

# *Thalloidima squamatum* comb. nov. – a distinct and common but overlooked lichen in Europe

Martin Westberg<sup>1\*</sup>, Stefan Ekman<sup>1</sup>, Laura Briegel-Williams<sup>2</sup>, Samantha Fernandez-Brime<sup>3</sup>, Mats Wedin<sup>3</sup>, Einar Timdal<sup>4</sup>

## Article info

Received: 6 Jul. 2023  
Revision received: 28 Sept. 2023  
Accepted: 3 Oct. 2023  
Published: 29 Dec. 2023

## Associate Editor

Martin Kukwa

**Abstract.** The new combination *Thalloidima squamatum* is proposed for a morphologically and phylogenetically distinct species, until now included within the variation of *T. sedifolium*. Compared to *T. sedifolium*, the species is characterized by its larger squamules and apothecia, shorter ascospores, the pale color of the excipulum, and its habitat growing on moss cushions over calcareous rock or directly on rock rather than on soil. Most of the material studied originates from Norway and Sweden, but specimens are also reported from Austria, Croatia, Germany, Greenland, Italy, Poland, Russia, Scotland and Switzerland.

**Key words:** *Ascomycota*, ITS, *MCM7*, mrSSU, nrLSU, phylogeny, *Ramalinaceae*, *Toninia*

## Introduction

The genus *Thalloidima* was described by Massalongo (1852), who originally included four species in the genus; *T. vesiculare* (Hoffm.) A. Massal. (= *T. sedifolium* (Scop.) Kistenich et al.), *T. candidum* (Weber) A. Massal., *T. mamillare* (Gouan) A. Massal. (= *Porpidinia tumidula* (Sm.) Timdal) and *T. conglomeratum* (Ach.) A. Massal. (= *Psorinia conglomerata* (Ach.) Gotth.Schneid.). *Toninia* was described in the same work, and throughout most of the subsequent taxonomic history, *Thalloidima* was considered a synonym of *Toninia* (see Timdal 1992 for a historical review). However, *Toninia* in the sense of major monographic treatments and checklists (e.g., Poelt 1969; Baumgärtner 1979; Hawksworth et al. 1980; Egan 1987; Timdal 1992; Santesson et al. 2004) was shown already by Ekman (2001), based on ITS sequence data, to be polyphyletic. The phylogeny and generic subdivision of the *Ramalinaceae* was studied thoroughly by Kistenich et al. (2018) and *Toninia* was split between several genera, among them *Thalloidima*, comprising a monophyletic clade including the type species *T. sedifolium*. In its current circumscription, *Thalloidima* comprises 17 species, twelve of which have had their position in *Thalloidima* confirmed by DNA sequence data (Kistenich et al. 2018).

Morphologically, the genus is characterized by mostly 1-septate, fusiform ascospores, a grey epithecium reacting K+ violet and N+ violet (except *T. toninianum* (A. Massal.) A. Massal.: olivaceous brown to green, K–), and a squamulose thallus (except two non-lichenized species) that in many species has a white pruina of calcium oxalate crystals. Most species, perhaps all, begin their life-cycle on cyanolichens or remain lichenicolous (Timdal 1992; Kistenich et al. 2018).

*Thalloidima sedifolium* is a well-known and widespread species with an almost worldwide distribution occurring on all continents except Antarctica (Timdal 1992). It is a characteristic component of biological soil-crust communities on calcareous ground, e.g., the widely distributed “Bunte Erdflechten-Gesellschaft” (colored soil lichen community, Reimers 1950, 1951), where it grows together with species like *Cladonia symphylicarpa* (Flörke) Fr., *Psora decipiens* (Hedw.) Hoffm., *Squamarina cartilaginea* (With.) P. James, *S. lentigera* (Weber) Poelt, *Gyalolechia bracteata* (Hoffm.) A. Massal., *G. fulgens* (Sw.) Søchting et al., and several different cyanobacterial lichens, e.g., *Enchylium tenax* (Sw.) Gray, *Scytinium pulvinatum* (Hoffm.) Otálora et al., and *S. schraderi* (Bernh.) Otálora et al. etc. The species was known for a long time under the name *Toninia coeruleonigricans* (Lightf.) Th.Fr., based on the now rejected name *Lichen coeruleonigricans* Lightf., the type of which was shown by Timdal (1992, p. 121) to belong to *Fuscopannaria praetermissa* (Nyl.) P.M. Jørg. *Thalloidima sedifolium*, as currently understood (Timdal 1992), is a variable species in many characters, e.g., thallus color (pale green or brown to dark green or brown), size of thallus and apothecia, pruina

<sup>1</sup> Museum of Evolution, Norbyvägen 16, SE-752 36 Uppsala, Sweden (Westberg, ORCID: 0000-0002-8346-0322)

<sup>2</sup> University of Applied Sciences Kaiserslautern, Department Integrative Biotechnology, Carl-Schurz-Straße 10-16, 66953 Pirmasens, Germany

<sup>3</sup> Swedish Museum of Natural History, Department of Botany, P.O. Box 50007, SE-104 05 Stockholm, Sweden

<sup>4</sup> Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway

\* Corresponding author e-mail: martin.westberg@em.uu.se

(lacking to entirely pruinose), coloration of proper exciple (medium to dark brown) and hypothecium (medium brown to dark reddish brown) and in ascospore size and shape (broadly to narrowly fusiform,  $12\text{--}24 \times 3\text{--}5 \mu\text{m}$ ). A number of described names are listed as synonyms of *T. sedifolium* (Timdal 1992). In addition, there are several similar species, e.g., *T. albilabrum* (Dufour) Flagey, *T. opuntioides* (Vill.) Kistenich et al. and *T. physaroides* (Opiz) Opiz that are all easy to confuse with *T. sedifolium* and probably are, at least in some regions, overlooked.

During fieldwork in 2012–2013 within an international project on soil crust communities in Europe (see Büdel et al. 2014), we became aware of a possibly distinct species within the traditional delimitation of *T. sedifolium* (Westberg et al. 2016). This was corroborated by Kistenich et al. (2018, see Suppl. Fig. S2), who showed that *T. sedifolium* specimens were divided between two clades in a phylogenetic tree based on ITS sequences, one corresponding to *T. sedifolium* s. str. and the other a hitherto overlooked species of *Thalloidima*. We propose the new combination *T. squamatum*, based on *Psora squamata* Hoffm., a replacement name for *Lichen squamatus* Dicks. that was listed as a synonym of *T. sedifolium* by Timdal (1992).

## Materials and methods

### Material

Specimens were collected in the field during excursions in Austria, Germany, Norway, Spain, Sweden, and Switzerland. Herbarium collections have been studied primarily in O, S, and UPS. Relevant type material was borrowed from GOET, H and M.

### Morphology and anatomy

Specimens were initially studied under a dissecting microscope. Measurements of finer anatomical structures (e.g., ascospores and paraphyses) were made under a light microscope of material mounted in water, using an oil-immersion lens, with a precision of  $0.5 \mu\text{m}$ . Only well-developed ascospores lying outside the asci were measured. To examine color reactions of pigments, we used a 10% solution of KOH (abbreviated K) and a 10% solution of  $\text{HNO}_3$  (abbreviated N). Ascospore dimensions are presented in the format “(minimum value observed–) mean value  $\pm$  standard deviation (–maximum value observed)” with n being the number of measurements.

### Chemical analyses

The secondary metabolites were analyzed using HPTLC and standard TLC, following the method described by Arup et al. (1993) and Orange et al. (2010), in both cases using solvent systems C. We refer to different chemotypes; 0 (acid deficient), C (unidentified depside) and Y (unidentified terpenoid), as defined by Timdal (1992).

### DNA extraction, amplification, and sequencing

DNA was extracted from recently collected material or from dried herbarium specimens (Table 1). Total DNA was extracted using the Qiagen DNEasy Plant Minikit, according to the manufacturer’s instructions. Selected markers for this study were the internal transcribed spacer complete repeat (ITS) and the large subunit of the nuclear ribosomal DNA (nrLSU), the small subunit of the mitochondrial ribosomal DNA (mrSSU), and the DNA replication licensing factor mini-chromosome maintenance complex component 7 (*MCM7*). The primers ITS1f (Gardes & Bruns 1993) and LR3 (Vilgalys & Hester 1990) were used to amplify and sequence the ITS and a fragment of  $\sim 600$  bp of the nrLSU. For the neotype of *T. sedifolium*, ITS4 (White et al. 1990) was used instead of LR3. The mrSSU was amplified and sequenced using the primers mrSSU1 and mrSSU3R (Zoller et al. 1999) and the *MCM7* was amplified and sequenced using the primers Mcm7-709for and Mcm7-1348rev (Schmitt et al. 2009). PCR amplifications were performed using Illustra™ Hot Start PCR beads, according to the manufacturer’s instructions. The PCR-products were purified using the enzymatic method Exo-sap-IT© provided by USB Corporation. The purified sequences were run on an automated sequencer (ABI Prism 377).

