Arthonia toensbergii, a new lichenicolous fungus on *Mycoblastus affinis* from the boreal rainforests in Norway

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Arthonia toensbergii is described from old-growth boreal rainforests in Norway. The new species parasitizes *Mycoblastus affinis* growing on branches and trunks of *Picea abies*. It can be recognised among related species by its combination of characters including the adnate, non-aggregated, matt, (brownish-)black ascomata not visibly breaking through the host thallus, $0.07-0.15 \mu m$ diam; medium olivish brown epi- and hypothecium without distinct apical caps on the tips of the paraphysoids; hyaline, slipper-shaped, 1-septate ascospores with slight constriction at the septum, $11-14 \times 4-5.5 \mu m$; hymenial gels I+ vinose, KI+ sky blue; and a KI+ blue ring in the tholus. *Arthonia toensbergii* is shown to belong to the *Bryostigma*-clade by RAxML and Bayesian analysis of mtSSU, nLSU, and *RPB2* sequence data. The related species *Arthonia parietinaria* is reported as new to Norway.

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Introduction

The boreal rainforests in Trøndelag and southern Nordland harbour a rich diversity of epiphytic lichens including a number of rare, clearly oceanic species of particular concern for biodiversity conservation (Holien & Tønsberg 1996 & 2012, Timdal et al. 2015). This so-called Trøndelag biogeographical element is in Europe largely confined to the boreal rainforests and is additionally found in similar oceanic forests in eastern and western North America (Holien & Tønsberg 1996, DellaSala 2011).

Limited data is currently available for the fungi growing as parasites or commensals on the lichens in the boreal rainforests. Published information is sparse and relates to few species including *Scutula lobariicola* Alstrup (Alstrup 1997), *Dactylospora microspora* Etayo (Holien 2001), *D. aeruginosa* Holien & Ihlen and *D. borealis* Holien & Ihlen (Ihlen et al. 2004a), *Unguiculariopsis manriquei* Etayo (Holien et al. 2016), and *Calycina alstrupii* Suija & Motiejūnaitė (Suija & Motiejūnaitė 2017). Lichenicolous *Arthonia* spp. in these forests include *A. biatoricola* Ihlen & Owe-Larss. (Ihlen et al. 2004b) growing on *Biatora efflorescens*, *A. excentrica* Th. Fr. (1867) growing on *Lepraria* spp., and *A. japewiae* Grube & Holien (Grube & Matzer 1997) growing on *Japewia subaurifera* Muhr & Tønsberg. Here, we describe an additional species of *Arthonia* parasitizing the thalli of *Mycoblastus affinis* (Schaerer) Schauer, which was occasionally

collected during the past 25 years in old-growth spruce forests including the boreal rainforests in Trøndelag.

Material and Methods

Materials and morphological investigations

Recent collections of *A. toensbergii*, *A. molendoi* (Frauenf.) R. Sant., and *A. parietinaria* Hafellner & A. Fleischhacker made within the species project *Three storied diversity: Mapping and barcoding crustose lichens and lichenicolous fungi in the Norwegian rainforests*, funded by the Norwegian Biodiversity Information Centre, are stored in TRH. Additional specimens of *A. toensbergii* were investigated from TRH collected by HH. The specimens were studied on hand sections mounted in water or lactic cotton blue. All measurements and indications of colour were made on water preparations. 10% potassium hydroxide (K), 0.2% and 1.5% iodine solutions (Idil/I, respectively) and 10% potassium hydroxide followed by 1.5% iodine solution (KI) were used for the study of the chemical properties of the ascomata.

