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Molecular systematics and species delimitation in Coniocarpon and Arthonia punctiformis s.lat. in Norway

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ABSTRACT

The diversity and distribution of many groups of crustose lichens are incompletely known, much due to their high levels of homoplasy and phenotypic plasticity. Lichens are indicator species for habitat quality and of great significance for biodiversity conservation. Increased knowledge is therefore important for improved natural resource management. The genus *Coniocarpon* and *Arthonia punctiformis* s.lat. represent two such insufficiently known groups in Norway. This study is aiming at delimiting species in *Coniocarpon* and *A. punctiformis* s.lat. in Norway based on an integrative taxonomy approach. The material studied comprises 115 specimens of *Coniocarpon* and 35 specimens of *A. punctiformis* s.lat., obtained through recent collecting efforts or received from major fungaria in Denmark, Finland, Norway and Sweden as well as from private collectors. This study investigated (1) phylogenetic relationship based on Bayesian and maximum likelihood analyses of four genetic markers (mtSSU, nITS, nLSU and *RPB2*), (2) morphology and anatomy using standard light microscopy, and (3) secondary lichen chemistry using HPTLC. The results show three genetically distinct lineages of *Coniocarpon* in Norway, representing *C. cinnabarinum*, *C. fallax* and *C. cuspidans*, the latter originally described as *Arthonia cinnabarina* f. *cuspidans* and herein raised to species level. All three species are supported by morphological and anatomical data (e.g., ascoma shape, distribution of pruina, ascospore size and septation) and phytochemistry. The molecular phylogenetic results on *A. punctiformis* s.lat. show two main lineages (*A. punctiformis* 1 and 4), in addition to two genetically distinct specimens (*A. punctiformis* 2 and 3). The two main lineages differ in their host tree distribution; *A. punctiformis* 1 is collected from *Betula pendula* and *B. pubescens*, while specimens of *A. punctiformis* 4 occur on *Corylus avellana, Fraxinus excelsior, Hippophae rhamnoides* and *Tilia cordata*. Specimens collected from *Sorbus aucuparia* occur in both lineages. Morphological differences were observed in ascospore size and shape, ascoma shape and chemical differences in the amyloidity of their ascomatal gels. The species descriptions of *A. punctiformis* 2 and 3 are preliminary due to a small sample size and might need adjustments in the future when more specimens are available. The nomenclature of the observed genetic lineages is currently unsolved. This is mainly due to the extensive synonymy of *A. punctiformis* and the inaccessibility of important type specimens.

SAMMENDRAG

Mangfoldet og utbredelsen av mange grupper skorpelav er ukjent, mye på grunn av homoplasi og fenotypisk plastisitet. Mange lav fungerer som indikator arter for habitatkvalitet og er dermed av stor betydning innen bevaringsbiologi. Økt kunnskap innen denne organismegruppen er derfor viktig for naturressursforvaltningen. Slekta *Coniocarpon* og artskomplekset *Arthonia punctiformis* s.lat. representerer to slike utilstrekkelig kjente lav-grupper i Norge. Denne studien tar sikte på å avgrense arter i *Coniocarpon* og *A. punctiformis* s.lat. i Norge basert på en tilnærming kalt integrert taksonomi. Materialet som studeres består av 115 eksemplarer av *Coniocarpon* og 35 eksemplarer av *A. punctiformis* s.lat. Materialet er dels tilkommet gjennom innsamlingsarbeid (2017 og 2018) og dels lånt fra fungarier i Danmark, Finland, Norge og Sverige, samt fra private samlere. Denne studien har undersøkt (1) det fylogenetiske slektskapet basert på Bayesiansk og maksimum likelihood analyse av fire genetiske markører (mtSSU, nITS, nLSU og *RPB2*), (2) morfologi og anatomi ved hjelp av standard lysmikroskopi og (3) sekundær lavkjemi ved hjelp av HPTLC. Resultatene viser tre distinkte evolusjonære linjer av *Coniocarpon* i Norge: *C. cinnabarinum*, *C. fallax* og *C. cuspidans*, sistnevnte beskrevet som *Arthonia cinnabarina* f. *cuspidans* og er i dette studiet hevet til artsnivå. Alle tre arter støttes av morfologiske og anatomiske data (for eksempel ascoma form, fordeling av pruina, størrelse og septering av ascosporer) og lavkjemi. De molekylære fylogenetiske resultatene av *A. punctiformis* s.lat. viser to distinkte evolusjonære linjer (*A. punctiformis* 1 og 4), i tillegg til to genetisk distinkte belegg (*A. punctiformis* 2 og 3). De to distinkte evolusjonære linjene skiller seg fra hverandre i preferansen av vertstre; *A. punctiformis* 1 er samlet fra *Betula pendula* og *B. pubescens*, mens *A. punctiformis* 4 forekommer på *Corylus avellana*, *Fraxinus excelsior*, *Hippophae rhamnoides* og *Tilia cordata*. *Sorbus aucuparia* forekommer som vertstre i begge de evolusjonære linjene. Morfologiske forskjeller ble observert i størrelse og form på ascosporer, formen på ascoma og forskjeller i amyloiditeten av gelen i ascoma. Artsbeskrivelsene av *A. punctiformis* 2 og 3 er midlertidig på grunn av få tilgjengelige belegg. Dermed kan tilpasninger skje i fremtiden når flere belegg blir tilgjengelig. Nomenklaturen for de observerte evolusjonære linjene er foreløpig uavklart. Dette på grunn av omfattende synonymi i *A. punctiformis* og manglende tilgang på viktig type materiale.

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1 INTRODUCTION

Species delimitation is crucial for improved natural resource management and biodiversity conservation (Lumbsch & Leavitt 2011). The basic units of conservation which usually are set to species needs to be recognized in order to develop conservation strategies. Lichens is a group where species delimitation may be challenging due to unclear species boundaries and/or cryptic diversity (e.g., Bendiksby et al. 2015, Carlsen et al. 2012, Leavitt et al. 2011, Lücking et al. 2014, Molina et al. 2011). This applies for instance to the genus *Coniocarpon* DC. and *Arthonia punctiformis* Ach. s.lat. in Norway.