### Taxon sampling

We assembled a dataset based on the four markers including as many species as possible of *Thalloidima* with an emphasis of *T. sedifolium* s. lat. from a wide geographic sampling. We included our own sequences from 41 specimens representing 7 species of *Thalloidima*. In addition, we added sequences from GenBank of two species where all markers except *MCM7* were present, as well as three species of the closely related genus *Bibbya*. As outgroup, we added new sequences from *Bacidia herbarum* (Stizenb.) Arnold.

### Sequence alignment

Sequences from the ITS, nrLSU, *MCM7* and mrSSU were aligned separately. The ITS, nrLSU, and mrSSU sequences were aligned using PASTA ver. 1.854 (Mirarab et al. 2015) with 100 iterations using MAFFT as aligner, OPAL as merger, and RAXML with a GTR+I+ $\Gamma$  model as tree estimator. The best alignment was kept and no sites were excluded from downstream analyses. *MCM7* nucleotide sequences were aligned with respect to their amino acid translation using MACSE ver. 2.07 (Ranwez et al. 2018) using standard translation code, standard optimization, and a BLOSUM62 scoring matrix. Finally, alignments were trimmed so that the 5’ and 3’ sites included at least 50% of the terminals.

### Phylogenetic analysis

IQ-TREE ver. 2.2.0 was used for model selection and maximum likelihood (ML) phylogeny estimation (Nguyen et al. 2015; Chernomor et al. 2016; Kalyaanamoorthy et al. 2017), including an initial assessment of topological

**Table 1.** Sequences newly produced (in bold) or downloaded from Genbank, and results from the chemical analyses (Ch. type).

Species	Isolate	Voucher	ITS	LSU	mrSSU	MCM7	Ch.type
<i>Bacidia herbarum</i>	C432	Sweden, Jämtland, Svensson 3777 (UPS L-1075754)	<b>OR230629</b>	<b>OR226010</b>	<b>OR229098</b>	<b>OR233359</b>	–
<i>Bibbya albomarginata</i>	5468	Peru, Tindal 10481 (O-L144851)	MG926024	MG926115	MG925927	–	–
<i>B. bullata</i>	SE251	Australia, Elix & Streimann 40393 (O-L68980)	MG926026	MG926116	MG925929	–	–
<i>B. ruginosa</i>	5469	Greenland, Tindal 10087 (O-L139109)	MG926033	MG926121	MG925937	–	–
<i>Thalloidima albilabrum</i>	T06	Spain, Andalucia, Westberg SCIN053 (S F298732)	<b>OR230630</b>	<b>OR226012</b>	<b>OR229127</b>	<b>OR233360</b>	Ch. 0
<i>T. albilabrum</i>	T07	Spain, Andalucia, Westberg SCIN069 (S F298730)	<b>OR230631</b>	<b>OR226013</b>	<b>OR229128</b>	<b>OR233361</b>	Ch. 0
	T57	Spain, Andalusia, Requena Mullor s.n. (UPS L-790424)	<b>OR230632</b>	<b>OR226015</b>	<b>OR229118</b>	<b>OR233362</b>	Ch. C
<i>T. alutaceum</i>	T42	Norway, Oppland, Westberg s.n. (S F298920)	<b>OR230633</b>	–	<b>OR229097</b>	<b>OR233363</b>	Ch. 0
<i>T. candidum</i>	SE59	Norway, Bratli & Tindal 8733 (O-L25779)	AF282117	MG926118	MG925932	–	–
<i>T. diffractum</i>	T11	Austria, Salzburg, Westberg HOCH051 (S F262276)	<b>OR230634</b>	<b>OR226011</b>	<b>OR229096</b>	<b>OR233364</b>	Ch. 0
<i>T. opuntioides</i>	T20	Austria, Salzburg, Westberg HOCH094 (S F261456)	<b>OR230635</b>	<b>OR226032</b>	<b>OR229131</b>	<b>OR233365</b>	Ch. Y
	T31	Norway, Oppland, Westberg s.n. (S F298919)	<b>OR230636</b>	<b>OR226033</b>	<b>OR229132</b>	<b>OR233366</b>	Ch. Y
	T50	Sweden, Pite lappmark, Westberg & Hedenäs 15-242 (S F278000)	<b>OR230637</b>	<b>OR226030</b>	<b>OR229130</b>	<b>OR233367</b>	Ch. Y
	T55	Scotland, East Lothian, Coppins & Yahr 25032 (UPS L-794042)	<b>OR230638</b>	<b>OR226031</b>	<b>OR229129</b>	<b>OR233368</b>	Ch. Y
<i>T. physaroides</i>	T01	Sweden, Öland, Westberg GYN013 (S F256993)	<b>OR230639</b>	<b>OR226009</b>	<b>OR229094</b>	<b>OR233369</b>	Ch. 0
	T12	Germany, Bavaria, Westberg GOS065 (S F262703)	<b>OR230640</b>	<b>OR226007</b>	<b>OR229092</b>	<b>OR233370</b>	Ch. 0
	T24	Sweden, Västergötland, Westberg & Prieto (S F283171)	<b>OR230641</b>	<b>OR226006</b>	<b>OR229093</b>	<b>OR233371</b>	Ch. 0
	T25	Sweden, Gotland, Prieto & Schultz (S F285802)	<b>OR230642</b>	<b>OR226008</b>	<b>OR229091</b>	<b>OR233372</b>	Ch. 0
<i>T. rosulatum</i>	T15	Italy, Piemonte, Westberg & Fontaneto s.n. (S F298953)	<b>OR230643</b>	<b>OR225994</b>	<b>OR229095</b>	<b>OR233373</b>	Ch. 0
<i>T. sedifolium</i>	T04	Sweden, Öland, Westberg GYN028 (S F257006)	<b>OR230644</b>	<b>OR226028</b>	<b>OR229125</b>	<b>OR233374</b>	Ch. 0
	T09	Spain, Andalucia, Westberg SCIN055 (S F298916)	<b>OR230645</b>	<b>OR226018</b>	<b>OR229111</b>	<b>OR233375</b>	Ch. C
	T13	Germany, Bavaria, Westberg GOS047 (S F262698)	<b>OR230646</b>	<b>OR226022</b>	<b>OR229116</b>	<b>OR233376</b>	Ch. 0
	T16	Spain, Andalucia, Westberg SCIN056 (S F298912)	<b>OR230647</b>	<b>OR226016</b>	<b>OR229122</b>	<b>OR233377</b>	Ch. 0
	T26	Norway, Oppland, Vågå, Westberg s.n. (S F298921)	<b>OR230648</b>	<b>OR226026</b>	<b>OR229119</b>	<b>OR233378</b>	Ch. 0
	T28	Sweden, Öland, Westberg s.n. (S F298954)	<b>OR230649</b>	<b>OR226027</b>	<b>OR229126</b>	<b>OR233379</b>	Ch. 0
	T33	Spain, Madrid, Westberg & Williams s.n. (S F283543)	<b>OR230650</b>	<b>OR226014</b>	<b>OR229114</b>	<b>OR233380</b>	Ch. C
	T35	Spain, Madrid, Westberg & Williams s.n. (S F283541)	<b>OR230651</b>	<b>OR226023</b>	<b>OR229117</b>	<b>OR233381</b>	Ch. 0
	T40	Norway, Finnmark, Tindal 12359 (O-L170859)	<b>OR230652</b>	<b>OR226024</b>	<b>OR229123</b>	<b>OR233382</b>	Ch. 0
	T45	Norway, Troms, Klepsland JK09-L474 (O-L165017)	<b>OR230653</b>	<b>OR226021</b>	<b>OR229115</b>	<b>OR233383</b>	Ch. 0
	T46	Norway, Finnmark, Klepsland JK11-L357 (O-L177200)	<b>OR230654</b>	<b>OR226029</b>	<b>OR229110</b>	<b>OR233384</b>	Ch. 0
	T47	Sweden, Gotland, Westberg et al. GTL49 (S F298913)	<b>OR230655</b>	<b>OR226020</b>	<b>OR229112</b>	<b>OR233385</b>	Ch. 0
	T48	Sweden, Pite lappmark, Westberg et al. 15-081 (S F277996)	<b>OR230656</b>	<b>OR226025</b>	<b>OR229113</b>	<b>OR233386</b>	Ch. 0
	T49	Sweden, Pite lappmark, Westberg & Hedenäs 15-239 (S F278002)	<b>OR230657</b>	<b>OR226019</b>	<b>OR229120</b>	<b>OR233387</b>	Ch. 0
	T58	Scotland, Perth & Kinross, Yahr et al. s.n. (UPS L-794039)	<b>OR230659</b>	<b>OR226017</b>	<b>OR229121</b>	<b>OR233388</b>	Ch. 0
T51	Italy, Friuli-Venezia Giulia, Hughes & Tindal 6808 (O-L00123, neotype)	<b>OR230658</b>	–	<b>OR229124</b>	–	Ch. C	
<i>T. squamatum</i>	T19	Sweden, Öland, Westberg GYN033 (S F257011)	<b>OR230660</b>	<b>OR226004</b>	<b>OR229100</b>	<b>OR233389</b>	Ch. 0
	T23	Sweden, Västergötland, Westberg & Prieto s.n. (S F283518)	<b>OR230661</b>	<b>OR226002</b>	<b>OR229099</b>	<b>OR233390</b>	Ch. 0
	T27	Sweden, Uppland, Westberg 08-419 (S F122068)	<b>OR230662</b>	<b>OR225999</b>	<b>OR229106</b>	<b>OR233391</b>	Ch. 0
	T29	Sweden, Öland, Westberg s.n. (S F298917)	<b>OR230663</b>	<b>OR226001</b>	<b>OR229105</b>	<b>OR233392</b>	Ch. 0
	T38	Norway, Hedmark, Breili L3647 (O-L167188)	<b>OR230664</b>	<b>OR226005</b>	<b>OR229108</b>	<b>OR233393</b>	Ch. 0
	T39	Norway, Sogn og Fjordane, Klepsland JK10-L121 (O-L183583)	<b>OR230665</b>	<b>OR226000</b>	<b>OR229102</b>	<b>OR233394</b>	Ch. 0
	T41	Sweden, Torne lappmark, Westberg s.n. (S F298955)	<b>OR230666</b>	<b>OR225998</b>	<b>OR229107</b>	<b>OR233395</b>	Ch. 0
	T43	Norway, Telemark, Haugan & Reiso 8201 (O-L160414)	<b>OR230667</b>	<b>OR225996</b>	<b>OR229109</b>	<b>OR233396</b>	Ch. 0
	T44	Norway, Nord-Trøndelag, Klepsland JK11-L208 (O-L177140)	<b>OR230668</b>	<b>OR225996</b>	<b>OR229104</b>	<b>OR233397</b>	Ch. 0
	T56	Italy, Veneto, Olariaga & Prieto s.n. (UPS L-790192)	<b>OR230669</b>	<b>OR225997</b>	<b>OR229103</b>	<b>OR233398</b>	Ch. 0
T59	Sweden, Gotland, Westberg et al. GTL176 (UPS L-793505, epitype)	<b>OR230670</b>	<b>OR226003</b>	<b>OR229101</b>	<b>OR233399</b>	Ch. 0	
<i>T. toninianum</i>	5768	Spain, Tindal 13773 (O-L200971)	MG926036	MG926124	MG925942	–	–