Direct PCR amplification and sequencing

Approx. $50 \times 50 \ \mu\text{m}$ large hand sections of the hymenium were used for direct PCR amplification with the Thermo ScientificTM PhireTM Plant Direct PCR Kit following the protocol of the manufacturer. The following primers were used for PCR amplification of the mtSSU (mtSSU1 and mtSSU3R; Zoller et al. 1999), nrITS (ITS4 and ITS1f; White et al. 1990), nrLSU (LIC24R and LSU-hypR2; Bendiksby & Timdal 2013, Miadlikowska & Lutzoni 2000) and *RPB2* (*RPB2*-7cF and *RPB2*-11aR; Liu et al. 1999). Annealing temperatures were 59°C for mtSSU and nrITS, and 57°C for nrLSU and *RPB2*. The PCR products were cleaned using the ExoSAP-ITTM PCR Product Cleanup Reagent (Applied BiosystemsTM) or cut from gel and cleaned with the E.Z.N.A.® Gel Extraction Kit (Omega Bio-Tek). Sequencing was done at Eurofins Genomics GmbH, Germany. Additional sequences of the mtSSU, nLSU, and *RPB2* were obtained from Genbank for 36 Arthoniaceae and for *Alyxoria varia* (Pers.) Ertz & Tehler, Lecanographaceae (operational outgroup) (Table 1).

Alignment

Sequences were aligned using the general MAFFT settings as implemented in the GUIDANCE WEB SERVER (Penn et al. 2010) and manually corrected. Longer insertions in the nLSU and ambiguously aligned regions in the mtSSU were removed prior to the analysis. The final concatenated alignment comprised 921 (mtSSU), 1220 (nLSU), and 876 (*RPB2*) nucleotide positions, resulting in a combined alignment of 3017 nucleotide positions. In total 1262 positions were variable and 961 informative. A partitioned dataset was used for the phylogenetic analyses to enable independent parameter estimation for the three gene loci. The *RPB2* data set was further partitioned according to codon positions to allow for the higher evolutionary rate of the 3rd codon position.

ML and Bayesian analyses

A general-time-reversible model with a proportion of invariable sites (GTR-I- Γ) was found to best explain the sequence evolution for the mtSSU, nLSU, and *RPB2* data set using the Akaike Information Criterion (AIC; Akaike 1973) implemented in MEGA7 (Kumar et al. 2016). Bayesian inference (Holder & Lewis 2003, Huelsenbeck et al. 2001) and Maximum Likelihood (ML) were used for inferring phylogenetic hypotheses. The single-gene alignments were tested for conflicting

Table 1.	Specimens	used	for	the	phylogenetic	analyses	and	their	GenBank	accession	numbers.	Newly
generated	sequences a	re ind	icate	ed in	bold.							

