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Taxonomy of selected groups of the genus *Caloplaca*

Ph.D. Thesis

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Annotation

The thesis deals with phylogeny, taxonomy and nomenclature of selected groups of the lichen genus *Caloplaca*. Particularly, the *C. cerina* group was closely investigated using molecular methods (ITS sequences), morphology and chemistry, based on material from Europe, and to some extent also from North America and western Asia. This approach resulted in the description of three new species (*C. sterilis*, *C. subalpina*, *C. thracopontica*), and detected an unexpected richness of lineages. Nomenclature, taxonomy, morphology and ecology of *C. aurantia* and *C. flavescens* from the *C. aurantia* group were studied in detail, including selection of the neotype of the former species. Their distribution was reviewed for the territory of the Czech Republic. Poorly known taxon *C. aurantiomurorum* from Algeria was lectotypified and synonymized with *C. aurantia*. Apart from the two groups, *C. phlogina* and *C. scythica*, differing partly in thallus colour and distinctly in distribution, were examined using both molecular (ITS sequences) and phenotypic data and found to be conspecific.

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Jaroslav Šoun

Author's contribution to the papers

I The author obtained all molecular and morphological data except most data for *Caloplaca sterilis*, performed all analyses except HPLC, collected a part of herbarium material used, and wrote the first draft of the ms. and edited the co-authors' amendments and revisions. Overall author's contribution is c. 90 %.

II The author performed the molecular analysis, participated in the fieldwork and contributed to writing the paper. Overall author's contribution is c. 30 %.

III This paper is based on the author's master thesis. The author (JŠ) added some new data and wrote the first draft of the ms. and edited the co-author's amendments and revisions. Overall author's contribution is c. 90 %.

V The author participated in obtaining the data and writing the paper. Overall author's contribution is c. 40 %.

VI The author performed the molecular and phylogenetic analyses and prepared them for publication. Overall author's contribution is c. 30 %.

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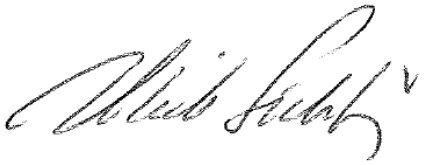

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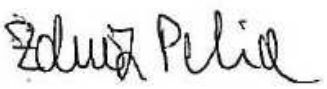

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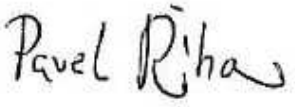

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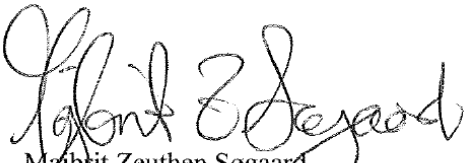

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Content

Introduction

Taxonomy of lichens – unique symbiotic associations between a filamentous fungus and at least one photosynthetic organism – is passing through a fast progress at this time. New insights from molecular data are considerably changing our understanding of Ascomycota, whose lichen-forming fungi are the indivisible part (e.g. Printzen 2010). Except a few representatives of lichens which belong to Basidiomycota. This thesis is devoted to several groups of one of the most species-rich genera in lichens, the genus *Caloplaca*.

According to the last outline of Ascomycota (Lumbsch & Huhndorf 2007), the genus *Caloplaca* belongs to the family Teloschistaceae, which is along with Letrouitiaceae, Megalosporaceae and Physciaceae included in the order Teloschistales (subclass Lecanoromycetidae, class Lecanoromycetes, subphylum Pezizomycotina). Close alliance of the large family Physciaceae was expected by several older authors, fascinated by many cases of their parallel phenotypic development as evidenced e.g. by the superficial similarity of *Caloplaca carphinea* (Teloschistaceae) and *Dimelaena oreina* (Physciaceae). Physciaceae (incl. Caliciaceae) was firstly assigned into Teloschistales by Miadlikowska et al. (2006) in a separate suborder Physciineae with remaining families sorted in Teloschistineae. For more detailed review of families' classification see Kärnefelt (1989). There is no single phenotypic character shared by all genera in the order but most representatives of the Teloschistaceae and Physciaceae possess polar diblastic ascospores.