incongruence between the four markers. For each marker, we used IQ-TREE to select the best 1-, 2-, or 6-rate likelihood model in the general time-reversible family, with or without a proportion of invariable sites and gamma-distributed rate heterogeneity across sites approximated with four discrete categories. Standard non-parametric bootstrapping with 1,000 replicates and default search settings was used to assess branch support. No conflicting relationships among markers with support  $\geq 70\%$  in the consensus topologies were identified, leading us to proceed and concatenate the data and repeat the phylogeny estimation, this time with a partitioning scheme. We divided the data into eight potential subsets, ITS1, 5.8S, ITS2, nrLSU, *MCM7* 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> codon positions, and mrSSU. IQ-TREE subsequently optimized model fit by merging potential subsets and selecting models for each subset, resulting in an overall model composed of three independently parameterized subsets with proportional rates: (1) GTR+ $\Gamma$  for ITS1, ITS2 and *MCM7* 3<sup>rd</sup> codon positions, (2) GTR+I+ $\Gamma$  for 5.8S, nrLSU and *MCM7* 1<sup>st</sup> codon positions, and (3) HKY+ $\Gamma$  for mrSSU and *MCM7* 2<sup>nd</sup> codon positions. Bayesian phylogeny estimation was carried out using MrBayes ver. 3.2.6 (Ronquist & Huelsenbeck 2003; Ronquist et al. 2012) with the same partitioned model as in the ML analysis. Priors included a uniform distribution on topology, a (1, 1, 1, 1) Dirichlet on the proportional subset rates, and (when applicable) a (1, 1, 1, 1, 1, 1) Dirichlet on the rate matrix, a (1, 1) beta distribution on the transition/transversion rate ratio, a (1, 1, 1, 1) Dirichlet on state frequencies, an exponential distribution with mean 1 on the gamma shape parameter describing rate heterogeneity across sites, and a uniform (0, 1) distribution on the proportion of invariable sites. We used a compound Dirichlet prior on branch lengths (Zhang et al. 2012), with the gamma distribution component set to  $\alpha = 1$  and  $\beta = 0.92$  (the expected tree length from the ML analysis being  $\alpha/\beta = 1.0861$ ) and the Dirichlet component to the default (1, 1). Five parallel Markov chain Monte Carlo runs were performed, each with four chains and the temperature increment parameter set to 0.2 (Altekar et al. 2004). The appropriate degree of heating was determined by observing swap rates between the cold and hot chains in preliminary runs. Every 1,000<sup>th</sup> tree was sampled. Topological convergence was assessed every 10<sup>6</sup> generations, removing the first 50% of the tree sample as burn-in. The analysis was halted when the average standard deviation of splits (with frequency 0.1) between runs fell below 0.01, which was achieved after 5 $\times$ 10<sup>6</sup> generations. Potential scale reduction factors ranged from 0.996 to 1.001. Effective sample sizes of model parameters in the posterior sample ranged from 4,115 to 9,005 as estimated by Tracer ver. 1.7.1 (Rambaut et al. 2018).

## Results

In the phylogenetic tree, samples of *Thalloidima sedifolium* s. lat. appear in two distinct monophyletic clades (Fig. 1). One set of samples that includes the neotype of *T. sedifolium* forms a clade together with *T. albilabrum*. The second set forms a well-supported and monophyletic

clade as sister species to *T. physaroides*. Specimens in the first clade are recognized as *T. sedifolium* (corresponds to *T. sedifolium* II in Kistenich et al. 2018) while the second clade is recognized as *T. squamatum* (corresponds to *T. sedifolium* I in Kistenich et al. 2018). The morphological distinctions between the two species are described in detail below. The results from the chemical analyses are presented in Table 1.

## Taxonomy

***Thalloidima sedifolium*** (Scop.) Kistenich, Timdal, Bendiksy & S. Ekman, *Taxon* 67(5): 897. 2018

(Figs 2A–C, 3C)

MycoBank MB 824415

Basionym: *Lichen sedifolius* Scop., *Fl. Carniol.* Ed. 2, 2: 395. 1772. = *Toninia sedifolia* (Scop.) Timdal, *Opera Bot.* 110: 93. 1992 [1991].

Type: Italy, Friuli Venezia Giulia, Trieste, Monrupino [=Sanuario di Monrupino], 45°42'N, 13°48'E, alt. 320 m, on soil-filled crevices in calcareous rock, 19 July 1988, Hughes & Timdal 6808 (O-L-00123 – neotype! designated by Timdal 1992, p. 93, Genbank Accession No.: OR230658 (ITS)).

= *Verrucaria grisea* Willd., *Bot. Mag.*, (Roemer & Usteri) 2: 12. 1788.

Type: Germany, Niedersachsen, “Goettingae”, Ehrhart, *Pl. Crypt.* Linn. No 206 (GOET – neotype! designated by Timdal 1992, p. 93 [also neotype (see Timdal 1992) for the names *Lichen radicans* Vill. (Villars 1789), *Patellaria vesicularis* Hoffm. (Hoffmann 1794) and *Psora paradoxa* Hoffm. (Hoffmann 1796)]).

= *Lecidea glebosa* Ach., *Lichenogr. Universalis*: 187(1810).

Type: Switzerland, “Helvetiae” [without collector] (H-ACH 298, specimen marked “884” – lectotype! designated by Timdal 1992, p. 93).

= *Toninia subtabacina* (Nyl.) H. Olivier, *Expos. Lich. Ouest France, Suppl.* 2: 13. 1900. Basionym: *Lecidea subtabacina* Nyl. *Lich. env. Paris*: 87(1896).

Type: France, “Paris, St. Germain”, 1855, W. Nylander (H-NYL 16629 – lectotype! designated by Timdal 1992, p. 93, as “holotype” (ICN Art. 9.10).

= *Toninia arenaria* Räsänen, *Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo* 20, 3: 21. 1944.