Taxon	Voucher	mtSSU	nLSU	RPB2
Alyxoria varia	Sweden; Frisch 11/Se1 (UPS)	KJ851006	KJ851027	KJ851147
Arthonia apatetica 1	Sweden; Svensson 2017 (UPS)	KJ850992	KJ851045	KJ851125
Arthonia apatetica 2	Sweden; Hermansson 17868b (UPS)	KJ850993	KJ851056	-
Arthonia apotheciorum	Sweden; Frisch 11/Se23 (UPS)	KJ850970	-	KJ851148
Arthonia atra	Great Britain (L10170)	KY983978	-	KY983985
Arthonia biatoricola	Japan; Thor 24350 (UPS)	KJ850990	-	KJ851149
Arthonia calcarea	France; Ertz 7539 (BR)	EU704064	-	EU704028
Arthonia didyma	Belgium; Ertz 7587 (BR)	EU704047	EU704083	EU704010
Arthonia lapidicola	Sweden; Frisch 11/Se47 (S)	KJ850997	KJ851070	KJ851119
Arthonia molendoi 1	Norway; Frisch 17/No10 (TRH)	MH177777	MH177781	MH177770
Arthonia molendoi 2	Sweden; Frisch 11/Se36 (UPS)	KJ851000	KJ851051	KJ851117
Arthonia neglectula	Sweden; Frisch 10/Se90 (UPS)	KJ850989	KJ851037	KJ851118
Arthonia parietinaria	Norway; Frisch 17/No25 (TRH)	MH177778	MH177782	MH177771
Arthonia peltigerina	Sweden; Frisch 11/Se46 (S)	KJ850998	-	KJ851122
Arthonia phaeophysciae	Belgium; Ertz 16900 (UPS)	-	KJ851067	KJ851112
Arthonia punctiformis	Sweden; Thor 21658 (UPS)	KJ850973	KJ851044	KJ851113
Arthonia radiata	Sweden; Frisch 11/Se25 (UPS)	KJ850969	-	KJ851109
Arthonia spadicea	Sweden; Frisch 11/Se31 (UPS)	_	KJ851029	KJ851115
Arthonia stereocaulina	Sweden; Frisch 11/Se48 (S)	KJ850999	KJ851062	-
Arthonia toensbergii 1	Norway; Frisch 17/No131 (TRH)	MH177776	MH177780	-
Arthonia toensbergii 2	Norway; Frisch 17/No132 (TRH)	MH177775	MH177779	-
Arthothelium norvegicum	USA; McCune 31061 (UPS)	KJ851003	KJ851038	KJ851114
Arthothelium spectabile	Japan; Frisch 12/Jp179a (TNS)	KP870144	-	KP870160
Bryostigma muscigenum	Sweden; Thor 26206 (UPS)	KJ850991	KJ851052	KJ851124
Coniocarpon cinnabarinum	Uganda; Frisch 11/Ug297 (UPS)	KJ850977	KJ851059	KJ851104
Coniocarpon fallax	Great Britain (L10175)	KJ850979	-	KJ851101
Crypthonia palaeotropica	Uganda; Frisch 11/Ug457 (UPS)	KJ850961	-	KJ851084
Crypthonia vandenboomii	Uganda; Frisch 11/Ug21 (UPS)	KJ850960	-	KJ851085
Cryptothecia subnidulans	Réunion; v.d. Boom 40613 (herb. v.d. Boom)	KJ850952	-	KJ851087
Herpothallon inopinatum	Mexico; Rudolphi 12 (UPS)	KJ850964	-	KJ851099
Herpothallon rubrocinctum	Mexico; Rudolphi 5 (UPS)	KF707643	-	KF707655
Inoderma byssaceum	Japan; Thor 25952 (UPS)	KJ850962	KJ851089	KJ851040
Inoderma nipponicum	Japan; Frisch 12/Jp227a (TNS)	KP870146	-	KP870162
Inoderma subabietinum	Azores; Ertz 16885 (BR)	KP870150	-	KP870164
Myriostigma candidum	Uganda; Frisch 11/Ug125 (UPS)	KJ850959	-	KJ851096
Pachnolepia pruinata	Sweden; Frisch 11/Se34 (UPS)	KJ850967	-	KJ851098
Reichlingia syncesioides	Uganda; Frisch 11/Ug14 (UPS)	KF707651	KF707636	KF70765
Reichlingia zwackhii	Sweden; Thor 26800 (UPS)	KF707652	KF707637	KF707662
Sporodophoron cretaceum	France; Ertz 17547 (BR)	KP870151	-	KP870165
Sporodophoron gossypinum	Japan; Frisch 12/Jp186 (TNS)	KP870154	-	KP870168
Tylophoron hibernicum	Uganda; Frisch 11/Ug220 (UPS)	KJ850966	KJ851065	KJ851097

tree topologies prior to concatenation. Serious conflict was assumed when deviant tree topologies were supported by \geq 70 % bootstrap values (BS) and \geq 0.95 posterior probabilities (PP).

Maximum likelihood was performed with the RAxML-HPC BLACK BOX v. 8.2.10 implemented in the CIPRES SCIENCE GATEWAY (Miller et al. 2010) using rapid bootstrapping and full ML analysis under the GTR+GAMMA approximation allowing for a proportion of invariable sites. The analysis was stopped automatically after 402 bootstrap replicates using the bootstopping option implemented in RAxML (Pattengale et al. 2009).

Bayesian analysis was performed with MRBAYES 3.2.6 (Ronquist & Huelsenbeck 2003) implemented in the CIPRES SCIENCE GATEWAY (Miller et al. 2010). A GTR-I-Γ model of

sequence evolution was applied to the partitioned dataset, and the model parameters were estimated during the run for each gene partition separately starting from a default flat Dirichlet distribution. The analysis was run for 5.000.000 generations in 8 chains and every 100th generation was sampled. The first 50 % of trees were discarded as burnin and a 50 % majority rule consensus tree was calculated.

Results

We generated new mtSSU and nLSU sequences for two specimens, and new ITS barcode sequences for 3 specimens, of *A. toensbergii*. Sequencing of the *RPB2* failed for all three specimens. In addition, we generated mtSSU, nLSU, and *RPB2* sequences for one specimen each of *A. molendoi* (*Arthonia molendoi* 1) and *A. parietinaria* from Norway. Serious conflicts were not observed among the three single-gene alignments for both the ML and Bayesian analysis and the three gene loci were analysed together.

