the specimen “T.H. Nash 38931 (C)” is placed within the *G. epiphyta* clade. We have also appraised several specimens of *G. arizonica* from Arizona (T. H. Nash 16456 in PRA-V, T. H. Nash 21219 in PRA-V, O. Breuss 27.7.1991 in W) and morphologically they fit collections of *G. epiphyta* with coarse granules. They were collected from *Juniperus*, a typical substratum for Asian populations of *G. epiphyta*.

We have seen type specimens of *Caloplaca juniperi* from northern Himalaya and *Gyalolechia juniperina* from Central Asia and we consider them conspecific with *G. epiphyta*. Rondon (1963) described *Caloplaca laricina* from the Alps; although we did not locate its type, we appraised the specimen collected by Rondon in 1963 from *Larix* wood in Basses-Alpes, Méolans (A. Vězda: *Lich. Sel. Exs.* 250 in PRA-V) and it has *G. epiphyta* morphology. The photograph showing thallus morphology in the description by Rondon (1963) also represents *G. epiphyta*. The protologue of *Caloplaca tarani* with a photograph of the type (Kondratyuk *et al.* 2013) indicates that this taxon described from the Far East is also *G. epiphyta*. We have assessed specimens collected from Kamchatka in the Far East (in the list below) that have *G. epiphyta* morphology but, unfortunately, repeated attempts to sequence these specimens were unsuccessful.

Despite *Gyalolechia epiphyta* having been described from many parts of the world under different names, we disagree with the synonymization of *G. xanthostigmoidea* (Räsänen) Søchting *et al.* in Arup *et al.* (2013: 72) with *G. epiphyta* proposed by Søchting & Tønsberg (1997). *Gyalolechia xanthostigmoidea*, described from New Brunswick in Canada (Räsänen 1933), is probably a distinct taxon more similar to *G. persimilis*/*G. ussuriensis*, because it forms soralia (Fig. 5F) and its ITS sequence (see Table 1 for specimen details) does not place it in the *G. epiphyta* clade (Fig. 4). Arctic-alpine, blastidiate specimens belong to *G. epiphyta*,