A decade before the start of molecular studies on Teloschistales, Kärnefelt (1989) in his throughout revision of the order attempted to implement modern phylogenetic analyses using morphological data. His results were naturally different from following molecular phylogenies (Gaya et al. 2008b), but can serve as an example of limits of morphological taxonomy. Twelve genera were accepted in the family Teloschistaceae in the last outline of ascomycetes (Lumbsch & Huhndorf 2007): *Caloplaca*, *Cephalophysis*, *Fulgensia*, *Huea*, *Ioplaca*, *Josefpoeltia*, *Seirophora*, *Teloschistes*, *Xanthodactylon*, *Xanthomendoza*, *Xanthopeltis* and *Xanthoria*. Some other recently circumscribed xanthorioid genera *Oxneria*, *Rusavskia*, *Xanthoanaptychia* (Kondratyuk & Kärnefelt 2003), distinguished only by phenotypic characters, were not accepted in that treatment. Three new genera *Jackelixia*, *Ovealmbornia*, *Xanthokarrooa* were recently described in a phylogenetic study of xanthorioid lichens by Fedorenko et al. (2009), but they have not been accepted in the recent notes to the ascomycete systematics (Lumbsch & Huhndorf 2009). Detailed review of generic classification history in Teloschistales provided Gaya et al. (2008b).

As in other lichen groups, the taxonomic research in Teloschistaceae progresses from two opposite directions. Several phylogenetic works tried to find borders among the genera within the family (Fedorenko et al. 2009; Gaya et al. 2003, 2008b; Kasalicky et al. 2000; Søchting & Lutzoni 2003; Søchting et al. 2002), while the other group of studies focused at the species delimitation in difficult species aggregates. Nevertheless, none of these studies involved representatives of all accepted genera. The most exhaustive sampling for phylogenetic studies were conducted by Gaya et al. (2008b) using one locus (ITS) and focusing particularly at *Caloplaca*, and by Fedorenko et al. (2009) using two loci (ITS, mtSSU), and focusing on xanthorioid taxa. Polyphyly of all traditionally recognized genera *Caloplaca*, *Fulgensia* and *Xanthoria* was detected in these studies, finding the distinguishing morphological characters to be homoplastic, and implying thus the need for a complete generic reassessment of Teloschistaceae or even Teloschistineae. Although the monophyly of some xanthorioid genera was recently proven by molecular data and some new genera were described (Fedorenko et al. 2009), countless members of the polyphyletic *Caloplaca* still remain to be accommodated, awaiting ultimate large-scale multi-gene study of the suborder and final generic consensus

among lichenologists studying Teloschistineae. The first step to multi-gene study was accomplished by Gaya et al. (2008a), reporting selecting new generation of genes.

Caloplaca is far the most species-rich genus within Teloschistineae, and even one of the richest within lichen-forming fungi, comprising an estimated 800 to 1000 species (Arup & Åkelius 2009). Species richness of *Caloplaca* is the biggest in non-tropic parts of the world. The genus was never monographed as a whole. However, many taxonomic studies of the genus treating a particular group and/or region have been published, but only some of the recent ones were done using molecular methods (see above). The best explored part is Europe, irrespective of the fact that new species are described from that territory almost every year (Arup 2006b, c; Gaya 2009; Khodosovtsev et al. 2002, 2003; Kondratyuk et al. 2006; Navarro-Rosinés et al. 2000a, b; **paper I**; **paper II**; Roux et al. 2009; Søchting & Stordeur 2001; Søchting et al. 2007; Tretiach & Muggia 2006; van den Boom & Rico 2006; Vondrák & Hrouzek 2006; Vondrák et al. 2008, 2009c). Given this situation in well-explored Europe, it is not hard to imagine what could be found by specialists in other parts of the world. *Caloplaca* in North and Central America is much better known thanks to series of recent works of C. Wetmore and U. Arup, and some other papers (e.g. Arup 1995, Breuss 2001; Nimis et al. 1994; Søchting 2004; Wetmore 1994, 1996, 2001, 2003, 2004a, b, 2007, 2009; Wetmore & Kärnefelt 1998). Polar regions are also quite well explored (e.g. Hansen et al. 1987; Søchting & Olech 1995; Søchting et al. 2008). Asia is still not well investigated, but there are some recent comprehensive treatments (e.g. Khodosovtsev et al. 2004; Poelt & Hinteregger 1993) and on-going research is carried out mainly in India (e.g. Joshi & Upreti 2006, 2007; Joshi et al. 2009). The research on *Caloplaca* in Australia is also in fast progress (Kärnefelt & Kondratyuk 2004; Kondratyuk et al. 2007a, b, 2009a, b, 2010). Africa and South America are still the least investigated continents, although probably host an extensive amount of the *Caloplaca* diversity. Thus the world-wide *Caloplaca* monograph is so far unforeseeable.

