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Additional species in *Tetramelas*

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Abstract: *Tetramelas phaeophysciae*, a new obligately lichenicolous species occurring in Scandinavia, Iceland and Greenland, is described, and the closely related *Buellia pulverulenta*, together with *B. triphragmioides*, are transferred to *Tetramelas*. Phylogenetic reconstructions based on sequence data from nITS1-5.8S-ITS2 rDNA, using Bayesian inference and parsimony analyses, support the segregation of the new species from *B. pulverulenta* as well as the segregation of *Tetramelas* and *Diplotomma* from *Buellia* s. str.

Key words: Bayesian inference, *Buellia*, Greenland, Iceland, ITS, maximum parsimony, phylogeny, Scandinavia, *Tetramelas*, *Tetramelas phaeophysciae*

Introduction

During work with material collected by G. Einar Du Rietz on riverbanks and shores of lakes in northern Sweden (see Nordin 2002, 2003), it became evident that *Buellia pulverulenta* Anzi, as conceived in earlier publications by Nordin (1996, 2000), is heterogeneous. In the specimens studied earlier by Nordin (*loc. cit.*) the spores were usually 3-septate at maturity and a mixture of 1–—3-septate spores was often seen. In a few specimens, however, the spores were invariably 1-septate, and also the appearance of the apothecia differed slightly from the collections with 3-septate spores. Because of the sparse material these differences were not given any attention. In the Du Rietz-material studied, however, specimens with 1-septate spores were found in several collections of *Phaeophyscia* species. This prompted further studies of the material.

Recently *Buellia pulverulenta* was transferred to *Diplotomma* Flot. in a work based on molecular data (Molina *et al*. 2002). However, *B. pulverulenta* was not included in the analysis; the transfer was based mainly on the phylogenetic analysis presented by Nordin (2000), where *B. pulverulenta* formed part of the ''*Diplotomma*-group''. In order to investigate species delimitation and the phylogenetic relationships of the two putative taxa observed, a phylogenetic analysis based on nITS1-5.8S-ITS2 rDNA data has been carried out. A number of supposedly related species, including representatives from *Buellia* De Not, *Diplotomma* and *Tetramelas* Norman, all members of the ''B-clade'' in the *Physciaceae* (Helms *et al*. 2003), were also included in the analysis.

Tetramelas was reintroduced by Marbach (2000) and new species were added to the genus by Kalb (2004) and Nordin (2004). In this paper a new species in *Tetramelas* is described and two additional species are added. Furthermore the monophyly of the genus is tested.

Material and Methods

Sampling

Sequence data from nITS1-5.8S-ITS2 rDNA of 27 specimens representing 23 species of *Buellia*, *Diplotomma*, *Hafellia* Kalb, H. Mayrhofer & Scheid., and *Tetramelas*, were used in this study. Four species from the ''A-clade'' in the *Physciaceae* (Helms *et al.* 2003), *Heterodermia leucomela* (Fée) Swinscow & Krog, *Phaeophyscia orbicularis* (Neck.) Moberg, *Physcia stellaris*

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TABLE 1. *Sequences downloaded from GenBank and newly produced sequences* (*in bold*)

Species	Origin	Collection (herbarium)	GenBank no.
Amandinea punctata	Austria		AF540492
Buellia aethalea	Sweden		AF540496
B. capitis-regum	USA		AF540497
B. disciformis	Sweden		AF540498
B. elegans	Austria		AJ421415
B. erubescens			AF250786
B. griseovirens	Sweden		AF540500
B. muriformis	USA		AF540501
B. ocellata	Faeroe Islands		AF540502
B. penichra	USA		AF540503
B. triphragmioides	Sweden		AF450505
B. zoharyi	Canary Islands		AJ421418
Diplotomma alboatrum 1	UK		AJ549958
D. alboatrum 2	Sweden		AJ549959
D. alboatrum 3	Sweden	*Nordin* 3205 (UPS)	**DQ198357**
D. lutosum	Sweden		AF540510
D. venustum	Spain		AF352320
Dimelaena oreina	Austria		AJ421417
Hafellia dissa	South Africa		AF540515
Heterodermia leucomela	El Salvador		AF540520
Rinodina pyrina	Austria		AF540549
Phaeophyscia orbicularis	Germany		AF540528
Physcia stellaris	Germany		AJ421421
Tetramelas confusus	New Zealand	*Galloway* 0239 (UPS)	**DQ201954**
T. geophilus	Sweden		AF540499
T. insignis	Sweden	*Nordin* 5464 (UPS)	**DQ198358**
T. papillatus			AF250790
T. phaeophysciae	Iceland	*Nordin* 4922 (UPS)	**DQ198359**
T. phaeophysciae	Norway	*Nordin* 5663 (UPS)	**DQ201951**
T. pulverulentus	Iceland	*Nordin* 4917 (UPS)	**DQ201952**
T. pulverulentus	Sweden	*Nordin* 4427 (UPS)	**DQ201953**