Arthoniales is one of the largest orders accommodating crustose and fruticose lichens (Sundin & Tehler 1998), comprising in total around 1500 species of lichenized, lichenicolous and saprotrophic fungi (Frisch et al. 2014, Van den Broeck et al. 2018). About 800 species belong to the family Arthoniaceae Rchb. (Frisch & Thor 2010). The most species rich genus in Arthoniaceae is *Arthonia* Ach., with around 500 species (Grube 1995). *Arthonia* is a polyphyletic genus with high diversity in morphology, ecology, distribution and habitat preferences (Frisch et al. 2015). In the process of splitting *Arthonia* into monophyletic groups, several genera have been described or resurrected recently, e.g., *Bryostigma* Poelt & Döbbeler, *Coniarthonia* Grube, *Felipes* (Ach.) Frisch & G.Thor, *Inoderma* (Ach.) Gray, *Melarthonis* Frisch & G.Thor and *Pachnolepia* A.Massal. (Frisch et al. 2014, Frisch et al. 2015, Grube 2001). The genus affiliation of *A. punctiformis* s.lat. is questioned due to its phylogenetic placement on a clade separated from *A. radiata* (Pers.) Ach., the type species of *Arthonia* (Frisch et al. 2014).

Coniocarpon is mainly distributed in humid tropical to warm-temperate regions of the world, reaching higher latitudes, for instance, in the boreo-nemoral rainforests and other highly oceanic habitats in Norway. The boreo-nemoral rainforests in Norway, located between 58–62° N (DellaSala et al. 2011), are categorized as vulnerable (VU) in the *Norwegian Red List of Nature Types 2018* (Blom 2018). *Coniocarpon* and other taxa restricted to the boreo-nemoral rainforests are of particular importance for biodiversity conservation due to their limited distribution, which makes them vulnerable to extinction.

Coniocarpon is characterized within Arthoniaceae mainly by crystalline orange, red and purple quinoid pigments in the ascomata, dissolving with purple solution in K, macrocephalic transversely septate ascospores and ascoma morphology (Frisch et al. 2014, Frisch et al. 2018, Van den Broeck

et al. 2018). The colorful pigmentation of the ascomata, together with its high value of nature conservation, are two reasons why *Coniocarpon* has frequently been collected in Norway. However, the morphological delimitation between the two reported species, C. *cinnabarinum* DC. and *C. fallax* (Ach.) Grube, is challenging due to ambiguous interpretation of the morphological characters (Blom et al. 2015).

In databases and scientific collections in Norway, *C. cinnabarinum* and *C. fallax* are often still included under the names *Arthonia cinnabarina* (DC.) Wallr. and *A. elegans* (Ach.) Almq., respectively, in the sense of *The Lichen Flora of Great Britain and Ireland* (Smith et al. 2009). *Coniocarpon* was resurrected by Frisch et al. (2014) and *C. fallax* was accepted as the correct name for *A. elegans* in the 7th edition of *An Illustrated Guide to the British and Irish Species* (Dobson 2018), with *A. elegans* as its synonym (Van den Broeck et al. 2018). Both species are listed as vulnerable (VU) on the *Norwegian Red List of Species 2015* (as *A. cinnabarina* and *A. elegans*; Henriksen & Hilmo 2015).

Preliminary morphological and molecular evidence indicates three distinct taxa of *Coniocarpon* in Norway. At the world level, *C. cinnabarinum* has been reported from Europe, America, Asia, Africa and Oceania (Smith et al. 2009), while *C. fallax* has been reported from the West British Isles, temperate Europe, the Azores and Asia (Aptroot & Sparrius 2003, Smith et al. 2009). The distribution of *Coniocarpon* is well established in Norway, while the frequency and distribution of its species is insufficiently known. Collection data prior to this study report *C. cinnabarinum* from Vest-Agder, Rogaland, Hordaland and Møre og Romsdal, while *C. fallax* occurs in the same counties except Møre og Romsdal (Henriksen & Hilmo 2015). Moreover, *C. cinnabarinum* is reported in Scandinavia from Gotland and Skåne in Sweden (ArtDatabanken 2015, Santesson et al. 2004) and from Denmark (Søchting & Alstrup 2008), while *C. fallax* in Scandinavia has not been reported from outside Norway.

The non-lichenized fungi within *A. punctiformis* s.lat. occur in a family where most members are lichenized. Their biology has never been studied in detail, but they are often described as saprophytic in literature (Frisch et al. 2014). The species in this complex are typically growing as pioneers in the bark of living twigs and branches of various trees and shrubs causing no visible damage. In addition to not being lichenized, they are characterized morphologically by black, maculate, rounded to lirellate ascomata breaking through the bark substrate, oliveish to brownish

ascomatal pigments, the lack of lichen compounds demonstrable by HPTLC and hyaline, transversely septate ascospores resembling those of *A. radiata* (Smith et al. 2009).

Preliminary molecular data indicate that *A. punctiformis* s.lat. is heterogeneous both at the world level and in Norway. Specimens of *A. punctiformis* s.lat. collected in Japan and Sweden are genetically distinct and separated by the lichenized *A. dispersa* (Schrad.) Nyl. in a molecular phylogeny by Frisch et al. (2014). Initial molecular data of *A. punctiformis* s.lat. in Norway show that specimens collected from *Hippophae rhamnoides* L. and *Betula pubescens* Roth. differ in their mtSSU sequences (A. Frisch, pers. comm.). Preliminary morphological data, however, indicate no differences. At the world level, *A. punctiformis* has been reported from Europe, North America, Asia and Africa (Smith et al. 2009). In Norway, *A. punctiformis* s.lat. is widely distributed from the sea level up to 400 m elevation, being reported from all counties except Akershus, Aust-Agder, Hedmark, Telemark, Vest-Agder and Østfold (Timdal 2019).