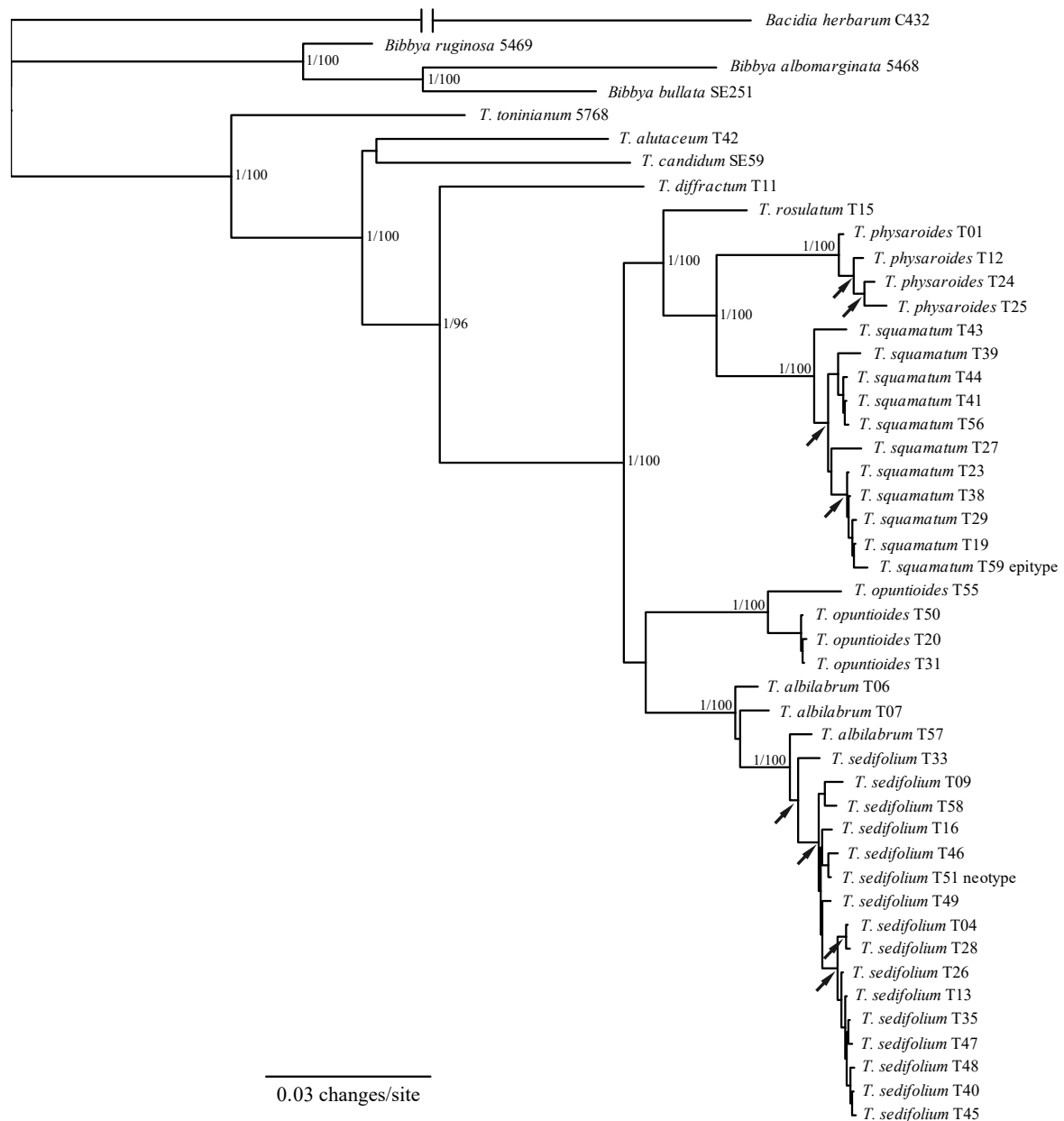
Type: Argentina, Mendoza, Las Heras, “in collibus siccis ca. Villa Hipodromo, in terra, haud parce” 17 Nov. 1939, A. Ruiz Leal 6386 (H – lectotype! designated by Timdal 1992, p. 93, as “holotype” (ICN Art. 9.10)).

= *Toninia muricola* B. de Lesd., *Bull. Soc. Bot. France* 95: 198. 1948.

Type: France, Provence-Alpes-Côte, Alpes-Maritimes, “Nice, chemin de Brancolar. Mur de soutènement.” 12 July 1948, B. de Lesdain (UPS L-709008! – lectotype! designated by Timdal 1992, p. 93).

= *Toninia carolitana* (Bagl. ex Arnold) Nimis & Poelt, *Stud. Geobot.* 7, Suppl. 1: 231. 1987. Basionym: *Thalloidima caeruleonigricans* var. *carolitanum* Bagl. ex Arnold, *Verh. Zool.-Bot. Ges. Wien* 26: 403. 1876.

Type: Italy, Sardegna, “prope Carolim, Sard. merid.” comm. Baglietto (M-0163836 – lectotype! designated by Timdal 1992, p. 93, as “holotype” (ICN Art. 9.10)).



**Figure 1.** Majority-rule consensus tree resulting from Bayesian MCMC analysis of combined mrSSU, ITS, nrLSU, and *MCM7* data. Branch support is given as posterior probability (PP) /bootstrap support (BS) for nodes with  $>0.95$  PP and  $>75$  BS. Supported nodes within species are indicated with arrows (support values not shown). The long branch to the outgroup *Bacidia herbarum* of length 0.2763 changes per site has been truncated.

**Notes.** We have studied all of the types mentioned above and found them to belong to the *T. sedifolium* clade. Excluding *T. squamatum*, this species is characterized by a thallus of small, convex to bullate squamules, up to 1.5 mm large, that grow scattered or sometimes form dense cushions. The apothecia can be up to 2.5 mm wide (average  $0.97 \pm 0.39$  mm,  $n=120$ ), epruinose to rarely entirely pruinose. In section, the proper exciple is dark red-brown while the hypothecium has a rather dull, dark brown color. The spores are colorless, 1-septate, fusi-form,  $(11.0\text{--})18.5 \pm 3.2\text{--}(30.0) \times (2.5\text{--})3.4 \pm 0.6\text{--}(4.0)$   $\mu\text{m}$  ( $n=171$ ). *T. sedifolium* is usually without lichen substances (chemotype 0), but chemotype C occurs in  $\sim 10\%$  of the samples according to Timdal (1992), which agrees with our results (Table 1). In Scandinavia, the species is widespread and occurs on calcareous ground in most parts of the country, from xerothermic grasslands in the south

to alpine heaths in the north. It is often found growing directly on soil, but also on bryophyte cushions on the soil.

**Selected specimens examined** (see also Table 1). NORWAY. Oppland, Vågå, Nordherad, hill E of Svarthåmårbecken and Svarthåmårbecken canyon,  $61.87^\circ\text{N}$ ,  $8.99^\circ\text{E}$ , on calcareous soil, 28 June 2013, M. Westberg (S F298918). SPAIN. Andalucía, Almería, Tabernas Badlands,  $\sim 5$  km SW of the village Tabernas,  $37.01349^\circ\text{N}$ ,  $2.43612^\circ\text{W}$ , on calcareous soil, 21 Feb. 2012, M. Westberg SCIN054, SCIN068 (S F298915, F298731). SWEDEN. Gotland, Eksta par., St. Karlsö, Norderhamn, 4 June 1917, G.E. Du Rietz (UPS L-167832); Torne lappmark, Jukkasjärvi par., Låktatjåkcos SV-sida, 1,100–1,200 m, 30 Aug. 1936, R. Santesson (UPS L-797637); Öland, Persnäs par., Knisa Mosse, along road to the sea on the W side,  $57.05^\circ\text{N}$ ,  $16.83^\circ\text{E}$ , 23 May 1982, L. Tibell 13848 (UPS L-797387). UNITED KINGDOM. Scotland, Banff, V.C. 94, north bank of Water of Ailnack gorge, opposite Lochan Uaine, elev. 438 m, calcareous conglomerat gorge, on conglomerate rock ledges, with *Tortula*

*inermis*, 29 July 2008, D.G. Long 38011 (E 00757052); E. Perthshire, V.C. 89, N cliffs above E side of Loch Loch, elev. 540 m, slopes below limestone cliffs, on dry ledges, 20 May 1994, D.G. Long & G.P. Rothero 25372 (E 00757053).

**Exsiccates examined.** ITALY. Poelt, Lich. Alp. 360 (UPS L-526248). SWEDEN. Moberg, Lich. Sel. Exs. Upsal. 497 (UPS L-886719). UKRAINE. Elenkin, Lich. Fl. Ross. 40 (UPS L-726737). UNITED KINGDOM. Crombie, Lich. Brit. Exs. 179 (UPS L-724623).

***Thalloidima squamatum* (Hoffm.) M. Westb. & Timdal, comb. nov.** (Figs 2D–F, 3A–B, D)

Mycobank MB 849389

Basionym: *Psora squamata* Hoffm., *Deutschl. Fl., Zweiter Theil* (Erlangen): 161(1796) [1795]. ≡ *Lichen squamatus* Dicks., *Fasc. Pl. Crypt. Brit.* 2: 20. 1790. nom illeg., Art. 53.1 (*Lichen squamatus* Vill. 1789).

Type: Dillenius, *Hist. Musc.*, Tab. 30, Fig. 135A (1742), lectotype, selected by Laundon (1984, p. 234). Epitype: SWEDEN. Gotland, Hejnum par., Hejnum hällar, ~2 km NE of Hejnum church, N of the small road towards Kallgatburg, 57.69610°N, 18.64667°E, elev. 55 m, open alvar area, on bryophytes over limestone, 14 Sept. 2016, M. Westberg, M. Wedin & S. Fernandez-Brime GTL176 (UPS, L-793505 – epitype, designated here, MycoBank MBT: 10013962, Genbank Accession No.: OR230670 (ITS); E, O – isoeotypes).