(L.) Nyl. and *Rinodina pyrina* (Ach.) Arnold, were used as out-group. New sequences were produced from seven specimens, listed in Table 1, together with sequences downloaded from GenBank.

DNA extraction, amplification and sequencing

For the new sequences total DNA was extracted from one to five ascomata using the Qiagen DNeasy Plant Mini Kit. Lichen sample vouchers of the new sequences are listed in Table 1.

PCR amplification was conducted by using the primers ITS1-F (Gardes & Bruns, 1993) in combination with LR7 or LR1n (GTTGGTTTCTTTTCCT) to specifically amplify the fungal ITS1-5.8S-ITS2. When no or only weak bands were obtained in the first PCR, the product from this reaction was used for a nested PCR using primers ITS4 and ITS5 (http://www.biology.duke.edu/fungi/mycolab/primers.htm). The PCR ran for 35 cycles (1 min at 94°C, 1 min at 54°C, 45 sec at 72°C with a 4 sec/cycle extension at 72°C) using ABI or Promega Taq. Before sequencing the PCR product was purified using the Qiaquick Spin kit and protocol by Qiagen or Millipore Cleanup Plates.

Sequencing reactions were carried out with the following primers: ITS2, ITS3, ITS4 and ITS5 (White *et al.* 1990). The sequencing reaction ran for 26 cycles (30 s at 96°C, 15 s at 50°C, 4 min at 60°C) for sequencing by the BigDye labelling method (Perkin-Elmer). Sequences were assembled manually.

The sequences were aligned using ClustalW as implemented by the Bioedit software packet (http://www.mbio.ncsu.edu/RNaseP/info/programs/BIOEDIT/bio edit.html), and optimized manually. The alignment can be obtained from the second author on request.

Phylogenetic analyses

The data set was subjected to Bayesian inference using the program MrBAYES version 3.0 beta4 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). Character polarity was assessed with outgroup comparison, using *Heterodermia leucomela*, *Phaeophyscia orbicularis*, *Physcia stellaris* and *Rinodina pyrina* as outgroup.

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Priors for the trees and other parameters of the model were implemented as the default settings. The models for nucleotide substitutions were selected prior to the MCMC. The model of evolution was chosen with MrModeltest Version 1.1b (Nylander 2002) in conjunction with PAUP* (Swofford 2002). The general time reversal model of evolution (GTR) with a gamma distribution of substitution rates (G) and a proportion of invariant sites (I) was suggested as the best model. Under MrBayes four Markov chains were run for 1 000 000 generation and every one hundredth tree was sampled. The tree samples of the burn-in phase (1000) were discarded. Groups with posterior probabilities above 50 are shown in the tree in Fig. 1.

Maximum parsimony analyses.

The data matrices were processed by the computer software PAUP* 4.0 (Swofford, 2002). Analyses applied a heuristic search using 1000 random addition sequences, TBR branch swapping algorithm, collapse branches if maximum branch length is zero, save multiple trees, gaps treated as missing data, and characters given equal weight. Jack-knife support values were obtained from an heuristic search using 1000 replicates with 5 random additional replicates, TBR branch swapping algorithm, save multiple trees, collapse zero length branches when maximum length is zero, gaps treated as missing data, characters given equal weight, actual deletion of characters 36·9%.