Hence, it can conceivably be hypothesised that 1) *Coniocarpon* consists of three genotypes in Norway, 2) *A. punctiformis* is a heterogeneous species in Norway, 3) the genotypes of *A. punctiformis* differ in their preferred host tree species. This study aims at delimiting the taxa of *Coniocarpon* and *A. punctiformis* s.lat. in Norway based on an integrative taxonomic approach, including morphological, chemical and molecular data. All available specimens of *Coniocarpon* and selected specimens of *A. punctiformis* s.lat. housed in fungaria in Denmark, Norway and Sweden will be revised. Finally, the species distributions of *Coniocarpon* in Scandinavia and *A. punctiformis* s.lat. in Norway will be mapped, potentially new species will be described and keys for the Norwegian species of *Coniocarpon* and *A. punctiformis* s.lat. will be provided.

2 MATERIAL AND METHODS

2.1 Taxon selection

New specimens of *Coniocarpon* for this study were collected in the boreo-nemoral rainforests on the west coast of Norway from Vest-Agder to Møre og Romsdal. New specimens of *A. punctiformis* s.lat. were collected in various habitats from Vest-Agder to Nordland, including coastal shrub and heathland, boreo-nemoral and boreal rainforests, and open agricultural landscape and parkland. Additional herbarium specimens of *Coniocarpon* were made available from Bergen (BG), Copenhagen (C), Helsinki (H), Oslo (O), Paris (PC), Prag (PRA), Stockholm (S), Trondheim (TRH) and Uppsala (UPS). All specimens of *A. punctiformis* s.lat. needed for this study were available in Trondheim (TRH).

2.2 DNA extraction and sequencing

DNA was isolated from specimens collected less than one year ago, due to prior knowledge of fast DNA degradation in these taxa (e.g., Frisch et al. 2014). Genomic DNA was extracted following one of three methods. (1) Five to eight ascomata were sampled in 2 ml microcentrifuge tubes with metal beads and crushed into a fine powder using a crushing machine. Subsequently, genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions. (2) Three to five ascomata were sampled directly in 0.2 ml Eppendorf PCR Tubes with 30 µl Dilution Buffer (Phire Plant Direct PCR Kit, ThermoFisher Scientific) and crushed with tweezers. (3) Small cuttings (ca. 50–100 µm × 50–100 µm in size) of the hymenium were sampled in 0.2 ml Eppendorf PCR Tubes and directly used for PCR amplification. The Phire Plant Direct PCR Kit (ThermoFisher Scientific) was used for PCR amplification in all three methods. Each 20 µl of PCR reaction contained 10 µl 2× Phire Plant PCR Buffer, 0.4 µl Phire Hot Start II DNA Polymerase, 1 µl of each primer for all genetic markers except *RPB2* (1.5 µl of each primer), 1 µl genomic DNA (1:1) or the lichen samples, and was filled with H_2O to the final volume. If PCR amplification resulted in weak products, 2 µl genomic DNA (1:10) was added. PCR amplification of *Coniocarpon* was done for the mtSSU, nITS and the protein-coding gene *RPB2* with the following primers: mtSSU1 + mtSSU3R (Zoller

et al. 1999), ITS-1F + ITS4 (Larena et al. 1999, White et al. 1990) and *RPB2*-7cF + *RPB2*-11aR (Liu et al., 1999), respectively. PCR amplification of *A. punctiformis* s.lat. was done for the mtSSU and *RPB2* using the same primer sets, whereas nLSU and ITS2 were amplified using LIC24R + LSU-hypR2 (Bendiksby & Timdal 2013, Miadlikowska & Lutzoni 2000) and ITS-LichF + ITS4 (Bendiksby & Timdal, 2013, Miadlikowska & Lutzoni 2000), respectively. PCR cycling conditions for *RPB2* and nLSU started with an initial denaturation at 98 °C for 5 min, followed by 40 cycles of 98 °C for 5 s, 57 °C for 5 s, and 72 °C for 20 s, followed by a final extension of 72 °C for 7 min. For mtSSU and nITS, annealing temperature was set to 59 °C. For ITS2 the annealing temperature was set to 62 °C. The PCR products were visualized on a 1 % agarose gel stained with SYBR Safe DNA gel stain (ThermoFisher Scientific) under UV light. Clean PCR products lacking visible contaminations were purified by adding 5 µl ExoSAP-IT Express PCR Cleanup (1:3 concentration; ThermoFisher Scientific) to the PCR reactions. PCR reactions resulting in more than a single product were purified using the E.Z.N.A. Gel Extraction Kit (Omega BIO-TEK) following the manufacturer's instructions, except for step 8 where the second wash buffer step was repeated. The PCR products were sent to Eurofins Genomics (Germany) for Sanger sequencing using the same primers as for the PCR reactions.

2.3 Sequence alignment and phylogenetic analyses

The sequences were edited and aligned using BioEdit v.7.0.5.3 (Hall 1999). The identity of the sequences was verified using the BLAST search in GenBank. Outgroup taxa and additional sequences of *Coniocarpon* and *A. punctiformis* s.lat. were downloaded from GenBank. Outgroup taxa were selected based on their phylogenetic position in Frisch et al. (2014) and Van den Broeck et al. (2018). To examine topological incongruence among data sets, maximum likelihood (ML) bootstrapping analyses were carried out on each of the single-gene data sets using the RAxML-HPC Blackbox ver. 8.2.10 (Stamatakis 2014). Topological incongruence was assumed if conflicting tree topologies were supported by ≥ 70 % ML support. Since topological incongruence could not be observed, maximum likelihood (ML) bootstrapping analyses were carried out on the concatenated three-locus dataset of 43 accessions for *Coniocarpon* and the concatenated four-locus dataset of 54 samples for *A. punctiformis* s.lat. using the same settings as for the single-gene analyses.