Phylogenetic studies using molecular data (ITS or rarely mtSSU sequences) on particular groups of species within the genus *Caloplaca* started to appear at the end of the last century. Molecular data were firstly used by Arup & Grube (1999), who revealed where sterile *Lecanora demissa* really belonged. Muggia et al. (2008), Tretiach et al. (2003) and Vondrák et al. (2008) studied and also newly described some black-fruited species from the section *Pyrenodesmia*. Corrected phylogenetic position of the *C. aurantia* group was presented by Søchting & Arup (2002). Several species from the *C. ferruginea* group were studied by Arup & Åkelius (2009) and Arup et al. (2007). Søchting et al. (2007) described new species within the *C. lactea* group exceptionally using mtSSU sequences. The first newly described Asian species supported by DNA data was *C. lenae* by Søchting & Figueras (2007). In the **paper VI** molecular data and phenotype examinations convinced us that two previously distinguished species *C. phlogina* and *C. scythica*, believed to differ in colour of soredia and geographical distribution, are conspecific. The *C. citrina* group (Arup 2006b; Vondrák et al. 2009c) and the *C. holocarpa* group (Arup 2009) are the only ones, which taxonomy were studied by molecular data, at least in restricted regions (Scandinavia and Black Sea region respectively). The *Caloplaca cerina* group has usually been taxonomically used in a broader morphological sense (Clauzade & Roux 1985; Hansen et al. 1987; Wetmore 1996, 1997, 2004b, 2007b), but in the **paper I** and **paper II** is treated for the first time in a narrower sense as a monophyletic group of species around *C. cerina*. The **paper I** presents phylogeny and revised taxonomy of the group in Europe and in some extent also North America and western parts of Asia. Results show unexpected richness of lineages only partly supported by morphology and pointing out on the problem with cryptic or semi-cryptic species (sensu Vondrák et al. 2009c). First data about the phylogeny of the group was published in the **paper II**, where two new species *C. subalpina* and *C. thracopontica* were described. DNA data were several times used to help in determination of peculiar *Caloplaca* species (Arup 2006a; Rosato & Arup 2010; Vondrák et al.

2009a, b, 2010). The standard use of molecular methods in the taxonomy on the species level, with increasing accessibility of them, is anticipated. Nevertheless, another problem has arisen with deeper view into species phylogeny – cryptic or semi-cryptic species and species delimitation in general (see e.g. Crespo & Pérez-Ortega 2009; Del-Prado et al. 2010; Grube & Kroken 2000; **paper I**; Vondrák et al. 2009c).

Xanthoria has been also studied by molecular methods. Franc & Kärnefelt (1998), Lindblom & Ekman (2005), Lindblom & Søchting (2008) investigated differences between closely related *Xanthoria* species. Population genetics of *X. elegans* was studied by Dyer & Murtagh (2001) and Murtagh et al. (2002) and that of *X. parietina* by Honegger et al. (2004), Lindblom (2009), Lindblom & Ekman (2006, 2007) at different spatial scales. Widespread and conspicuous *X. parietina* has been used as a model organism in a wide spectrum of studies on developmental anatomy, physiology, element accumulation, chemistry, cultivation, reproduction etc., for examples see Nash (2008). The genome of *X. parietina* will be one of the two going to be sequenced in lichen-forming fungi (Lutzoni & Miadlikowska 2009).