Morphology

Morphological details were studied on material in UPS. Microscopical measurements were made in water. Spore measurements are given as (min.–)M − SD–[M]–M+SD(–max.), rounded to the nearest 0·5 µm, where 'min.' and 'max.' are the extreme values recorded, M the arithmetric mean and SD the corresponding standard deviation. Measurements of other details represent extreme values. Preparation of material for Transmission Electron Microscopy was carried out as described by Nordin (2000). For the investigation a Zeiss Supra 35VP Scanning Electron Microscope with TEM detection was used.

Results

The parsimony analysis resulted in 18 most parsimonious trees with a length of 1165 steps. Jackknife support values are indicated at the nodes in Fig. 1. The topologies resulting from both the parsimony and the Bayesian analyses of resolved clades were fully congruent for jackknife values higher or equal to 90%, and conversely for posterior probabilities higher than 0·90, except for *Phaeophyscia orbicularis* and *Rinodina pyrina* which formed a clade with pp=0·91, while they formed part of a larger polytomy in the parsimony analysis. Furthermore *Dimelaena oreina* did not join *Buellia aethalea* and *Buellia ocellata* in a well-supported clade in the parsimony analysis. Here only the result of the Bayesian analysis is presented in detail (Fig. 1). Both the *Tetramelas* and the *Diplotomma* group are well-supported as monophyletic. '*Buellia*' *pulverulenta* is embedded in *Tetramelas* and does not belong to *Diplotomma*. The taxon described as *Tetramelas phaeophysciae* below is closely related to '*Buellia*' *pulverulenta*. Both these species share the sequence fragments GAGCCTTA and GCCGGAG (in ITS1) and TATAATC, TTGGAT, and CTCAC (in ITS2) as unique features in the alignment. There are numerous consistent differences between homologous bases in the ITS1 part between these two species, whereas in ITS2 only one difference was discovered in the present alignment and also in an alignment comprising only the specimens of *T. phaeophysciae* and '*Buellia*' *pulverulenta*. Sequences of these species were obtained both from Iceland and Scandinavia, and the sequences grouped together according to species. The type species of *Buellia*, *B. disciformis* (Fr.) Mudd, is part of a clade containing *B. capitis-regum* W. A. Weber, *B. muriformis* A. Nordin & Tønsberg, *B. penichra* (Tuck.) Hasse and *Hafellia dissa* (Stirt.) H. Mayrhofer & Sheard with a high posterior probablity (1.0) and moderate jack-knife support (89%).

Discussion

The ITS data support the separation of the new species *Tetramelas phaeophysciae* from *Buellia pulverulenta*, both of which are part of the well-supported *Tetramelas* group. The inclusion of *B. pulverulenta* in *Diplotomma* (Molina *et al.* 2002) was apparently premature. The *Tetramelas* group also includes *B. triphragmioides*. Together with *B. pulverulenta* it is combined into *Tetramelas* below. Also in the analysis of Helms *et al.* (2003) *B. pulverulenta* and *B. triphragmioides* were part of a strongly supported group including other *Tetramelas* species, but contrary to this analysis *B. elegans* Poelt and *B. zoharyi* Galun were also included. These two