The best-fit evolutionary models for each partition using the Bayesian information criterion (BIC; Schwarz 1979) were estimated in PartitionFinder2 ver. 2.1.1. (Lanfear et al. 2016). The input data included both ingroup and outgroup taxa. The pre-set partitions were mtSSU, *RPB2*/1st codon position, *RPB2*/2nd + 3rd codon position, nLSU, and ITS1, 5.8S, ITS2. Bayesian analyses were performed using MrBayes v.3.1.2 (Huelsenbeck et al. 2001, Ronquist & Huelsenbeck 2003). Each MCMC run was using four independent chains and 10 million generations, sampling trees every 1000th generation. The software TRACER ver. 1.7.1 (Rambaut et al. 2018) was used to ensure convergence by plotting the log-likelihood values of the sample points against generation time. All phylogenetic analyses were running on the CIPRES Science Gateway (Miller et al. 2010). Phylogenetic trees were visualized using FigTree ver. 1.4.4 (Rambaut 2018). Informative sites estimated for ingroup taxa for the single loci were tracked by using Winclada ver. 1.61 (Nixon 1999-2002).

2.4 Morphological and chemical investigations

The morphology of all specimens was examined using a Leica M80 stereomicroscope and a Zeiss Standard Binocular microscope. Macroscopic photographs were taken with a Leica MZ16A stereomicroscope fitted with a Leica DFC420 camera. Microscopic photographs were taken with a Leica CTR6000 microscope fitted with a Leica DFC365 camera. Sections of ascomata and lichen thalli were cut by hand and mounted in water or lactic acid cotton blue (LCB). Length and width were measured for single ascoma as well as for aggregations composed of several ascomata. For the epithecium, exciple, hymenium and hypothecium, measurements were performed in LCB. Measurements of asci and ascospores were performed in water using squashed preparations. Only fully developed ascospores and commonly asci containing mature ascospores were measured. Ascospore measurements are presented as (min.–)mean±STD(–max.). The amyloid reaction of the apothecia was tested by using 0.2 % (I_{dil}) and 1 % (I) iodine solution, and 1 % iodine solution after pretreatment with 10% potassium hydroxide (KOH) in water (KI). The quinoid pigments and Ca-oxalate crystals were measured in water and their shape studied. Later, the crystals reaction with KOH was observed. The quinoid pigments were identified in *Coniocarpon* by HPTLC (Arup et al. 1993) in solvent C. HPTLC was not performed for *A. punctiformis* s.lat. as lichen secondary compounds are unknown in this group.

2.5 Distribution maps

Based on occurrence information of the revised specimens, the species distributions of *Coniocarpon* in Scandinavia and *A. punctiformis* s.lat. in Norway were illustrated by adding a delimited text layer to a Wikimedia map from QuickMap services in QGIS ver. 3.6.2. (QGIS Development Team 2019). Specimens collected from the mid-80s and onwards were placed on the maps by their geographical coordinates, while specimens collected 1870–1983 and lacking geographical coordinates were placed on the maps based on locality information. All geographical coordinates were converted to degrees, minutes and seconds when necessary. The Earth Point coordinate converter (http://www.earthpoint.us/Convert.aspx) was used to convert coordinates.

3 RESULTS

3.1 Molecular data

A total of 206 new sequences were obtained for this study and 50 additional sequences were retrieved from GenBank. Seventy five of the 206 new sequences were generated for 25 specimens of *Coniocarpon* from Norway and 1 specimen from Great Britain (mtSSU 26, nITS 25, *RPB2* 24). Fourteen sequences (mtSSU 8, *RPB2* 6) for 8 specimens of *Coniocarpon* from Great Britain, Japan, Norway, Rwanda and Uganda were added from GenBank.

One hundred and eleven of the 208 new sequences were generated for 33 specimens of *A. punctiformis* s.lat. collected in Norway (mtSSU 33, nITS2 20, nLSU 28, *RPB2* 30). Additional 5 sequences (mtSSU 2, nLSU 2, *RPB2* 1) for 2 specimens of *A. punctiformis* s.lat. from Sweden and *A.* aff. *punctiformis* from Japan, respectively, were added from GenBank. Further 20 (mtSSU 6, ITS2 2, nLSU 6, *RPB2* 6) of the 206 new sequences were generated for 6 specimens of *A. atra* (Pers.) Schneid. (2), *A. expendienda* (Nyl.) Leight. (2) and *A. radiata* (2). The remaining 31 sequences from GenBank (mtSSU 15, nLSU 2, *RPB2* 14) represent the 13 outgroup taxa used for the phylogenetic analyses (Table A1, Appendix A; Table B2, Appendix B).

Two of the four genetic markers (nITS and nLSU) amplified differently in the two target taxa. The PCR amplification and sequencing of the nLSU failed for *Coniocarpon* with the selected set of primers, while the ITS2 amplified more successfully in *A. punctiformis* s.lat. than the entire nITS. Phylogeny informative sites were found for the ingroup taxa of *Coniocarpon* (mtSSU 61, ITS1 160, 5.8S 0, ITS2 84, *RPB2* 127) and *A. punctiformis* s.lat. (mtSSU 53, ITS2 21, nLSU 24, *RPB2* 151).

The software PartitionFinder2 ver. 2.1.1. (Lanfear et al. 2016) suggested the following substitution models for five subsets in *Coniocarpon*: GTR+G for mtSSU, K80+1 for *RPB2*/1st, F81+I for 5.8s and *RPB2*/2nd, HKY+G for *RPB2*/3rd, HKY+I for ITS1 and ITS2. The same software suggested the following substitution models for five subsets in *A. punctiformis* s.lat.: HKY+I+G for mtSSU, GTR+I+G for *RPB2*/1st and nLSU, F81+I for *RPB2*/2nd, HKY+G for *RPB2*/3rd and ITS2. The RAxML (Pattengale et al. 2010) analysis was stopped automatically after 402 bootstrap replicates in *Coniocarpon* and 408 bootstrap replicates in *A. punctiformis* s.lat. using the MRE-based bootstopping criterion. Bayesian phylogenetic analyses sampled every

1000th out of 10 000 000 generations, resulting in 10 000 sampled trees for each analysis. After removal of a burnin of 25 %, 7500 trees were summarized in the final Bayesian 50% majority-rule consensus trees.