**Notes on typification.** The epithet *squamata* was validly and legitimately published as *Psora squamata* by Hoffman (1796) as a replacement name for Dickson's illegitimate name *Lichen squamatus*, the type of which is a drawing and not possible to identify. The material in Dillenius' herbarium in Oxford, which the drawing is based on (Fig. 3A), is small and sterile, but nevertheless identifiable to the species forming a monophyletic clade as sister to *T. physaroides* in Fig. 1. We therefore find it appropriate to use the name *T. squamatum* for the discussed species. The collection originated from the Swiss botanist Albrecht von Haller, but the locality is unknown. The only locality Dickson mentioned when he described *L. squamatus* was “Scotia”. As there are similar species occurring in Scotland, we cannot know with certainty which species Dickson actually referred to, although we can confirm the presence of *T. squamatum* in Scotland. We prefer, however, to epitypify the lectotype on modern, sequenced material to avoid possible confusion in the future and have selected a specimen from the rich populations on Gotland, an island off the Swedish east coast.

**Description.** Thallus squamulose, indeterminate, often forming compact patches, up to 8 cm across. Squamules up to 6 mm long, contiguous to crowded to sometimes imbricate, bullate from a young age, rounded to becoming irregularly lobed, sometimes columnar, larger squamules sometimes horizontally flattened. Upper surface pale brown to greenish brown to dark green, smooth or with a leathery texture, usually partly covered with a white, farinose pruina of calcium oxalate crystals, but can be entirely epruinose to densely white pruinose, pseudocyphellae absent. Lower side pale brown to whitish. Upper cortex of thick-walled, irregularly to mainly anticlinally arranged

hyphae with rounded to elongated cells, 20–40 µm thick including an up to 15 µm thick epinecral layer, often containing or covered by crystals of calcium oxalate. Medulla white to pale yellowish, lacking crystals, consisting of a spongy tissue formed by thin-walled hyphae. Algal layer continuous, algae trebouxoid, to ~15 µm diam. Lower cortex resembles the upper cortex, but is thinner.

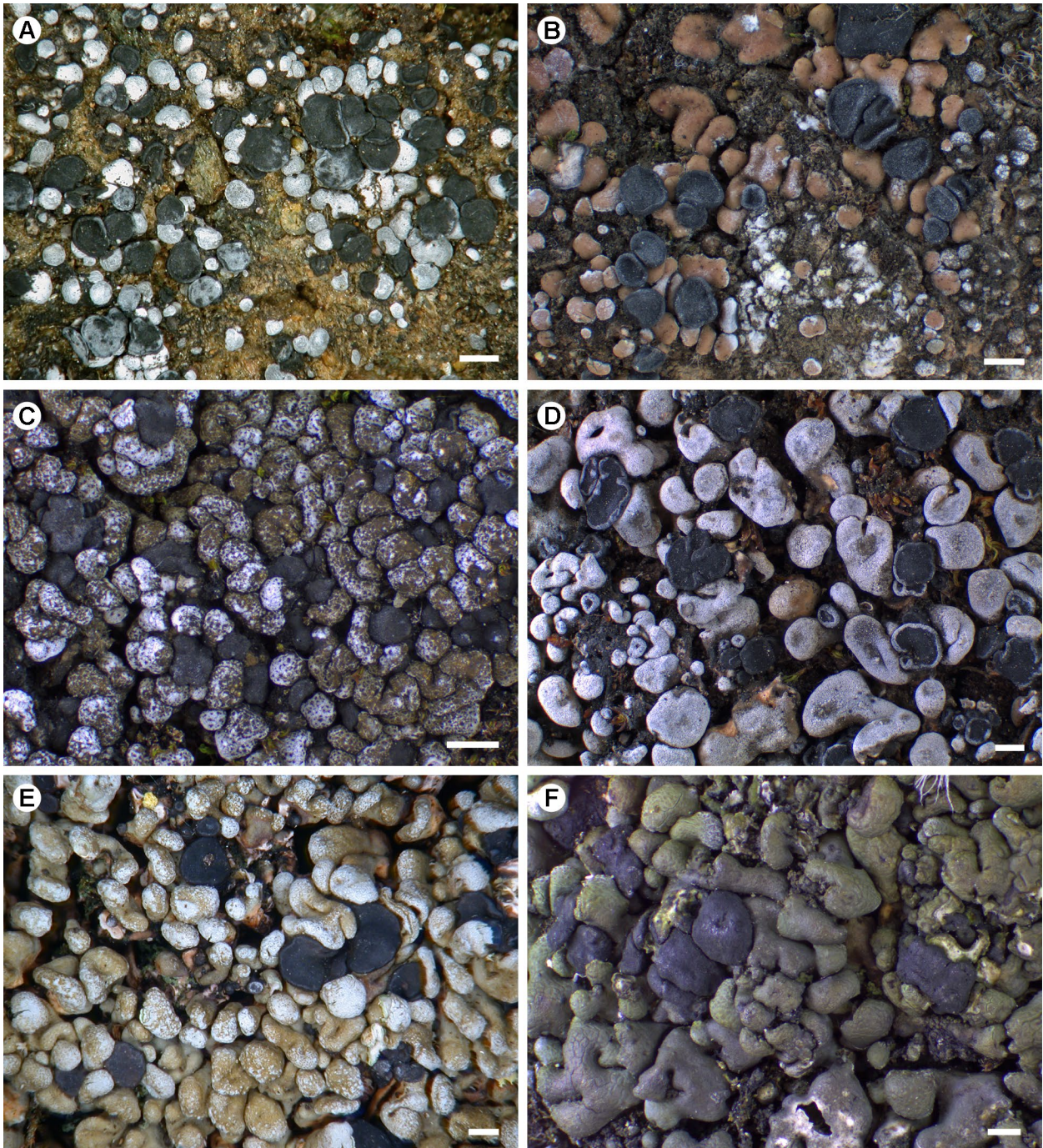
Apothecia common and usually present, often sparse, but sometimes numerous and crowded, rounded at first, but becoming strongly irregular in older apothecia, up to 4 mm wide (average  $1.92 \pm 0.76$  mm,  $n = 112$ ), marginate when young, but later often becoming immarginate, epruinose or rarely entirely pruinose, pruina often confined to the margin. Proper exciple colorless to pale golden brown in the outer part, darker golden brown towards the inner part. Hypothecium golden brown to red-brown. Hymenium colorless, 65–80 µm tall. Epithecium grey, often with a faint violet tone, K+ purple, N+ purple. Paraphyses simple, stout, ~3 µm in midhymenium, tips nearly cylindrical to clavate, to 6 µm broad. Asci 8-spored, narrowly clavate. Ascospores colorless, 1-septate, fusiform or with one end rounded, (12–)  $14.6 \pm 1.6$  (–20) × (3.0–)  $3.8 \pm 0.5$  (–5.0) µm ( $n = 109$ ).

Pycnidia not seen.

**Chemistry.** Chemotype 0, no lichen substances detected by TLC or HPTLC.

**Distribution and ecology.** *Thalloidima squamatum* is usually overgrowing bryophyte cushions on calcareous rocks or sometimes growing directly on rock, particularly along cracks in the stone. More rarely, it is found growing on soil or bryophytes over soil. In Scandinavia, the species is widely distributed and occurs in many areas where calcareous rocks are present, also in alpine localities in the north. Outside Scandinavia, we report it from several localities in the Alps (Austria, Germany, Italy and Switzerland), as well as scattered localities in Croatia, Greenland, Poland, Russia and Scotland.

**Notes.** *Thalloidima squamatum* is generally easy to identify based on its overall habit and large size. The amount of pruina on the thallus squamules ranges from absent to completely and densely white pruinose. This wide variation may cause confusion, although extremes are rare. The species is distinguished from *T. sedifolium* by its larger, more upright, sometimes columnar squamules, thicker and larger apothecia, a paler proper exciple lacking a reddish tone, and shorter and slightly broader spores. It should be noted, however, that the variation in spore size within *T. sedifolium* is large and partially overlapping with *T. squamatum*. Unlike *T. squamatum*, *T. sedifolium* prefers to grow directly on soil or bryophytes over soil. The two species often occur together in the same sites, but as *T. squamatum* is the more conspicuous of the two species, it has frequently been collected to document “*T. sedifolium*” and is consequently overrepresented in the herbaria. Among the 191 specimens of *T. sedifolium* from Sweden currently housed in UPS, 143 (=75%), turned out to belong to *T. squamatum*. *Thalloidima rosulatum* Anzi (Fig. 4D) is also similar to *T. squamatum*, but