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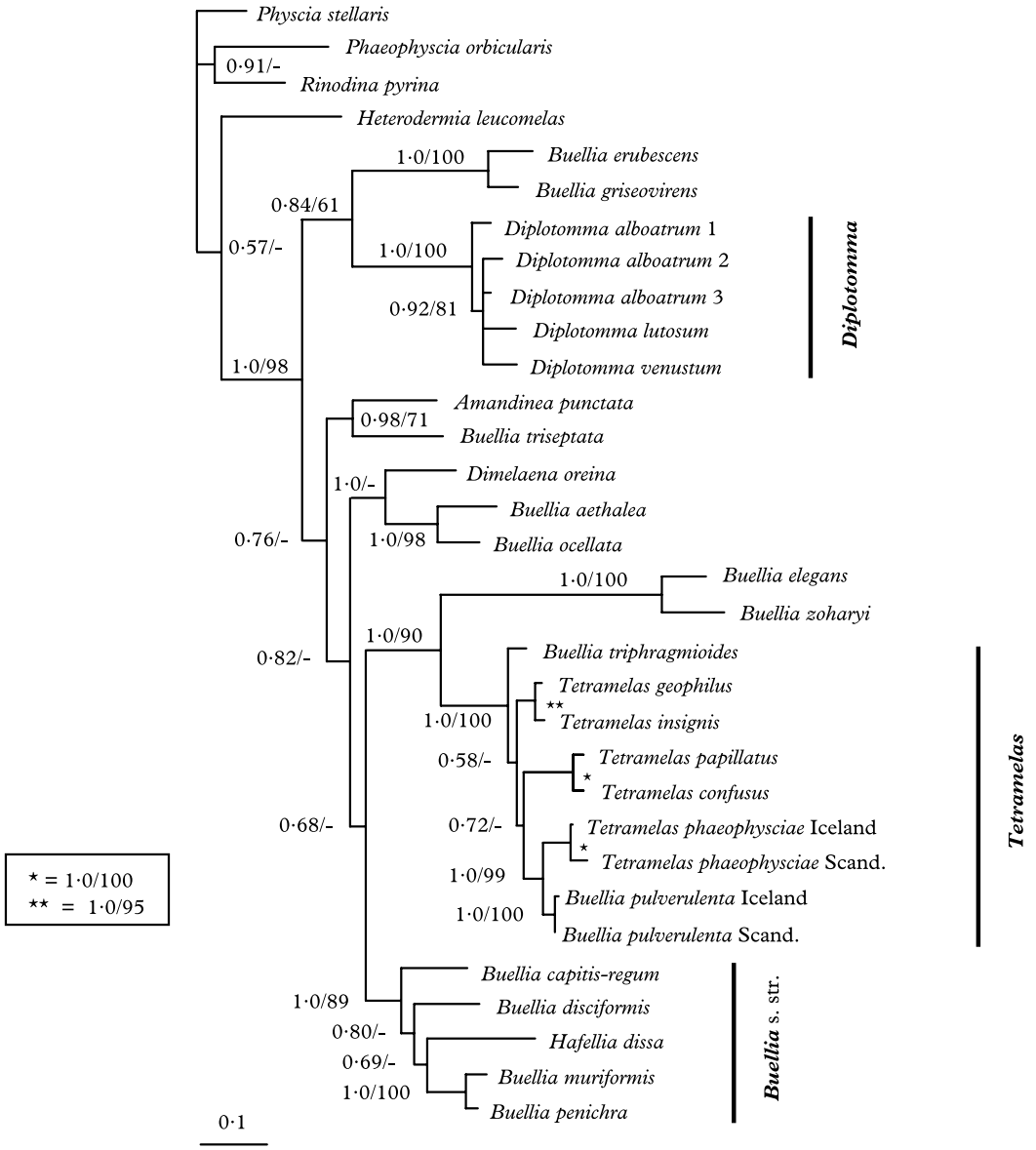


FIG. 1. Tree resulting from the Bayesian analysis. Posterior probabilities/Jackknife values are indicated at the nodes. Branch lengths correspond to the number of character changes per site.

species are apparently more closely related to *Tetramelas* than to *Buellia* s. str., but probably do not really belong to *Tetramelas* either. In both analyses this is indicated by the long branches. The recently described *Tetramelas confusus* A. Nordin (Nordin 2004) seems to be most closely related to *T. papillatus* (Sommerf.) Kalb. However, since the voucher specimen for the sequence used, unlike the Scandinavian material of *T. papillatus* (including the type), was reported to contain 6-*O*-methylarthothelin (Grube & Arup 2001), its identity remains uncertain.

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Like the *Tetramelas* group, the *Diplotomma* group has strong support, and it has been well supported also in other analyses based on molecular data (e.g. Molina *et al.* 2002; Helms *et al.* 2003). However, the relationships within the group are more problematic. At least, *D. alboatrum* 1 seems to represent a distinct taxon. It contains norstictic acid and was collected on calcareous seashore rocks in S England, and was originally labelled *D. chlorophaeum* (Hepp ex Leight.) Kr. P. Singh & S. R. Singh, a name regarded as synonymous with *D. alboatrum* (Hoffm.) Flot. by Nordin (2000). Apparently it is distinct from *D. alboatrum* 2 and 3, both lacking norstictic acid and growing on siliceous rocks and bark of *Fraxinus* respectively. For a better understanding of the group a separate analysis of the *Diplotomma* group based on well-designed sampling is needed.