3.2 Phylogeny

The phylogenetic hypothesis of *Coniocarpon* in Norway based on Bayesian and maximum likelihood analyses shows three distinct and well supported lineages of *Coniocarpon* (Fig. 1). The tree recovers *Coniocarpon* as monophyletic using the selected taxon and outgroup sampling from the Arthonioid sub-clade in Arthoniaceae. *Coniocarpon cinnabarinum* from Rwanda and Uganda are phylogenetic sisters to *C. cinnabarinum* in Norway, while *C. cinnabarinum* from Japan (low RAxML support and lacking Bayesian support) is genetically distinct and sister to the remaining taxa. The two sampled specimens from Great Britain are genetically close to *C. cuspidans* (Nyl.) Moen, Frisch & Grube and *C. fallax* in Norway, respectively.

The phylogenetic hypothesis of *A. punctiformis* s.lat. in Norway based on Bayesian and maximum likelihood analyses shows two well supported lineages of *A. punctiformis* s.lat. (*A. punctiformis* 1 and 4) (Fig. 2). Moreover, two genetically distinct specimens (*A. punctiformis* 2 and 3) form a clade with *A. punctiforms* 1 in the RAxML and Bayesian analyses, but the two analyses disagree in which lineage is the closest relative of *A. punctiformis* 1. The study recovers *A. punctiformis* s.lat. including *A. dispersa* as monophyletic using the selected outgroup sampling from the Arthonioid sub-clade in Arthoniaceae.

Arthonia aff. *punctiformis* growing on *Betula* sp. in Japan is sister to *A. punctiformis* 4 growing on *Betula* spp. and *Sorbus aucuparia* in Scandinavia, supported by the RAxML but not the Bayesian analysis. A specimen of *A. punctiformis* collected from *B. pendula* Roth in Sweden is placed among *A. punctiformis* 4 from Norway. *Arthonia excipienda* is included in a molecular phylogeny for the first time. It is phylogenetic sister to a clade accommodating a monophyletic *A. radiata*-group (including *A. apotheciorum* A. Massal., *A. calcarea* (Sm.) Ertz & Diederich, *A. radiata*, *A. subfuscicola* (Linds.) Triebel), and *A. punctiformis* s.lat. incl. *A. dispersa*.