A half of the thesis is devoted to the *Caloplaca aurantia* group, a small but distinct group of lobate, saxicolous species unique within the genus by their lemon-shaped ascospores. The group was studied recently by various authors (e.g. Gaya 2009; Søchting & Arup 2002; Śliwa & Wilk 2008; Wetmore & Kärnefelt 1998) and five species were accepted: *C. aurantia*, *C. aegaea*, *C. flavescens*, *C. fuerteventurae* and *C. thallincola*. Confusing situation with respect to their distribution and distinguishing between *C. aurantia* and *C. flavescens* in the Czech Republic was elucidated in the **paper III**. A neotype of *C. aurantia* was selected and historical circumstances associated with this name were discussed in the **paper IV**. In the **paper V,** the identity of *C. aurantiomurorum* as another potential member of the group was studied. The type exsiccate revealed to be a mixture of different species including *C. aurantia*, *C. saxicola* and *Candelariella senior*. The lectotype of *C. aurantiomurorum* was selected and the name was put into synonymy of *C. aurantia*.

Contents of lichen substances, mainly anthraquinones, in Teloschistaceae and especially in the genus *Caloplaca* have been studied for a long time (e.g. Bohman 1969, Santesson 1970, Søchting 1997, 2001). Formerly TLC and nowadays HPLC or HPTLC have been employed. Their assessment became a standard part of recent taxonomical treatments (e.g. Arup 2006b; **paper I**; **paper II**; **paper VI**; Søchting & Fröberg 2003; Vondrák & Hrouzek 2006).

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Paper I

Taxonomy and phylogeny of the *Caloplaca cerina* group in Europe

Šoun, J., Vondrák, J., Søchting, U. Hrouzek, P., Khodosovtsev, A. & Arup, U. (2011) *Lichenologist* (accepted)

Using ITS nrDNA sequence data, the *Caloplaca cerina* group (*Teloschistaceae*) is defined here as a monophyletic, but internally richly branched lineage. The group is also characterized by a combination of morphological and anatomical characters. Its internal lineages are supported by phenotypic characters in addition to ecology and distribution. Within the large *C. cerina* group, we have found at least 20 phylospecies in the temperate zone of the Northern Hemisphere. Two species complexes do not produce any vegetative diaspores; the polyphyletic, corticolous *Caloplaca cerina* s. lat. (six separated cryptic or semi-cryptic species) and the monophyletic *C. stillicidiorum* s. lat. that grows mainly on plant debris, small shrubs and bryophytes and consists of at least four internal lineages. All lineages producing vegetative diaspores (soredia, blastidia, isidia or lobules) are phenotypically characteristic and represent fairly easily distinguishable species; *C. chlorina*, *C. isidiigera*, *C. monacensis*, *C. subalpina*, *C. thracopontica*, *C. turkuensis* and *C. ulmorum*. Only the North American sorediate *C. pinicola* possibly represents an aggregate of species. *Caloplaca sterilis* is described as a new species. A key to the phenotypically distinguishable species is provided here.
Lectotypes are designated here for *C. albolutea*, *Caloplaca cerina* f. *coronulata* and for *C. monacensis*. The Australian *C. hanneshertelii* belongs to this group, but this and other possible species from the Southern Hemisphere are not treated here in detail. Some species traditionally placed into the *C. cerina* group due to their similar morphology are excluded here on the basis of our phenotype examinations and molecular data. *Caloplaca albolutea*, *C. mydalaea* and *C. virescens* are intricate taxa and their identities still remain unclear.

Skupina *Caloplaca cerina* (*Teloschistaceae*) je pomocí molekulárních dat (sekvence nrDNA ITS) definována jako monofyletická, vnitřně bohatě rozvětvená linie. Dále je skupina charakterizována kombinací morfologických a anatomických znaků. Kromě ekologie a rozšíření jsou její vnitřní linie podpořeny fenotypickými znaky. V rámci této velké skupiny jsme v mírném pásu severní polokoule nalezli nejméně 20 fylogenetických druhů. Dva komplexy druhů netvoří žádné vegetativní diaspory; polyfyletická, kortikolní *C. cerina* s. lat. (šest samostatných kryptických nebo semikryptických druhů) a monofyletická *C. stillicidiorum* s. lat., která roste hlavně na zbytcích rostlin, keříčcích a meších, a obsahuje nejméně čtyři linie. Všechny linie tvořící vegetativní diaspory (sorédie, blastídie, isídie nebo lalůčky) jsou fenotypicky charakteristické a představují dosti snadno rozlišitelné druhy; *C. chlorina*, *C. isidiigera*, *C. monacensis*, *C. subalpina*, *C. thracopontica*, *C. turkuensis* a *C. ulmorum*. Pouze severoamerická sorediózní *C. pinicola* pravděpodobně představuje agregát druhů. *C. sterilis* je popsána jako nový druh. V práci je uveden klíč k fenotypicky rozlišitelným druhům.
Stanoveny jsou lektotypy *C. albolutea*, *C. cerina* f. *coronulata* a *C. monacensis*. Do této skupiny také náleží australský druh *C. hanneshertelii*, který ale není spolu s dalším potenciálně novým druhem z jižní polokoule zpracován. Některé druhy, řazené tradičně pro svou podobnou morfologii do skupiny *C. cerina*, jsou zde na základě fenotypových a molekulárních dat vyloučeny. *C. albolutea*, *C. mydalaea* a *C. virescens* jsou problematické taxony a jejich identita zůstává nevyjasněna.