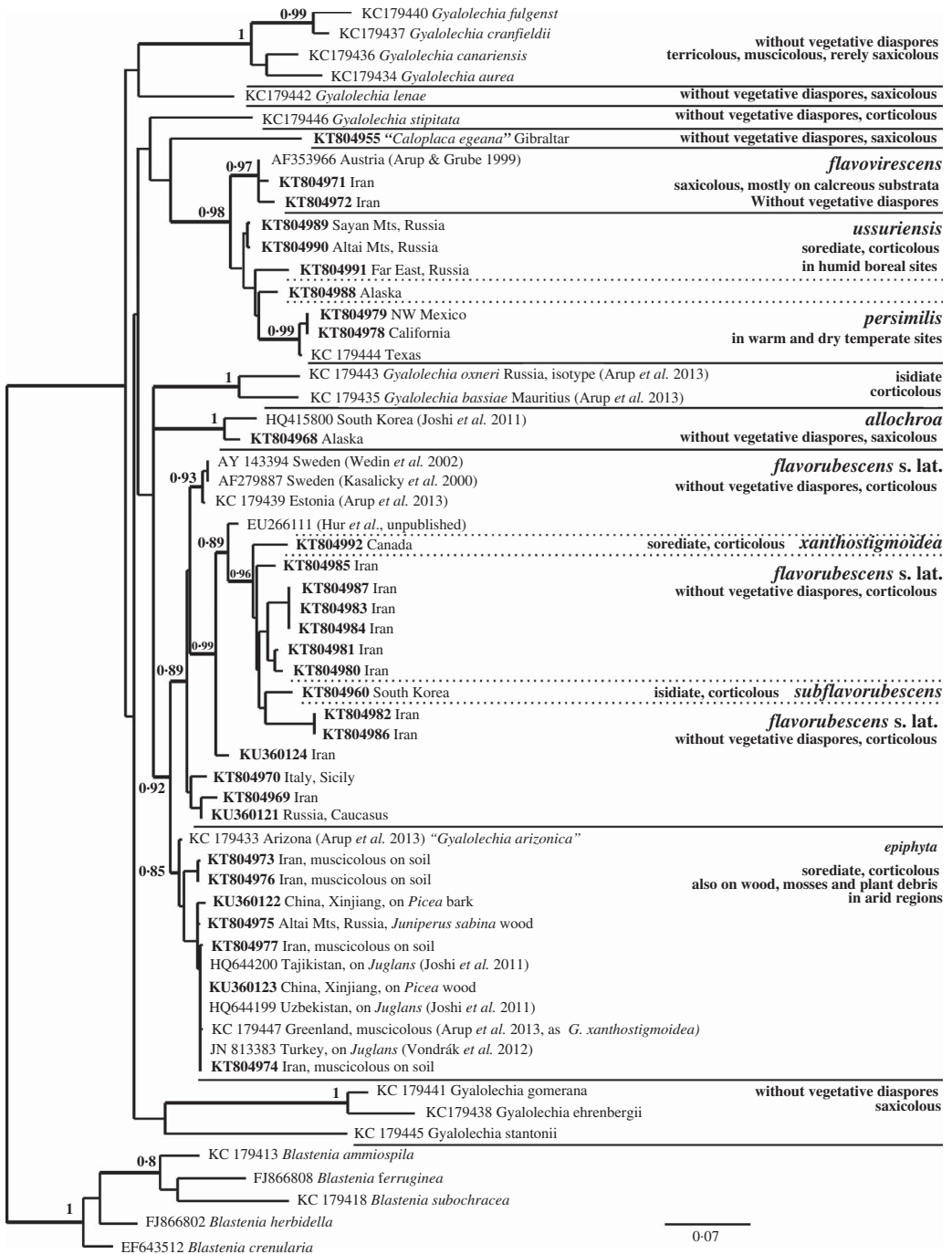


FIG. 4. Maximum likelihood ITS phylogeny of *Gyalolechia* showing positions of *G. epiphyta* and *G. ussuriensis*. New sequences are in bold; bootstrap supports (BS > 0.7) are shown at nodes.

as supported by the ITS sequence KC179447 from the Greenland specimen (Fig. 4), called “*G. xanthostigmoidea*” by Arup *et al.* (2013).

Russian specimens. Russia: Republic of Altai: Altai Mts, Kosh-Agach district, Kuray Steppe, limestone hills c. 4 km W of Kuray, alt. 1470–1680 m, on wood of *Juniperus sabina*, 2012, I. Frolov & J. Vondrák 12710 (PRA); *ibid.*, on mosses in limestone crevices, J. Vondrák 10319 (PRA); Kosh-Agach district, SE part of Kuray Ridge, NE of Chagan-Uzun Village, alt. 3000–3100 m, over mosses on limestone outcrop in alpine zone, 2012, I. Frolov & J. Vondrák 10353 (PRA). *Kamchatka Krai:* Ust'-Bol'sheretsk district, Praviy Kihchik River basin, alt. 250 m, 53-558224°N, 156-738025°E, on *Lonicera caerulea*, 2004, D. Himelbrant s. n. (PRA, ex LECB); *ibid.*, alt. 220 m, 53-581380°N, 156-683090°E, on *Populus suaveolens*, 2004, D. Himelbrant s. n. (PRA, ex LECB); *ibid.*, alt. 250 m, 53-548477°N, 156-697123°E, on *Populus suaveolens*, 2004, D. Himelbrant s. n. (PRA, ex LECB).

***Gyalolechia ussuriensis* (Oxner, S. Y. Kondr. & Elix) Vondrák comb. nov.**

Mycobank No.: MB 814537

Caloplaca ussuriensis Oxner *et al.* in Kondratyuk *et al.*, *Folia Cryptogamica Estonica* 48: 21–23 (2011); type: Russia, Primorsky Krai, in the vicinity of Okeanicheskaya [= Okeanskaya] railway station, on *Acer pseudosieboldianum*, 1927, A. Oxner (LE—isotype seen).