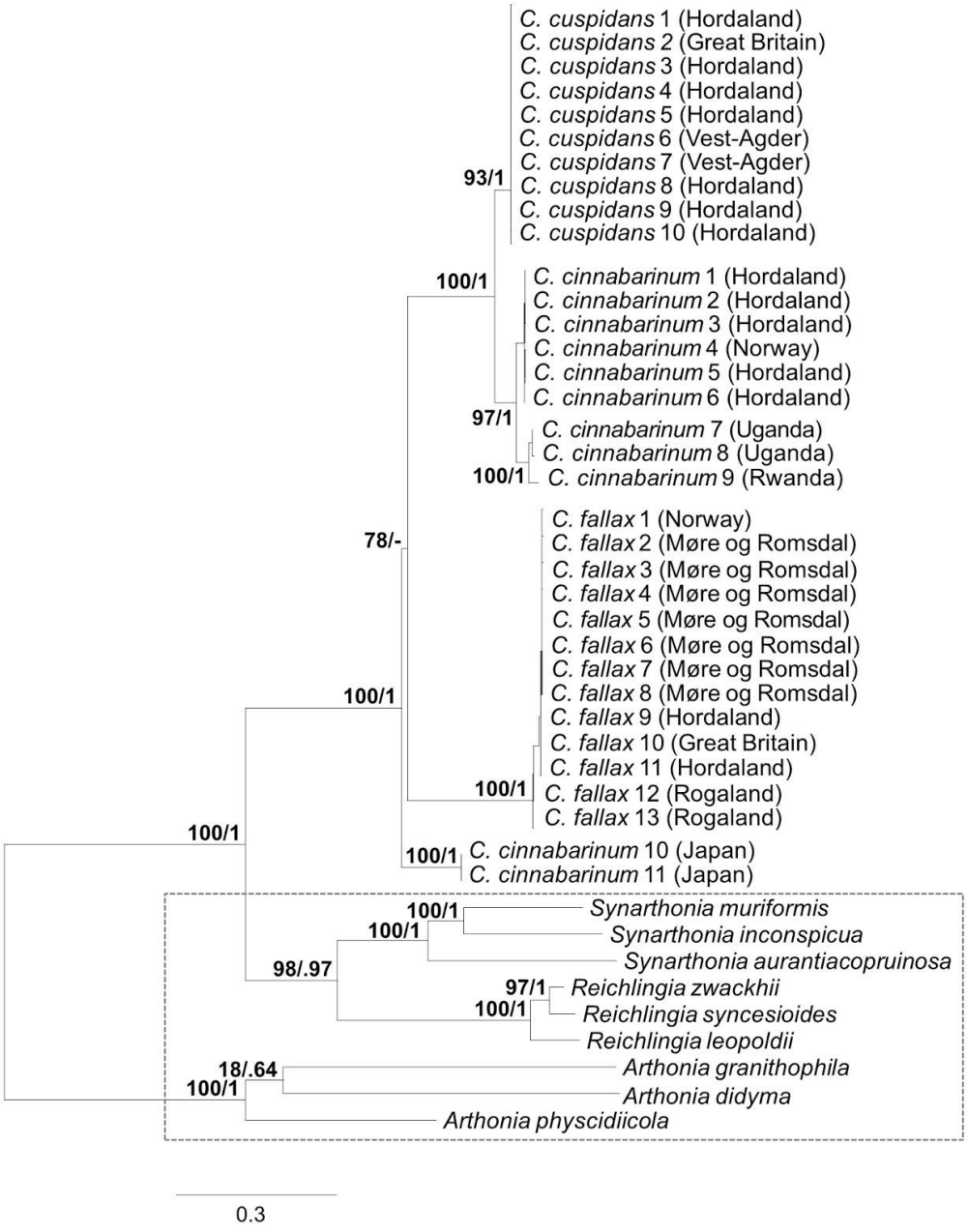

Fig. 1. RAxML phylogenetic tree of *Coniocarpon* in Norway based on mtSSU, nITS and *RPB2* sequence data. Additional specimens of *Coniocarpon* from Great Britain, Japan, Rwanda and Uganda are shown among the ingroup taxa. Outgroup taxa are marked by a dashed rectangle. RAxML bootstrap (first) and Bayesian (second) support values are indicated.

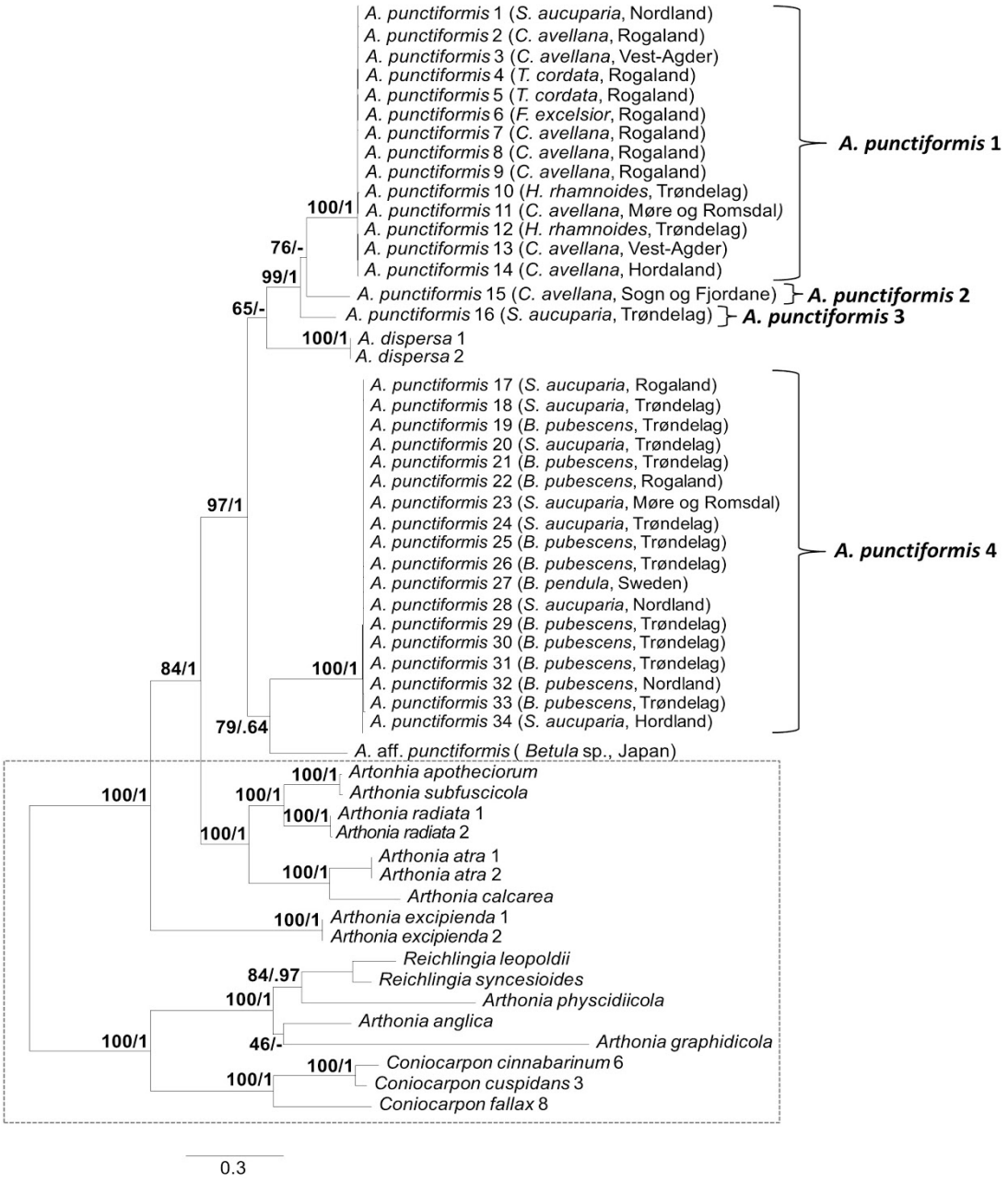

Fig. 2. RAxML phylogenetic tree of *Arthonia punctiformis* s.lat. in Norway based on mtSSU, nITS2, nLSU and *RPB2* sequence data. The brackets indicate the four lineages of *A. punctiformis* s.lat. Additional specimens of *A. punctiformis* from Japan and Sweden are included. Outgroup taxa are marked by a dashed rectangle. RAxML bootstrap (first) and Bayesian (second) support values are indicated.

3.3 Morphology and chemical characters

The morphology of 115 specimens of *Coniocarpon* (Norway 87, Sweden 8, Denmark 16, Great Britain 1, Austria 1, Turkey 1, Scotland 1) was studied. Forty-four specimens were identified as *C. cinnabarinum*, 29 as *C. cuspidans* and 42 as *C. fallax.* Ascospore size (Fig. 3), ascospore septation (Fig. 4A–C), ascoma shape and the distribution of pruina (Fig. 5A–D) were identified as useful characters for species distinction. Moreover, differences were observed in the quinoid pigment patterns revealed by HPTLC (Fig. 6) and the amyloidity of the ascomatal gels. Four quinoid pigments were identified showing different colors on the HPTLC plates prior to sulphuric acid treatment and charring (A1 reddish, A2 purple, A3 yellow, A4 reddish). The quionid pigments were named according to Frisch et al. (2018), except for the newly identified A4. The chemical results for all species are summarized in the taxonomy section. The identification of species based on morphology and chemical properties alone was usually possible, but scanty or poorly preserved specimens might be difficult to assign to their respective taxon.