Letter of acceptance

17-Oct-2010

Dear Mr. Šoun:

It is a pleasure to accept your manuscript entitled "Taxonomy and phylogeny of the Caloplaca cerina group in Europe" in its current form for publication in The Lichenologist.

Thank you for your fine contribution. We look forward to your continued contributions to the Journal.

Yours sincerely

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Paper II

***Caloplaca subalpina* and *C. thracopontica*, two new saxicolous species from the *Caloplaca cerina* group (*Teloschistales*)**

Vondrák, J., Šoun, J., Hrouzek, P., Říha, P., Kubásek, J., Palice, Z. & Søchting, U. (2008) *Lichenologist* 40: 375–386.

Caloplaca subalpina Vondrák, Šoun & Palice and *C. thracopontica* Vondrák & Šoun are described here as new to science. The former is a sorediate, often sterile, saxicolous species inhabiting subalpine base-rich overhanging rocks in European mountains; the latter grows on maritime cliffs of the Black Sea and is conspicuous by the lobules and pustules which are usually present on its thallus and by its apothecia which are typically large and abundant. The placing of the two species in the *C. cerina* group was confirmed by molecular studies using nrDNA ITS sequences. The chemosyndromes of both new species correspond to chemosyndrome A, which is in accordance with their position in the *C. cerina* group. A key to the saxicolous species of the *C. cerina* group is provided.

V příspěvku jsou pro vědu nově popsány druhy *Caloplaca subalpina* Vondrák, Šoun & Palice a *C. thracopontica* Vondrák & Šoun. První z nich je sorediózní, často sterilní, saxikolní druh, rostoucí na subalpínských bazických převislých skalách v evropských horách. Druhý roste na přímořských útesech Černého moře a je nápadný jak svými lalůčky a puchýřky, které jsou na jeho stélce obvykle přítomny, tak svými apotécii, která jsou typicky velká a početná. Umístění těchto dvou druhů do skupiny *C. cerina* bylo molekulárně potvrzeno použitím sekvencí nrDNA ITS. Chemosyndromy obou nových druhů se shodují s chemosyndromem A, což je v souladu s jejich umístěním ve skupině *C. cerina*. Uveden je klíč k saxikolním druhům skupiny *C. cerina*.

Paper III

***Caloplaca aurantia* and *Caloplaca flavescens* (*Teloschistaceae*, lichen-forming fungi) in the Czech Republic; with notes to their taxonomy and nomenclature**

Šoun, J. & Vondrák, J. (2008) *Czech Mycology* 60: 275–291.

A revision of *Caloplaca aurantia* and *C. flavescens* in the Czech Republic is provided. Both species are confirmed from the territory; their distribution is reviewed and their ecological demands commented upon. Morphological investigations have confirmed the structure of the cortex and shape and colour of the lobes as the best diagnostic characters of both species; the thickness of the cortex has been found to be another useful character. Nomenclatural confusions regarding both species are discussed and clarified.

V příspěvku je zpracována revize druhů *Caloplaca aurantia* a *C. flavescens* v České republice. Oba druhy jsou z tohoto území potvrzeny. Zrevidováno je jejich rozšíření a okomentovány ekologické nároky. Studium jejich morfologie potvrdilo, že struktura kůry spolu s tvarem a barvou laloků jsou nejlepšími rozlišovacími znaky mezi oběma druhy. Dalším užitečným rozlišovacích znakem byla shledána tloušťka kůry. Diskutovány a vyjasněny jsou nomenklatorické zmatky týkající se obou druhů.