The tree obtained from the RAxML and Bayesian analyses (fig. 1) conforms with the results of previous phylogenetic studies of the Arthoniaceae (Frisch et al. 2014a, 2014b, 2015, 2017). *Arthonia toensbergii* falls in the *Bryostigma*-clade (Frisch et al. 2014b) that includes both lichenicolous fungi and lichens. The closest relatives in our phylogeny are the lichenicolous *A. peltigerina* (Almq.) H. Olivier, growing on *Peltigera* spp. with cyanobacterial photobionts, and the lichenized *Bryostigma muscigenum* (Th. Fr.) Frisch & G. Thor.

ITS sequences for specimens Frisch 17/No131, 132, and 133 (see under Additional specimens examined below; GenBank nos MH177772, MH177773, MH177774) show no variation in nucleotide composition.

The Species

Arthonia toensbergii Holien & Frisch, sp. nov.

MycoBank: MB824915

Diagnosis: New lichenicolous *Arthonia* on *Mycoblastus affinis* affiliated to the *Bryostigma*-clade; characterized by the adnate, non-aggregated, matt, (brownish-)black ascomata not visibly breaking through the host thallus, 0.07–0.15 μ m diam.; medium olivish brown epi- and hypothecium without distinct apical caps on the tips of the paraphysoids; hyaline, slipper-shaped, 1-septate ascospores with slight constriction at the septum, 11–14 × 4–5.5 μ m; hymenial gels I+ vinose, KI+ sky blue; and a KI+ blue ring in the tholus. Figures 1, 2.

Type: **Norway**. *Sør-Trøndelag*: Meldal, along river Svorka, 63.1344°N, 9.8231°E, ED50, on twigs of *Picea abies* in old spruce forest, c. 220 m alt., 1992-10-16, H. Holien 5482 (TRH L-1848, holotype).

Etymology: We dedicate this new species to our colleague Tor Tønsberg on the occasion of his 70th birthday.

Description: Infection causing or not a pale brownish discolouration of the host thallus; c. $2-3 \mu m$ wide thick-walled (0.5–1.0 μm) vegetative hyphae, I+ vinose, KI+ pale blue, were observed in the host thallus near the ascomata. Ascomata in small colonies, not aggregated, irregularly rounded to short elliptical, adnate, moderately to strongly convex, not visibly breaking through the host



Figure 1. Maximum likelihood tree of selected taxa in Arthoniaceae showing the phylogenetic position of *Arthonia toensbergii* (in bold) within the *Bryostigma*-clade. ML (first) and Bayesian (second) support values are presented for each node. The inlay picture shows *Mycoblastus affinis* infested by *A. toensbergii* (Holien 7644, TRH-L-17501); scale bar = 1 mm.

thallus, (brownish-)black, matt, emarginate, minutely scabrid-verruculose, 0.07–0.15 mm diam., in section 0.07–0.1 mm tall. Proper exciple 5–10 μ m wide, medium olivish brown, of more compacted paraphysoidal hyphae. Epithecium 10–15 μ m tall, medium olivish brown. Hymenium hyaline to pale brownish, 35–40 μ m tall, conglutinated; asci distantly spaced. Hypothecium up to 45 μ m tall, medium olivish brown, conglutinated. Paraphysoids loosely branched and netted, c. 1–2 μ m wide, embedded in dense gelatinous matrix; tips densely intertwined, horizontally extending above the asci, widened to 2.5–4.0 μ m, with coarse granules to small plaques of a dark brownish pigment attached to the outer walls, more rarely with distinct dark brown caps. Asci *Arthonia*-type, (broadly) clavate, with thin lateral walls (c. 1.0–1.5 μ m), 30–40 × 15–20 μ m (n=6), 8-spored (spores in 2–3 irregular rows), with broadly triangular ocular chamber. Ascospores slipper-shaped, hyaline, 1-septate, (11.0–) 11.7–13.5 (–14.0) × (4.0–) 4.3–5.1 (–5.5) μ m (n=51; 1: mean=12.6, STDV=0.86; w: mean=4.7, STDV=0.36), constricted at the septa, with thin walls and septa (\leq 0.5 μ m), with narrow, smooth perispore (\leq 0.5 μ m); browning of over-aged ascospores not observed. Pycnidia not seen.