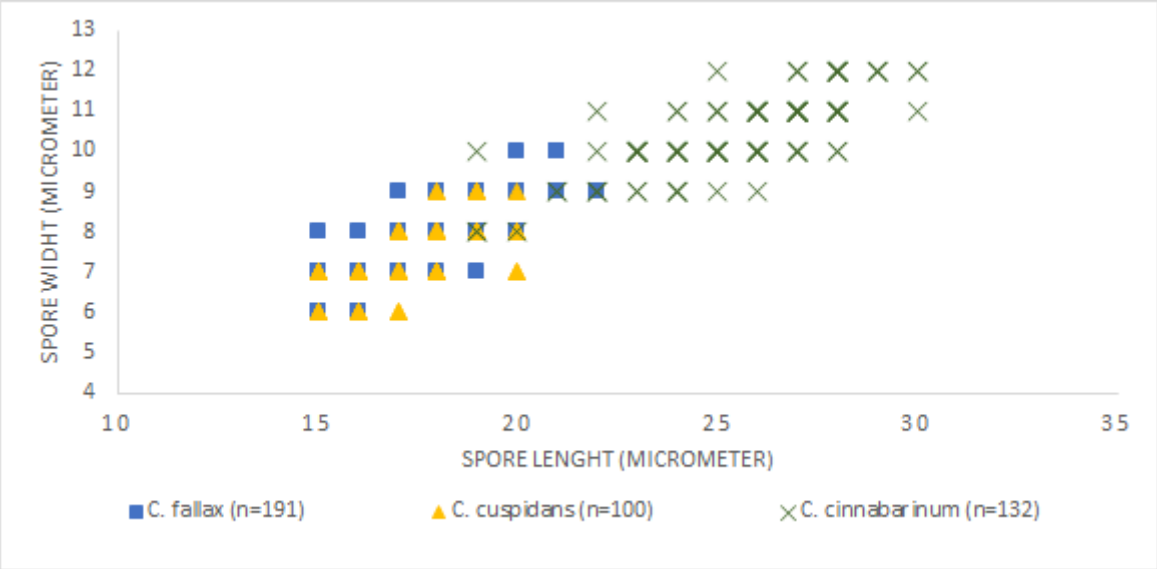

Fig. 3. Ascospore size of *C. cinnabarinum* (n= 132; 20 ascospores from Denmark, 85 ascospores from Norway; 27 ascospores from Sweden), *C. cuspidans* (n=100, all ascospores from Norway) and *Coniocarpon fallax* (n=191, all ascospores from Norway).