(Fig. 2C, distribution map; Fig. 5D)

Gyalolechia ussuriensis is a humid-temperate to boreal taxon described from the Far East (Kondratyuk *et al.* 2011). Although it is paraphyletic in our ITS tree with *G. persimilis* (Fig. 4), we consider these taxa to be distinct because *G. persimilis* is known from quite different conditions in dry, temperate regions of western North America (Wetmore 2004) (see Fig. 2C). ITS sequences of *G. ussuriensis* also differ from those of *G. persimilis* in 15 nucleotide positions. The sequence of the Alaskan *G. aff. ussuriensis* (KT804988 in Fig. 4) is short, without the ITS2 region. It has affinities with both *G. persimilis* and *G. ussuriensis*, but it also has unique nucleotides in seven positions. This specimen (KT80498) may represent another taxon because it has a more reduced thallus than either *G. persimilis* or *G. ussuriensis*

(compare Fig. 5C, *G. persimilis* and D, *G. ussuriensis* with E, *G. aff. ussuriensis*), and it has a rather specific ecology, growing on the bark of *Cupressus nootkatensis* in places not favourable for other lichens. (Note that all published specimens of *G. persimilis*/*G. ussuriensis* have been collected from broad-leaved trees.) *Gyalolechia xanthostigmoidea* (Fig. 5F) is morphologically very similar to both *G. persimilis* and *G. ussuriensis*, but it is geographically distinct (Fig. 2C) and its ITS sequence KT804992 is not related to either (Fig. 4).

Gyalolechia ussuriensis was known only from a small territory in the Russian Far East (Kondratyuk *et al.* 2011), but our records from the Salair Range, Sayan Mountains and Kamchatka suggest a much broader range in humid taiga forests in Siberia.

Russian specimens. Russia: Altai Krai: Zalesovsky district, Salair Range, headwaters of Berd' River at 20 km NE from the Kordon settlement, in *Abies sibirica* - *Populus tremula* forest, alt. 430 m, 54-4166°N, 85-1166°E, on *Populus tremula*, 2012, E. Davydov 11220 (ALTB). *Kamchatka Krai:* Mil'kovo district, Nature Reserve, S of Nikolka volcano, alt. 270 m, 55-0958°N, 159-9950°E, 2009, D. Himelbrant & I. Stepanchikova s. n. (LECB); *ibid.*, 55-1013°N, 159-9894°E, on *Populus suaveolens*, 2009, D. Himelbrant & I. Stepanchikova s. n. (LECB); SW slope of Tolbachik Volcano, c. 40–43 km SE of Kozyrevsk, alt. 683 m, 55-7317°N, 160-1974°E, on *Populus suaveolens*, 2006, D. Himelbrant s. n. (PRA, ex LECB). *Krasnoyarsk Krai:* West Sayan Mts, Minusinsk, Shushenskoe, 10 km SE of Tanzibey Village, forest in valley of Bolshoy Kebezh River, alt. 440 m, 53-0830°N, 93-0944°E, 2013, I. Frolov & J. Vondrák 13417 (PRA). *Primorsky Krai:* Terney district, Northern Sikhote-Alin', 30 km WNW of Amgu settlement, alt. 570 m, 45-8963°N, 137-3130°E, on bark, 2014, L. Yakovchenko & E. Davydov 11500 (ALTB).

Discussion

Work by the first author in and around the Mediterranean (Vondrák *et al.* 2009, 2012b) has previously suggested that many species of *Teloschistaceae*, for example those in *Flavoplaca* or the *Caloplaca xerica* group, have a narrow range. However, our recent data from Russia shows quite the opposite. Some species previously known only from Europe (e.g. *Caloplaca subalpina*) occur as far east as the Sayan Mountains in South Siberia. *Caloplaca ussuriensis*, formerly thought to be