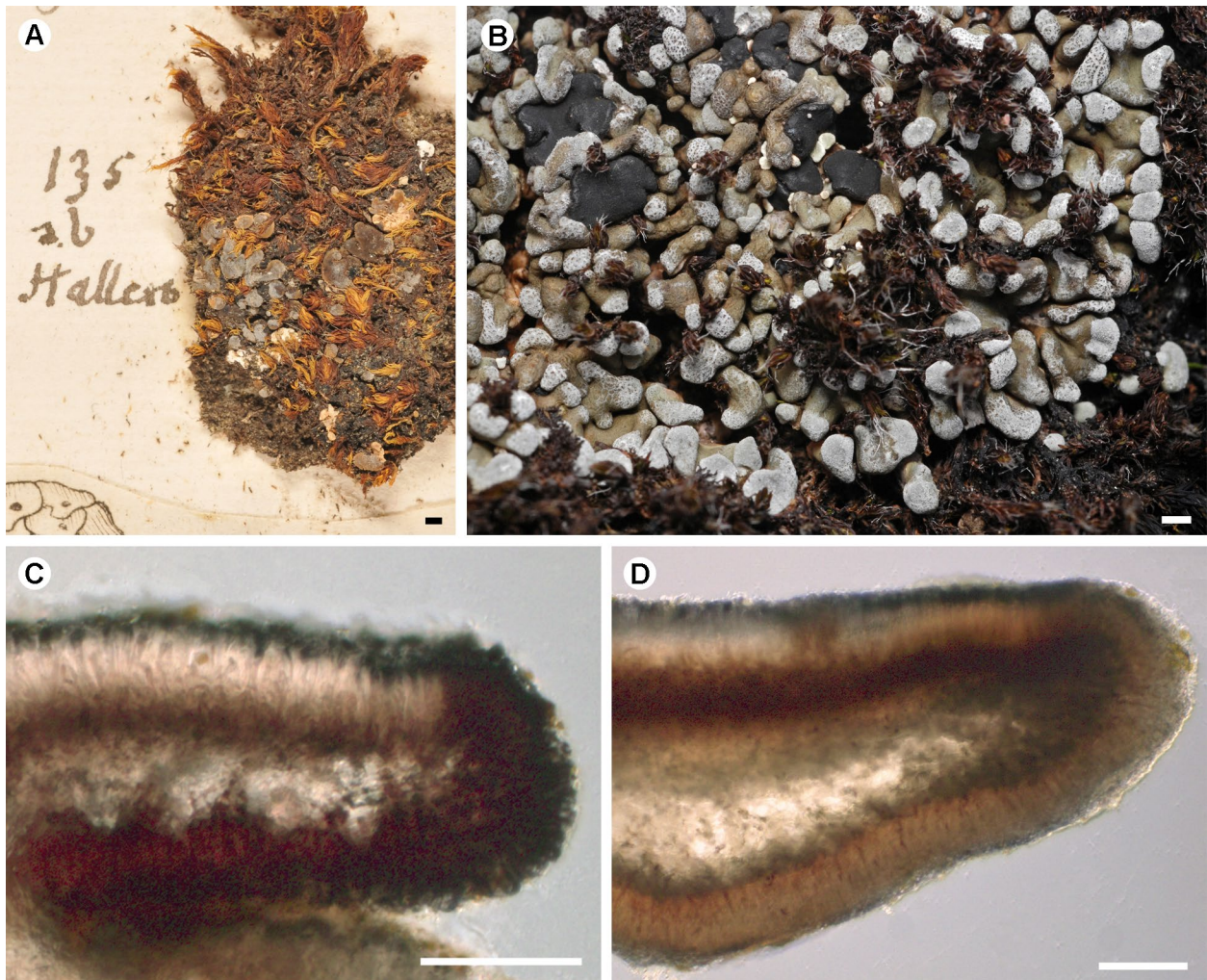


**Figure 2.** Morphological variation in *Thalloidima sedifolium* and *T. squamatum*. A – *T. sedifolium* with pruinose thallus, Norway, Westberg s.n. (S F298921); B – *T. sedifolium*, brown, mainly epruinose thallus, Spain, Westberg SCIN054 (S F298915); C – *T. sedifolium*, compact, cushion-forming thallus, Sweden, Westberg et al. GTL49 (S F298913); D – *T. squamatum*, pruinose thallus and apothecial margins, Sweden, Albertson s.n. (UPS L-797698); E – *T. squamatum*, pale thallus with pruinose lobe ends, Sweden, Westberg & Prieto s.n. (S F283518); F – *T. squamatum* with epruinose thallus, Sweden, Westberg s.n. (UPS L-901809). Scale = 1 mm.

has a hyaline hypothecium and distinctly lobate squamules covered by a coarser pruina. *Thalloidima squamatum* can also be similar to well-developed samples of *T. physaroides* (Fig. 4C), but the latter species has white pseudocypellae (sometimes few and inconspicuous) and thick-walled medullary hyphae, characters that also separates this species from *T. sedifolium* (Timdal 1992; see also Farkas & Suija 2008). Dark green specimens of *T. squamatum* without or with a thin pruina at the edges of the squamules can be confused with *T. opuntoides*. This species is otherwise often recognized by its large

squamules with a dark green, waxy surface and pruinose squamule margins, and typically form imbricate thalli (Fig. 4B). Doubtful specimens can be identified with TLC, as *T. opuntoides* always has chemotype Y.

**Selected specimens examined** (see also Table 1). CROATIA. 10 km SSE of Slunj, 45.04835°N, 15.62780°E, 400 m, on boulders in a southern slope, 8 May 1972, R. Moberg 1800 (UPS L-002187). GREENLAND. Blomsterdalen, ~5 km N of Narsarsuaq airport, 61.1958°N, 45.3388°E, 30–45 m, on mosses on calciferous, vertical rocky outcrop facing N, 24 July 2005, B. Owe-Larsson 9591 (UPS L-175165). NORWAY. Akershus,

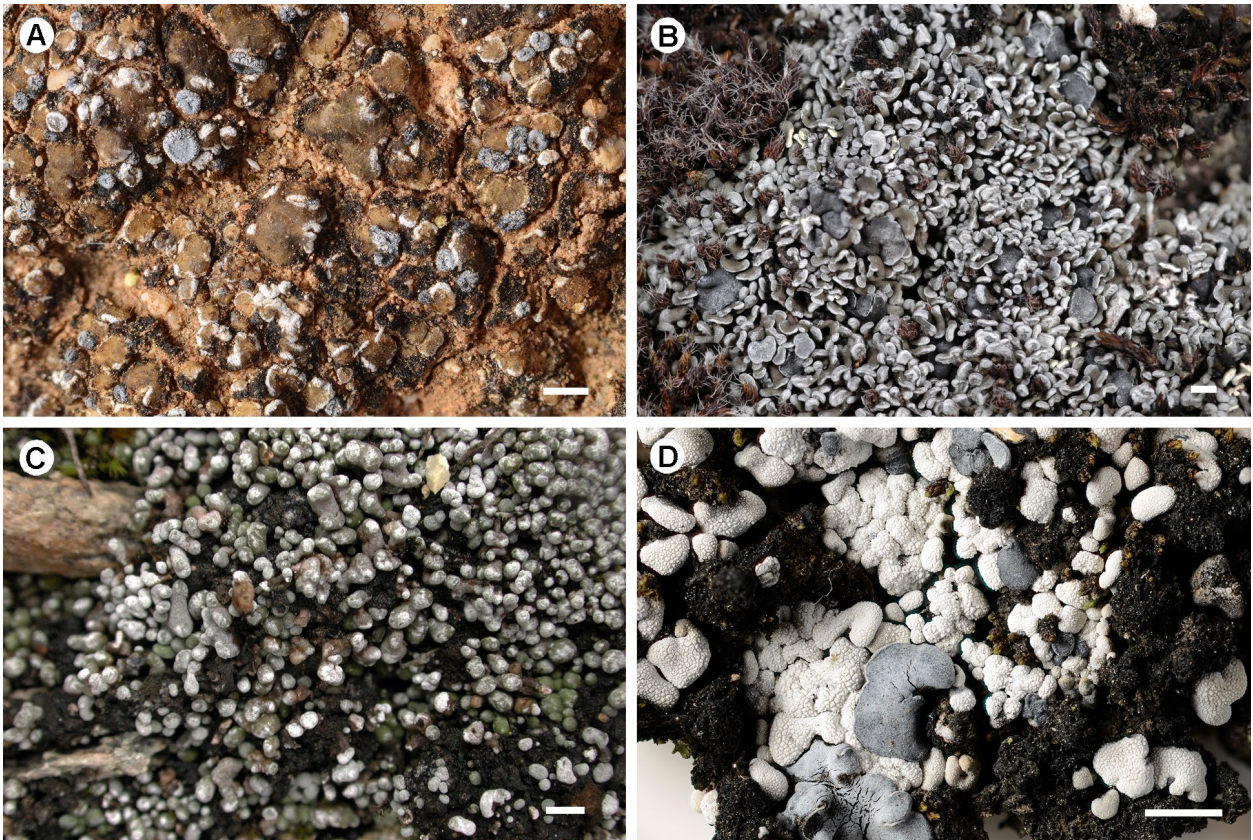


**Figure 3.** A – *Thalloidima squamatum*, specimen in the herbarium of Dillenius in OXF, “Specimina Muscorum in Historia Muscorum descriptorum agglutinata Februario 1744”, p. 228, No. 135a, b (HM-sheet\_079a (BRAHMS), courtesy of Oxford University Herbaria, Dept. of Biology); B – *T. squamatum*, habitus in the field, Sweden, Öland, Hulterstad, N of Gösslunda, over moss on limestone boulder, 13 Sept. 2007 (photo Leif Stridvall, courtesy of Anita Stridvall); C – *T. sedifolium*, apothecium section showing the reddish color of the excipulum (S F298921); D – *T. squamatum*, apothecium section showing pale excipulum (S F283518). Scales: A–B = 1 mm; C–D = 100  $\mu$ m.