Paper IV

Typification and taxonomy of *Caloplaca aurantia*

Šoun, J. (2010) *Mycotaxon* 111: 331–336.

The sample from the Arnold's Lichenes Exsiccati no 989: *Physcia aurantia*, deposited in M, is designated to serve as neotype of *Caloplaca aurantia*. The sample appears to be a topotype of *C. aurantia*. An overview is presented of the complicated history of the application and misuse of the name. Old literature references to *C. aurantia* should be confirmed by herbarium material, since the species was often confused with *C. flavescens*.

Položka Arnoldových Lichenes Exsiccati no 989: *Physcia aurantia*, uložená v M, je vybrána jako neotyp *Caloplaca aurantia*. Položka se jeví být topotypem *C. aurantia*. Prezentován je přehled komplikované historie používání tohoto jména, včetně nesprávného. Starší literární údaje o *C. aurantia* by měly být potvrzeny herbářovým materiálem, protože tento druh byl často zaměňován za *C. flavescens*.

Paper V

An appraisal of the syntype material of *Caloplaca aurantiomurorum* (*Teloschistaceae*, lichenized fungi)

Vondrák, J. & Šoun, J. (2006) *Mycotaxon* 97: 67–71.

Sample no. 54 of Flagey: Lichenes Algerienses exsiccati represents the syntype of *Placodium aurantiomurorum* (≡ *Caloplaca aurantiomurorum*). However, the samples of this exsiccatum distributed to FH, H, M, PC and UPS contain different lichen species. The lectotype of *P. aurantiomurorum* is selected here (sample in UPS) and this name is treated as a synonym to *Caloplaca aurantia*. In this exsiccatum, *Candelariella senior* has been identified (in H, FH, and PC), which is reported here as a new species to Algeria. The known distribution of *Can. senior* is described.

Položky číslo 54 z Flageyova exsikátu Lichenes Algerienses exsiccati představují syntyp *Placodium aurantiomurorum* (≡ *Caloplaca aurantiomurorum*). Položky tohoto exsikátu, umístěné v FH, H, M, PC a UPS, nicméně obsahují různé druhy lišejníků. Vybrán je zde lektotyp *P. aurantiomurorum* (položka v UPS) a toto jméno je synonymizováno s *Caloplaca aurantia*. V exsikátu (v H, FH a PC) byla identifikována také *Candelariella senior* a je zde zaznamenána jako nový druh pro Alžírsko. Popsáno je známé rozšíření *Can. senior*.

Paper VI

***Caloplaca phlogina*, a lichen with two faces; an example of infraspecific variability resulting in the description of a redundant species**

Vondrák, J., Šoun, J., Søgaard, M. Z. & Søchting, U. & Arup, U. (2010) *Lichenologist* 42: 685–692.

Caloplaca phlogina is shown here to have two kinds of soralia, yellow soralia with anthraquinones versus whitish or white-green soralia lacking pigments. Both kinds are present,

growing side by side, in some localities in Scandinavia, but yellow soralia appear to be more common. In contrast, the populations from halophilous shrubs on the Black Sea coast have predominantly white soralia, and they were described as a separate species, *C. scythica*. A single collection from Chile also has white soralia. Molecular data and phenotype examinations convinced us that Scandinavian and Black Sea populations are conspecific. We consider the North European, phenotypically variable population as a source for the Black Sea population which is ecologically and phenotypically more uniform.

V příspěvku je ukázáno, že *Caloplaca phlogina* má dva druhy sorálů: žluté sorály s antrachinony a bělavé nebo zelenobílé sorály postrádající pigmenty. Na některých lokalitách ve Skandinávii rostou oba druhy vedle sebe, ale žluté sorály se zdají být hojnější. Populace ze slanomilných keříků z černomořského pobřeží mají oproti tomu převážně bílé sorály a byly popsány jako samostatný druh, *C. scythica*. Jediný sběr z Čile má také bílé sorály. Molekulární a fenotypová data nás přesvědčila, že skandinávské a černomořské populace jsou stejným druhem. Severoevropskou, fenotypicky variabilní populaci, uvažujeme jako zdroj pro ekologicky i fenotypicky jednotvárnější černomořskou populaci.