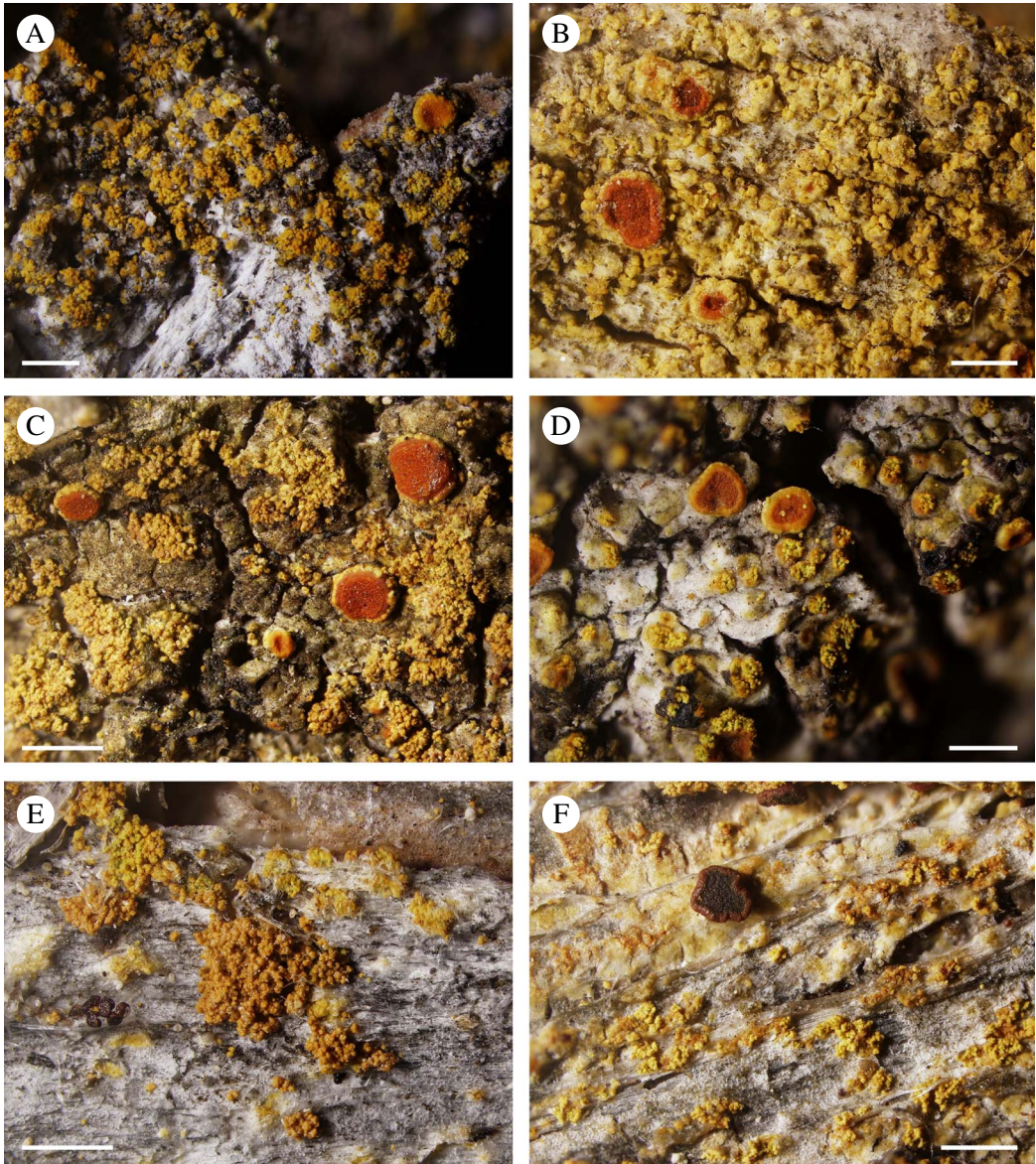


FIG. 5. A, *Calogaya bryochryson*, corticolous specimen from Altai Mts (ED11499, KT804937); B, *Gyalolechia epiphyta* with blastidiate thallus and without soralia from Tajikistan (hb. Halda 174, HQ644199); C, *Gyalolechia persimilis* with pale yellow thallus and bright yellow soralia from California (JV7486, KT804978); D, *Gyalolechia ussuriensis* with pale yellow thallus and bright yellow soralia from the Russian Far East (ED11500, KT804991); E, *Gyalolechia* aff. *ussuriensis* with an inconspicuous endophloedal thallus and bright yellow soralia from Alaska (TS38925, KT804988); F, *Gyalolechia xanthostigmoidea* from eastern Canada (TS32410, KT804992), a taxon morphologically similar to *G. persimilis*/*G. ussuriensis*. Scales: A–F = 0.5 mm.

restricted to the Far East, occurs from Kamchatka to the Altai Mountains in South Siberia. Other species (*Calogaya bryochryson*

and *Caloplaca isidiigera*) are almost circumpolar, and *Flavoplaca flavocitrina* may be almost cosmopolitan.