Bærum, Snarö, June 1859, Th.M. Fries (UPS L-797441); Oslo, Tidselöen, 20 May 1870, Th.M. Fries (UPS L-797443); Hedmark, Ringsaker, by the lake Mjøsa, 600 m NE of farm Nordgrefsheim, 10.98°N, 60.80°E, 130 m alt., 29 Aug. 1981, E. Timdal 2944 (O L-45306); Oppland, Vang, Sparstadodden Ø, 8.5806°N, 61.1463°E, 590 m alt., on small shelf in S-exposed rock wall, 28 Sept. 2018, J.T. Klepsland JK18-812 (O L-226685); Buskerud, Hole, the island Storøya in lake Tyrifjorden, 10.25°N, 60.04°E, 65 m alt., 14 Nov. 1981, E. Timdal 3139 (O L-26691); Telemark, Porsgrunn, Gravastranda, 9.6456°N, 59.0897°E, 5 m alt., on limestone in dry heath, 18 Oct. 2003, B.P. Løfall bpl-L10513 (O L-124122); Aust-Agder, Bygland, Heddeviki, 58.9354°N, 7.7297°E, 400 m alt., on mossy rock face just below rock wall with lime precipitation, 25 June 2010, J.T. Klepsland JK10-L156 (O L-183585); Hordaland, Ulvik, Finse, Jomfrunut, kalkbrant, 19 July 1916, G.E. Du Rietz (UPS L-901466); Sogn og Fjordane, Sogndal, Hamrestølen E, 6.7941°N, 61.1913°E, 370 m alt., S-facing, sun-exposed rock outcrop, 20 May 2019, J.T. Klepsland JK19-067 (O L-227362); Sør-Trøndelag, Trondheim, Hladehameren, 1880, C.S. Kindt (O L-26708); Nord-Trøndelag, Stjørdal, Vifstad, 10.8565°N, 63.4893°E, 100 m alt., sun-exposed limestone rock outcrop, 12 June 2001, H. Bratli & G. Rønning 5648 (O L-101604); Nordland, Bodø, Hjellevika, 14.6349°N, 67.4137°E, 30 m alt., on sand in cracks of feldspar rock, 22 July

2001, B.P. Løfall bpl-L8366 (O L-105762); Troms, Tromsø, Tromsøen, Langnes, 1 May 1911, B. Lyng (O L-26732); Finnmark, Porsanger, Børselv, 1 km E of Rautakoppa, 70.3128°N, 25.4913°E, 10 m alt. S-facing rock wall, dolomite, 5 July 2014, E. Timdal 13442-2 (O L-195599). RUSSIA. Karelyia, Karelia Onegensis, Walkeamäki, 1870, J.P. Norrlin (UPS L-783876). SWEDEN. Öland, Mörbylånga par., E of Amossen, N of the road between Södra Bärby and Alby, just W of the Middle Wall, 56.49561°N, 16.51082°E, 23 m, open alvar area, on the ground, 13 June 2017, M. Westberg (UPS L-921761); Resmo par., Stora Alvaret, about 4 km SSE of the church of Resmo, on open calcareous rocks, 2 July 1957, R. Santesson 11930 (UPS L-135882); Stenåsa par., Stenåsa alvar, 13 June 1912, G.E. Du Rietz (UPS L-167831); Ventlinge par., 1 km E of Grönhägen, on the alvar (limestone pavement), 8 July 1957, R. Santesson 11972 (UPS L-797626); Gotland, Hejnum par., Hejnum hällar, ~2 km NE of Hejnum church, N of the small road towards Kallgatburg, 57.6961°N, 18.64667°E, 14 Sept. 2016, M. Westberg, M. Wedin, S. Fernandez-Brime GTL 181 (UPS L-793516); Fårö par., 1.2 km WSW of Lansa, by the sea-shore, 57.91167°N, 19.04690°E, on mosses on limestone, 15 Sept. 2016, M. Westberg & S. Fernandez-Brime GTL208 (UPS L-793889); Dalsland, Skällerud par., ~3.5 km NE of Skällerud church, W side of the peninsula Ryrhalvön, 58.80305°N, 12.47019°E. on mosses on calcareous rock, 4 July 2017, M. Westberg (UPS L-851881);





**Figure 4.** Habitus images of related *Thalloidima* species. A – *T. albilabrum*, Spain, Timdal 4379 (O L-144396); B – *T. opuntiooides*, Italy, Rui & Timdal 10558 (O L-149069); C – *T. physaroides*, Norway, Timdal, not collected; D – *T. rosulatum*, Norway, Timdal 3424 (O L-26469). Photos: E. Timdal. Scale = 1 mm

Västergötland, Vilske-Kleva par., “Kleva klintar”, 7 Sept. 1913, E.P. Vrang (UPS L-797699); Östergötland, Västra Tollstad par., Kråkeryd Nature Reserve at Lake Vättern, S part, 58.2°N, 14.6°E, 110 m, on mosses in seepage track on steep rock ~20 m above water level, 1 Nov. 2002, A. Nordin 5540 (UPS L-124821); Närke, Glanshammar par., Glanshammar, 300 m NE of the church, 59.32118°N, 15.40583°E, on vertical calcareous rock, 23 April 2017, M. Westberg (UPS L-926910); Södermanland, Hölö par., Fridö, small promontory on the south side of the island, 58.94116°N, 17.61701°E, on mosses on calcareous rock, 26 April 2018, M. Westberg (UPS L-901809); Västmanland, Nora par., Oskarsvik, kalkudden vid Fåsjön, 7 Sept. 1947, G. Degelius (UPS L-797763); Lycksele lappmark, Tärna par., Ume älv, Över-Uman, holmen SV om Högstabynäset, östsidan, sydudden, 66.1°N, 14.67°E, 525–530 m, Dryadion-hed, 28 Aug. 1960, G.E. Du Rietz 2147z (UPS L-119188); Lule lappmark, Jokkmokk par., Padjelanta National Park, 11 km WNW Staloluokta, N of the river Duvgejåhkå, E slope of Mt. Unna Duvge, 1.05 km NE of small cabin, 67.35236°N, 16.46162°E, 737 m, on bryophytes/soil over calcareous, schistose rocks, 4 Aug. 2020, M. Westberg PAD331 (UPS L-1009800). SWITZERLAND. Graubünden, Ardez (Steinberg), on rocks around the ruined castle, 46.77445°N, 10.20460°E, 1450 m, 27 July 1976, R. Moberg 3271 (UPS L-002185); Valais, Sion, NW outskirts of the town, S of Lac du Mont d’Orge, 46.2315°N, 7.33858°E, on calcareous rock, 23 Sept. 2020, M. Westberg & G. von Hirschheydt (UPS L-1008063). UNITED KINGDOM. Scotland, West Inverness, V.C. 97, Coire Cheap, Aonach Beag, Ben Alder Range, elev. 975 m, soil amongst exposed limestone rock, 8 Aug. 1994, A. Fryday 5537 (E 00745319).

**Exsiccates examined.** AUSTRIA. Obermayer, Dupla Graec. Lich. 1279 (UPS L-1073597); Obermayer, Dupla Graec. Lich.

1280 (UPS L-1073598); Pl. Graec. Lich. 110 (UPS L-047280); Pl. Graec. Lich. 173 (O L-121054, UPS L-047343); GERMANY. Migula, Krypt. Germ., Austr. Helv. Exs. (Flechten), 346 (O L-121479, UPS L-660037). NORWAY. Havaas, Lich. Exs. Norveg. 382 (O L-26704, UPS L-137176). POLAND. Tobolewski, Lichenoth. Polon. 181 (UPS L-572861). SWEDEN. Malme, Lich. Suec. Exs. 238 (O L-6729, UPS L-108833). SWITZERLAND. Hepp, Flechten Eur. 237 (O s.n., UPS L-069258); Schaerer, Lich. Helv. Exs. Ed. 1, 168 (O L-192620, UPS L-115318). EUROPE. [without locality] Flotow, Lich. Exs. 240A, 240B, (UPS L-133210, UPS L-133211).