The group containing *Buellia capitisregum*, *B. muriformis*, *B. penichra* and *Hafellia dissa* also includes *B. disciformis*, the type species of *Buellia*. The support for this group is not high, but all these species are here provisionally referred to *Buellia* s. str. This is in accordance with the decision made by the Committee for Fungi (Gams 2004) not to decide anything(!) for the time being concerning the proposal to conserve *Buellia* with another type (Moberg *et al.* 1999). Thus *B. disciformis* is retained as the type of *Buellia*. The group includes both a *Hafellia* species and three species with pluriseptate spores and corresponds to *Hafellia sensu* Marbach (2000). Consequently *Hafellia sensu* Marbach could not possibly be retained but should be regarded as synonymous with *Buellia*. It should also be noted that *Buellia penichra* does not belong in *Diplotomma* (into which it was validly combined by Szatala in 1941, a fact that was neglected by Nordin 2000).

The seemingly close relationships between *Dimelaena oreina* (Ach.) Norman and *Buellia aethalea* (Ach.) Th.Fr./*B. ocellata* (Flot.) Körb. and *B. erubescens* Arnold and *B. griseovirens* (Turner & Borrer ex Sm.) Almb., respectively, might be an effect of the sampling. In Helms *et al.* (2003) the former are distinctly separated, while the latter go together as in this study.

Taxonomy

Tetramelas phaeophysciae A. Nordin & Tibell sp. nov.

Buelliae pulverulentae similis, sed differt sporis semper 1-septatis, hospitibus aliis, plerumque *Phaeophyscia* spp.

Typus: Sweden, Lycksele Lappmark, Tärna par., Vilasund, shore of lake Över-Uman below Martensson's boarding-house, alt. 520 m, 66°02′N 15°00′E, on thallus and apothecia of *Phaeophyscia endococcina*, 29 August 1963, *G. E. Du Rietz* 1963: 631a (UPS—holotypus; ASU, BM, CANL, CBG, GZU, H, HMAS, LD, M, MIN, O, TNS, UPS, US—isotypi, to be distributed in Moberg, *Lich. sel. exs. Ups.*)

(Figs 2 & 3)

Obligately lichenicolous. *Thallus* consisting of hyphal system developed inside host thallus.

Apothecia 0·10–0·55 mm diam., sparse to abundant on host thallus or apothecia, sessile; disc first urceolate, later flat to convex, epruinose; margin usually distinct but excluded in strongly convex apothecia. *Excipulum* 25–50 µm thick, dark brown in major part, slightly paler in inner part; carbonized cells, secondary products, and accessory pigments absent. *Hymenium* 50–70 µm high, without oil droplets; subhymenial layers <230 µm. *Asci* 43–50 × 12–20 µm. *Paraphyses* with tips 4·0–6·0 µm wide; apical caps distinct. *Spores* (16·5–) 19·0–[19·5]–21·0(–22·0) × (6·5–)6·5–[7·0]–7·5(–9·0) µm (n=40), ellipsoid, 1-septate, usually curved; uneven wall thickenings absent; perispore rugulate, slightly thinner than proper wall (Fig. 3).

Pycnidia not observed.

Chemistry. K −, P −, C −. No substances detected with TLC.

Distribution and habitat. Tetramelas phaeophysciae is an arctic-subalpine species so far known only from Greenland, Iceland, Norway and Sweden (Fig. 4). It grows in thalli of *Phaeophyscia* and *Physcia* species, growing on rocks or rarely on the ground. So

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FIG. 2. *Tetramelas phaeophysciae*, habitus (holotype), apothecia growing on the thallus and on apothecia of *Phaeophyscia endococcina*. Scale: 0·5 mm.