Figure 2. Arthonia toensbergii, microscopical characters. **A**, **C** Section through an ascoma on the thallus of *Mycoblastus affinis*, showing the pigmentation of epi- and hypothecium and the arrangement of hyphae; **B** Ascus apex in KI, showing the minute blue ring in the tholus; **D**–**F** Ascospores. Note the gelatinous perispore of the young ascospore in D; **G** Ascus with ascospores. Scale bars: $A = 50 \mu m$; B, F, $G = 10 \mu m$; $C = 100 \mu m$; D, $E = 5 \mu m$.

Chemistry: Thallus not tested; ascomatal gels I_{dil} +, I+ vinose, KI+ sky blue. A tiny KI+ blue ring structure in the tholus observed. Ascospores with I+ pale vinose, KI+ pale blue perispore. Brown pigment of the granules, plaques and the gelatinous matrix of the epi- and hypothecium unchanged or slightly more greenish in K.

Ecology and Distribution: Arthonia toensbergii parasitizes the thallus of *Mycoblastus affinis* growing on branches and trunks of *Picea abies*. The species usually occurs in mixed infections with *Dactylospora borealis* Holien & Ihlen and/or a species of *Opegrapha* s.lat. that is still under investigation. *Arthonia toensbergii* is currently only known from Trøndelag. Most specimens were found in old-growth boreal rainforests rich in epiphytic cyanolichens. However, the type specimen was collected in a more species poor old-growth forest, but harbouring several lichen species characteristic of the boreal rainforest in the region including *Gyalideopsis piceicola* (Nyl.) Vězda & Poelt, *Lichinodium ahlneri* Henssen and *Szczawinskia leucopoda* Holien & Tønsb.

Additional specimens examined: **Norway**, *Sør-Trøndelag*: Rissa, Storlidalen along river Nordelva, 63°40'09.9"N, 09°58'03.9"E, on *Picea abies* branch in boreal rainforest, 170–185 m alt., 2017-09-27, A. Frisch 17/No131 (TSD N1-2-Pa6-1) (TRH L-17890), ITS: GenBank MH177774; Åfjord, Høydalmoan nature reserve, 64°02'29.0"N, 10°26'38.0"E, on *Picea abies* branch in boreal rainforest, 100–130 m alt., 2017-07-21, A. Frisch 17/No133 (TSD N3-1-Pa1-1) (TRH L-17891), ITS: GenBank MH177773; ibid., 64°02'28.7"N, 10°26'12.8"E, on *Picea abies* branch in boreal rainforest, 70–90 m alt., 2017-07-22, A. Frisch 17/No134 (TSD N3-2-Pa4-2) (TRH L-17892); Osen, Seterelva nature reserve, 64°13'24.4"N, 10°40'36.2"E, on *Picea abies* branch in boreal rainforest, 110–130 m alt., 2017-07-13, A. Frisch 17/No132 (TSD N4-2-Pa4-1) (TRH L-17893), ITS: GenBank MH177772). *Nord-Trøndelag*: Overhalla, W of Foss, 64.4795°N, 11.9944°E (ED50), on twigs of *Picea abies* in humid spruce forest, boreal rainforest, c. 80 m alt., 1997-03-13, H. Holien 7623, 7644 (TRH L-17502, TRH L-17501); Grong, W of river Gartlandselva, 64.546°N, 12.3793°E, on twigs of *Picea abies*, 100 m alt., 1995-09-05, H. Holien 6867 (TRH L-17810).