## Discussion

*Thalloidima sedifolium* in the sense of Timdal (1992) occurs world-wide and further studies of the variation in the *T. sedifolium* clade may reveal additional taxonomic entities. A shortcoming of our study is that only European specimens have been studied. In our analysis, samples identified as *T. albilabrum* are closely related to *T. sedifolium*, but do not form a monophyletic clade. *T. albilabrum* (Fig. 4A) is characterized by having a white margin of the squamules that is formed by the exposed medulla and not primarily by pruina. In addition, the upper cortex is typically set with a network of deep cracks. The phylogenetic distinction between these two species remains unclear, however. In addition, we observed a distinct morphological form of *T. sedifolium* at two locations in Spain that, upon closer examination, differs from typical *T. sedifolium* in having shorter spores, as well as the chemotype C. In the phylogenetic tree, this form is represented by samples

T09 and T33 within the *T. sedifolium* clade (Fig. 1). These specimens may be referred to as *Toninia subtabacina* or possibly *T. muricola*, both described from France, but for the time being we treat these names as synonyms of *T. sedifolium*.

## Acknowledgements

It gives us great pleasure to dedicate this paper to our colleague and friend Tor Tønsberg on the occasion of his 75<sup>th</sup> birthday, in recognition of his great contribution to the field of lichenology. This study began within the European research initiative SCIN (Soil Crust International) which was launched in 2012 to investigate biodiversity and functional aspects of biological soil crusts in Europe (Büdel et al. 2014). The project was funded by the ERA-Net BiodivERsA program as part of the 2010–2011 BiodivERsA joint call, with the national funder the Swedish Research Council Formas (grant number 226-2011-1795). We gratefully acknowledge the curators of all herbaria mentioned for loans or access to material. We are also grateful to Rebecca Yahr, Brian Coppins and Juan Miguel Requena Mullor for providing specimens and to Stephen Harris and staff at Oxford University Herbaria, Department of Biology for providing a high-resolution photograph of the material in Dillenius' herbarium. Anita Stridvall kindly permitted us to use a photo from www.stridvall.se. Måns Svensson generously provided us with sequences of *Bacidia herbarum*. We are grateful to Bodil Cronholm at the Molecular Systematics Laboratory at the Swedish Natural History Museum for laboratory assistance. We would also like to thank the two anonymous reviewers for their comments and corrections which helped to improve the paper.

## References

- Altekar, G., Dwarkadas, S., Huelsenbeck, J. P. & Ronquist, F. 2004. Parallel Metropolis coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* 20: 407–415. <https://doi.org/10.1093/bioinformatics/btg427>
- Arup, U., Ekman, S., Lindblom, L. & Mattsson, J-E. 1993. High performance thin layer chromatography (HPTLC), an improved technique for screening lichen substances. *The Lichenologist* 25: 61–71. <https://doi.org/10.1017/s0024282993000076>
- Baumgärtner, H. 1979. *Revision der europäischen Arten der Gattung Toninia (Massal.) Ampl. Th. Fr.* München.
- Büdel, B., Colesie, C., Green, T. G. A., Grube, M., Lazáro Suau, R., Loewen-Schneider, K., Maier, S., Peer, T., Pintado, A., Raggio, J., Ruprecht, U., Sancho, L. S., Schroeter, B., Türk, R., Weber, B., Wedin, M., Westberg, M., Williams, L. & Zheng, L. 2014. Improved appreciation of the functioning and importance of biological soil crusts in Europe – the Soil Crust International project (SCIN). *Biodiversity & Conservation* 23: 1639–1658. <https://doi.org/10.1007/s10531-014-0645-2>
- Chernomor, O., von Haeseler, A. & Minh, B. Q. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* 65: 997–1008. <https://doi.org/10.1093/sysbio/syw037>
- Egan, R. S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. *The Bryologist* 89: 123–131. <https://doi.org/10.2307/3242609>
- Ekman, S. 2001. Molecular phylogeny of the *Bacidiaceae* (Lecanorales, lichenized Ascomycota). *Mycological Research* 105: 783–797. <https://doi.org/10.1017/s0953756201004269>
- Farkas, E. & Suija, A. 2008. The species of the former *Toninia coeruleo-nigricans* group in Estonia. *Folia Cryptogamica Estonica* 44: 33–36.
- Gardes, M. & Bruns, T. D. 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118. <https://doi.org/10.1111/j.1365-294x.1993.tb00005.x>
- Hawksworth, D. L., James, P. W. & Coppins, B. J. 1980. Checklist of British lichen-forming, lichenicolous and allied fungi. *The Lichenologist* 12: 1–115. <https://doi.org/10.1017/s0024282980000035>
- Hoffmann, G. F. 1794. *Vegetabilia Cryptogamica* 2. Erlangen. pp. 1–42.
- Hoffmann, G. F. 1796. *Deutschlands Flora oder Botanisches Taschenbuch. Zweyter Theil für das Jahr 1795. Cryptogamie*. B. I. I. Palm, Erlangen. pp. 1–200. <https://doi.org/10.5962/bhl.title.126793>
- Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A. & Jermin, L. S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>
- Kistenich, S., Timdal, E., Bendiksby, M. & Ekman, S. 2018. Molecular systematics and character evolution in the lichen family *Ramalinaceae* (Ascomycota: Lecanorales). *Taxon* 67: 871–904. <https://doi.org/10.12705/675.1.s>
- Laundon, J. R. 1984. The typification of Withering's neglected lichens. *The Lichenologist* 16: 211–239. <https://doi.org/10.1017/s002428298400044x>
- Massalongo, A. 1852. *Ricerche sull'autonomia dei licheni crostosi e materiali pella loro naturale ordinazione*. Verona.
- Mirarab, S., Nguyen, N., Guo, S., Wang, L. S., Kim, J. & Warnow, T. 2015. PASTA: ultra-large multiple sequence alignment for nucleotide and amino-acid sequences. *Journal of Computational Biology* 22: 377–386. <https://doi.org/10.1089/cmb.2014.0156>
- Nguyen, L.-T., Schmidt, H. A., von Haeseler, A. & Minh, B. Q. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Orange, A., James, P. W. & White, F. J. 2010. *Microchemical Methods for the Identification of Lichens*. Second Edition. London: British Lichen Society.
- Poelt, J. 1969. *Bestimmungsschlüssel europäischer Flechten*. Vaduz.
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G. & Suchard, M. A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Ranwez, V., Douzery, E. J. P., Cambon, C., Chantret, N. & Delsuc, F. 2018. MACSE v2: Toolkit for the alignment of coding sequences accounting for frameshifts and stop codons. *Molecular Biology and Evolution* 35: 2582–2584. <https://doi.org/10.1093/molbev/msy159>
- Reimers, H. 1950. Beiträge zur Kenntnis der Bunten Erdflechten-Gesellschaft. I. Zur Systematik und Verbreitung der Charakterflechten der Gesellschaft besonders im Harzvorland. *Berichte der Deutschen Botanischen Gesellschaft* 63: 148–157. <https://doi.org/10.1111/j.1438-8677.1951.tb01500.x>
- Reimers, H. 1951. Beiträge zur Kenntnis der Bunten Erdflechten-Gesellschaft. II. Allgemeine Fragen. *Berichte der Deutschen Botanischen Gesellschaft* 64: 36–50. <https://doi.org/10.1111/j.1438-8677.1951.tb02103.x>
- Ronquist, F. & Huelsenbeck, J. P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A. & Huelsenbeck, J. P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/bioinformatics/btg180>
- Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. 2004. *Lichen-forming and lichenicolous fungi of Fennoscandia*. Museum of Evolution, Uppsala.
- Schmitt, I., Crespo, A., Divakar, P. K., Frankhauser, J. D., Herman-Sackett, E., Kalb, K., Nelsen, M. P., Rivas Plata, E., Shimp, A. D., Widhalm, T. & Lumbsch, H. T. 2009. New primers for promising single-copy genes in fungal phylogenetics and systematics. *Persoonia* 23: 35–40. <https://doi.org/10.3767/003158509x470602>

- Timdal, E. 1992 [1991]. A monograph of the genus *Toninia* (*Lecideaceae*, *Ascomycetes*). *Opera Botanica* 110: 1–137.
- Vilgalys, R. & Hester, M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
- Villars, D. 1789. *Histoire des plantes de Dauphiné: vol. III. cum tab. aen.* Grenoble, Lyon, Paris. pp. 1–1091. <https://doi.org/10.5962/bhl.title.116232>
- Westberg, M., Fernandez-Brime, S., Timdal, E., Williams, L. & Wedin, M. 2016. Species delimitation in the *Toninia sedifolia* group. Abstract. The 8<sup>th</sup> IAL Symposium: Lichens in deep time, p. 156.
- White, T. J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M. A., Gelfand, D. H., Sinsky, J. J. & White, T. J. (eds) *PCR Protocols: a guide to Methods and Applications*. Academic Press New York, pp. 315–32. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Zhang, C., Rannala, B. & Yang, Z. 2012. Robustness of compound Dirichlet priors for Bayesian inference of branch lengths. *Systematic Biology* 61: 779–784. <https://doi.org/10.1093/sysbio/sys030>
- Zoller, S., Scheidegger, C. & Sperisen, C. 1999. PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *The Lichenologist* 31: 511–516. <https://doi.org/10.1017/s0024282999000663>