TABLE 3. *Modes of reproduction of species in large Teloschistaceae genera with distribution centres in northern Eurasia.*

Genus	Apothecia; no vegetative diaspores	Vegetative diaspores and apothecia	Source
<i>Athallia</i>	12	1	Vondrák (unpublished)
<i>Blastenia</i>	14	8	Vondrák (unpublished)
<i>Calogaya</i>	10	2	Gaya <i>et al.</i> 2011; Arup <i>et al.</i> 2013
<i>Caloplaca</i>	7	10	Šoun <i>et al.</i> 2011
<i>Flavoplaca</i>	10	15	Vondrák <i>et al.</i> 2009; Arup <i>et al.</i> 2013
<i>Xanthocarpia</i>	14	2	Vondrák <i>et al.</i> 2011

Note: species dispersed solely by vegetative diaspores are not known in these genera. Those producing both apothecia and vegetative diaspores (third column) can be without apothecia locally, but samples with apothecia are not exceptional. Large genera without modern taxonomic revision are not treated (e.g. *Pyrenodesmia* and *Variospora*)

Our earlier conclusion about narrow ranges is therefore not applicable to *Teloschistaceae* as a whole. It was biased by the particular characteristics of the Mediterranean region, where a combination of history, climate and geography has indeed resulted in a high degree of endemism (Blondel & Aronson 1999). In contrast, our more recent data support the fact that numerous species known from Europe or North America have been merely unrecognized in North Asia (Davydov & Printzen 2012).

Within species pairs (*sensu* Poelt 1970), lineages which reproduce vegetatively often have larger geographical ranges than their strictly sexual counterparts. Such contrasts in distribution can be found in, for example, *Hypogymnia* (Miądlikowska *et al.* 2011), *Letharia* (Kroken & Taylor 2001), and *Ramalina* (Rundel & Bowler 1976). In phylogenies of many genera within *Teloschistaceae*, lineages producing vegetative diaspores randomly alternate with strictly sexual lineages, that is, those with apothecia (and with or without pycnidia). This pattern was also observed, for example, by Buschbom & Mueller (2006) in a section of *Porpidia*. Species that display only vegetative distribution are very few (e.g. *Leproplaca* spp.), but most *Teloschistaceae* that reproduce vegetatively produce both apothecia and vegetative diaspores (Table 3), although apothecia are not common in some cases. The ability to produce both sexual and vegetative diaspores combines all the advantages of evolutionary plasticity with the ability to retain favourable allele combinations (e.g. Williams 1975; Maynard Smith 1978). Vondrák *et al.* (2013,

pages 710–711) reported some examples where species with vegetative diaspores have wider geographical ranges than their strictly sexual relatives and here we provide additional evidence. Six of the eight species discussed reproduce both sexually (via ascospores) and asexually (by soredia/blastidia/isidia and also by conidia) and have wider ranges than their strictly sexual relatives. These are as follows:

- 1) The continental and arctic-alpine *Calogaya bryochryson* is related to a clade containing strictly sexual *C. biatorina*, *C. ferrugineoides* and *C. polycarpoides* (Fig. 1) that are widely distributed in Central Asia, but they are absent from arctic and alpine habitats. Another related sexual species, *C. pusilla*, is probably restricted to western Eurasia: our easternmost records are from Turkey (unpublished data).
- 2) Within the genus *Caloplaca*, three of ten species with vegetative diaspores are distributed in Eurasia and also in North America. Strictly sexual species, 15 lineages of *C. cerina* s. lat. and *C. stillicidiorum* s. lat. in Šoun *et al.* (2011), are usually known from rather small territories, with the exception of the lineage “*stillicidiorum* (5)”.
- 3) Sexual species closely related to *Flavoplaca flavocitrina* are *F. havaasii*, *F. marina*, *F. maritima* and *F. ora* (Arup *et al.* 2013). All these have rather restricted geographical ranges.
- 4) *Gyalolechia epiphyta* is related to sexual *G. flavovirescens* s. lat. (Fig. 4), an entity that has a wide range, but which probably consists of several geographically more restricted taxa. *Gyalolechia ussuriensis* is related to the sexual *G. flavovirescens* known from western Eurasia, Greenland and North America, but its wide range has not been tested by molecular data, and so more species may exist within *G. flavovirescens*.

Evidence is accumulating that various *Teloschistaceae* species have wide geographical ranges. Many of them are

characterized by dual reproductive modes (producing sexual and asexual diaspores), but a few species without vegetative diaspores may also have broad ranges. The influence of reproductive mode on the fitness, competitive success and geographical range of lichens seems a promising area for research. The evolutionary grounds for switches between reproductive modes are also a related and promising topic for future study.

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SUPPLEMENTARY MATERIAL

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