Discussion

The genus Arthonia as currently circumscribed includes a large number of lichenicolous taxa that are still rather poorly explored, despite considerable progress in recent years. In total 129 Arthonia species are listed in the most comprehensive checklist of lichenicolous fungi to date (Lawrey & Diederich 2018), of which no less than 77 have been described within the past 25 years. The lichenicolous species of Arthonia are not monophyletic as indicated by their morphological heterogeneity (e.g., Etayo 2002, Etayo & Sancho 2008, Frisch et al. 2014a, Grube et al. 1995, Ihlen & Wedin 2008, Wedin & Hafellner 1998) and recently shown in a phylogenetic study of the Arthoniaceae (Frisch et al. 2014b). Our phylogenetic analyses (fig. 1) confirm the placement of Arthonia toensbergii in the Bryostigma-clade as defined by Frisch et al. (2014b), which is concordant with its morphological characters including 1) the small rounded, strongly convex (brownish-) black ascomata adnate to the thallus, 2) olivish brown pigments in epi- and hypothecium, 3) small hyaline, thin-walled, 1-septate ascospores with slightly enlarged upper cell, and 4) Arthonia-type asci. This clade includes mostly lichenicolous fungi, besides some lichenized taxa with chlorococcoid photobionts such as Bryostigma muscigenum, Arthonia apatetica (A. Massal.) Th. Fr., A. lapidicola (Taylor) Branth & Rostrup, and A. patellulata Nyl. In the absence of a comprehensive revision, the number of lichenicolous Arthonia referable to the Brvostigmaclade can only be approximated to 40-50 from the available species descriptions. All parasitic species in the Bryostigma-clade described so far are restricted to a narrow range of closely related host taxa or to a single lichen species.

Arthonia toensbergii is the only parasitic Arthonia described from a species of Mycoblastaceae and can be distinguished from similar species in the *Bryostigma*-clade most easily by its habitat and host selection. Few parasitic Arthonia species are known from the boreal rainforests and adjacent old-growth spruce forests in central Norway, of which only A. biatoricola and A. excentrica (cf.) can be assigned to the Bryostigma-clade. The morphologically similar A. biatoricola parasitizes Biatora efflorescens and probably other Biatora species in the Northern Hemisphere (Frisch et al. 2014b, Ihlen et al. 2004b, Tarasova et al. 2017) and is shown in figure 1 to be genetically distinct from A. toensbergii. Arthonia excentrica is described from a saxicolous species of Lepraria, probably L. neglecta (Nyl.) Erichsen, from the Brennevinsfjorden on Svalbard (Fries 1867). It seems doubtful that the Arthonia parasitizing Lepraria spp. on trunk bases of spruce in the boreal spruce forests in Scandinavia represents the same taxon. Beside its habitat and host selection, A. excentrica differs from A. toensbergii in the less convex and distinctly larger (0.25-0.35 mm) pure black apothecia, and the much darker epi- and hypothecium. Arthonia neglectula Nyl., another parasitic species on Lepraria spp. that may occur in these forests, differs among other characters in the pure black ascomata with a dark brown epithecium, the smaller ascospores $(7-10 \times 3-4 \text{ µm})$, and the K+ purplish lower hymenium and hypothecium. This species is typically found in underhangs and crevices of rocks and tree bases shaded from direct rain. Arthonia digitatae, which is known for Scandinavia from northern Sweden (Ihlen & Wedin 2005), differs in the smaller ascospores $(9-11 \times 3-4.5 \ \mu\text{m})$, the often aggregated ascomata, and in causing strong concentric infections on the basal squamules of *Cladonia digitata* and *C. pleurota*, typically in slightly rain-shaded situations.

The recently described *A. parietinaria* (Fleischhacker et al. 2016), which is here reported for the first time from Norway (Rogaland, Rennesøy, Vikevåg, on apple tree in farm, Frisch 17/No25, TRH-L-17926), parasitizes *Xanthoria parietina* and is genetically separated (Fig. 1). Besides its host selection, this species differs in the darker dull black ascomata that are often grouped together and a more greyish-bluish epihymenium turning chestnut-brown in K.

The phylogenetic analysis places *A. toensbergii* in a common clade with the lichenized *Bryostigma muscigenum* and the lichenicolous *A. peltigerina*. The latter species could represent a week or facultative lichenicolous fungus, as minute, lichenized granules with green coccal algae were sparsely neighbouring the ascomata of a specimen sequenced for the phylogenetic study of Frisch et al. (2014b). *Arthonia toensbergii* may belong to the Trøndelag phytogeographical element that includes epiphytic lichens having their main distribution range within Europe in the boreal rainforests in Norway, but additional information on its distribution is needed for confirmation.

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