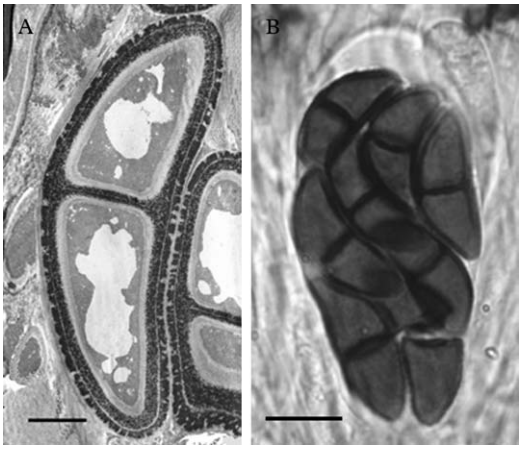


FIG. 3. *Tetramelas phaeophysciae* (holotype). A, TEM-micrograph of mature spore in ascus, the perispore (electron dense rugulate outer layer) is only slightly thinner than the proper wall (electron dense layer between the intermediate layer and the endospore); B, spores in ascus. Scales: A = 3 μm; B = 10 μm.

far known the most common host is *Phaeophyscia sciastra*, followed by *Physcia caesia*. Other known host species are *Phaeophyscia endococcina*, *Physcia dubia* and *P. tenella*. The species has mainly been found on riverbanks, shores of lakes and other humid areas.

Remarks. *Tetramelas phaeophysciae* differs from *T. pulverulentus* by the 1-septate, curved spores; the more markedly sessile, initially urceolate apothecia, long remaining flat and distinctly marginate; and the host preferences: *T. phaeophysciae* associates with *Phaeophyscia* but not *Physconia* species, while *T. pulverulentus*, associates with *Physconia* species, notably *Physconia muscigena*, but not *Phaeophyscia* species; both species, however, associate with *Physcia* species.

Tetramelas phaeophysciae, like *T. pulverulentus*, differs from other *Tetramelas* species by being obligately lichenicolous and by having a slightly thicker perispore (Fig. 3) – the other species having a perispore that is less than half as thick as the proper wall (Nordin 2004; for spore wall terminology, see Nordin & Mattsson 2001, Fig. 1). The two species also lack secondary substances, whereas most other *Tetramelas* species have xanthones, notably 6-*O*-methylarthothelin. Nonetheless, sequence data show they are closely related to the other species of the group.

In Nordin (2000: 86) some of the collections reported as *Buellia pulverulenta* refer to *Tetramelas phaeophysciae*. These are *Gelting* 10965b & 19756 (Greenland), *Nordin* 4922

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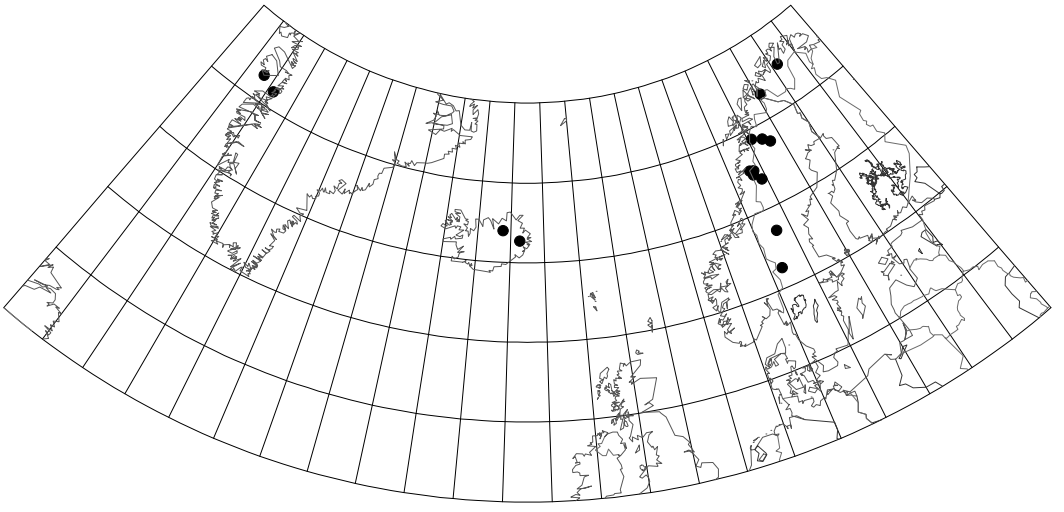


FIG. 4. Distribution of *Tetramelas phaeophysciae*.

(Iceland), *Hasselrot* (Dalarna, Sweden), *Nordin* 4788 (Jämtland, Sweden) and *Gilenstam* 322a (Lule Lappmark, Sweden).

Additional specimens examined (all in UPS). **Greenland:** Christianshaab, Igdluko, 8 m, 1952, *P. Gelting* 10965b; Godhavn, 30 m N of Arktisk Station, 22 m, 1953, *P. Gelting* 19756; Godhavn, 30 m N of Arktisk Station, 20 m, 1949, *P. Gelting* 11073b.—**Iceland.** *Austur-Island*: Nordur-Mulasýsla, Fljótsdalur, along Hengifossá River, 65°05′N 14°53′W, 65 m, 1997, *A. Nordin* 4922. *Nordur-Island*: Sudur-Thingeyjarsýsla Markhraun at Myvatn between Kálfaströnd and Geiteyjarströnd, 65°35′N 16°57′W, 300 m, 1997, *A. Nordin* 4918.—**Norway.** *Finnmark*: Porsangen, harbour bay NE of Lakselv, 1966, *I. Nordin* 3848d. *Troms*: Storfjord, River Skibotnelva at Gustavsvingen, *c*. 19 km SE of Skibotn, 69°16′N 20°29′E, 100 m, 2003, *A. Nordin* 5663.—**Sweden:** *Dalarna*: Lima par., in the ravine of Feman W of Rödhammarsgårdarna, 26 v 1961, *T. Hasselrot*. *Jämtland*: Berg par., Mt. Hoverberget, in the cleft Rämnan on W side of the mountain, 62°50′N 14°25′E, 440 m, 1997, *A. Nordin* 4788. *Lule Lappmark*: Gällivare par.,Vastenjaure, Puoltaketjejauratj, 67°30′N 16°30′E, 1965, *G. Gilenstam* 1202; Jokkmokk par., Lilla Luleälv, Blackälven, at the cascade Heliga fallet, 1963, *G. Eriksson* (*Gilenstam*) 322a; Jokkmokk par., Sarek, 1903, *B. Nilson Kajanus* (in collection of *Phaeophyscia sciastra*). *Lycksele Lappmark*: Tärna par., Ume River, small island in SW-most part of Lake Över-Uman, 66°06–07′N 14°32–33′E, 530 m, 1960, *G. E. Du Rietz* 920; Tärna par., Rönnbäck, the serpentine mountain, 65°29′N 15°27′E, 390 m, 1960, *G. E. Du Rietz* 2252e, 2258b, 2270b; Tärna par., NW of the lake Tängvattnet, SW slope of Rödingsnäset N of the end of the main road, 800 m, 1967, *R. Moberg* 886b (in collection of *Phaeophyscia sciastra*).

Tetramelas pulverulentus (Anzi) A. Nordin & Tibell comb. nov.

Abrothallus pulverulentus Anzi, *Cat. lich. Sonder.*: 116 (1860).—*Buellia pulverulenta* (Anzi) Jatta, *Syll. lich. Ital.*: 400 (1900); type: Italy, Valviola presso Premadio, Anzi (L—lectotype, not seen, UPS—isolectotype!).

This species is closely related to *Tetramelas phaeophysciae*, from which it differs mainly by its 3-septate spores (for more differences, see above). It has been characterized as an endoparasitic lichen (Hafellner & Poelt 1980), a characteristic that it shares with *T. phaeophysciae*. Both have a thicker perispore than other *Tetramelas* species, but distinctly thinner than in the *Diplotomma* species, and they lack secondary substances. For a more detailed description, see Nordin (2000).

Tetramelas triphragmioides (Anzi) A. Nordin & Tibell comb. nov.

Buellia triphragmioides Anzi, *Atti Soc. Ital. Sci. Nat.* 11: 171 (1868); type: Italy, Bormio, *Anzi* (TO, not seen).

This is a subalpine corticolous or lignicolous species having 3-septate, fairly large spores (19–27·5 × 7·5–10·5 µm), with a perispore that is about one third of the proper wall (see fig. 2c & 2d in Nordin 1997), and

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the thallus (and the apothecial pruina) contains arthothelin, a substance closely related to 6-*O*-methylarthothelin. Consequently it is well accommodated in *Tetramelas*.

We are indebted to Gert Helms, Universität Göttingen, for letting us use the unpublished ITS sequence of *Tetramelas confusus* and to Anette Axén and the Microscopy Unit, University of Uppsala, for technical assistance in connection with the TEM investigation.

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