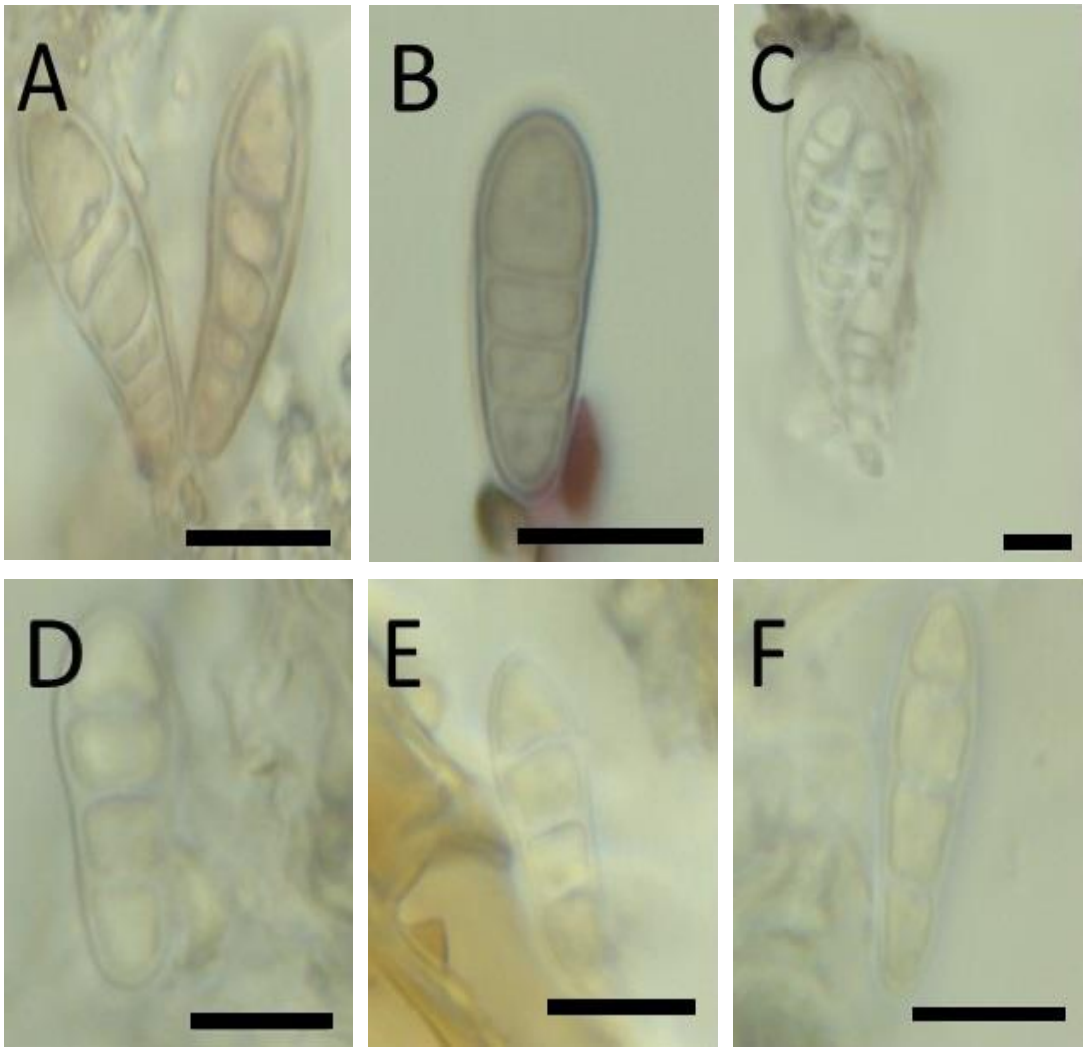

Fig. 4. Morphological diversity of ascospore shape and ascospore septation in *Coniocarpon* and *Arthonia punctiformis* s.lat. in Norway. **A** *Coniocarpon cinnabarinum* (*Frisch 17/No39*, TRH); **B** *Coniocarpon fallax* (*Frisch & Klepsland 17/No49*, TRH); **C** *Coniocarpon cuspidans* (*Frisch 17/No40*, TRH); **D** *Arthonia punctiformis* 1 (*Frisch 17/No136*, TRH); **E** *Arthonia punctiformis* 2 (*Frisch & Klepsland 18/No3*, TRH); **F** *Arthonia punctiformis* 4 (*Frisch 18/No142*, TRH). Scale bars: A–F = 10 µm.

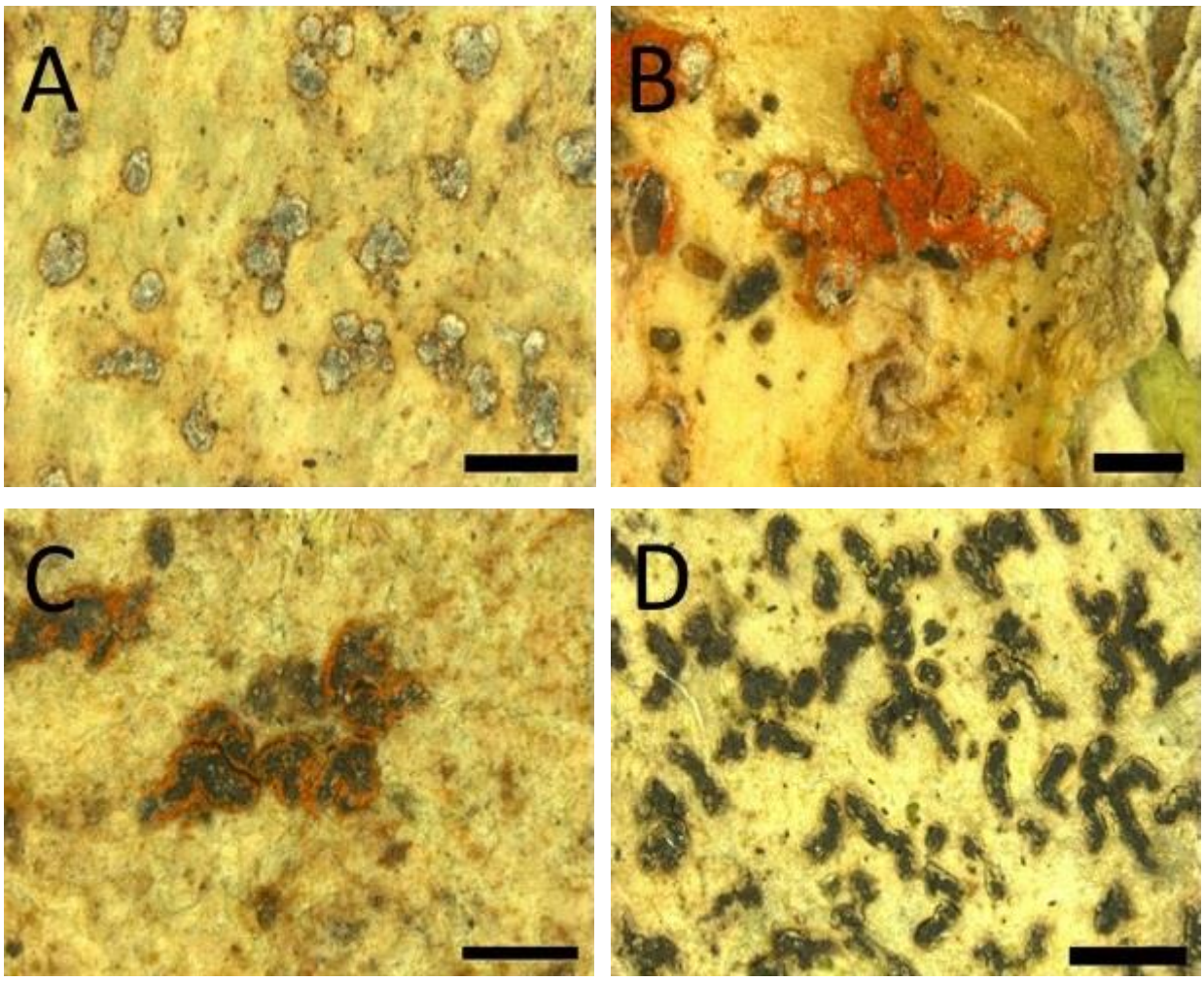

Fig. 5. Morphological diversity of *Coniocarpon* in Norway. **A** *Coniocarpon cinnabarinum* (*Frisch S06-1-Ca2-3*, TRH); **B** *Coniocarpon cinnabarinum* (*Frisch S06-1-Ca3-1*, TRH); **C** *Coniocarpon fallax* (*Frisch 17/No23*, TRH); **D** *Coniocarpon cuspidans* (*Gaarder*, TRH-L-18034). Scale bars: A, D = 1 mm, B–C = 500 µm.

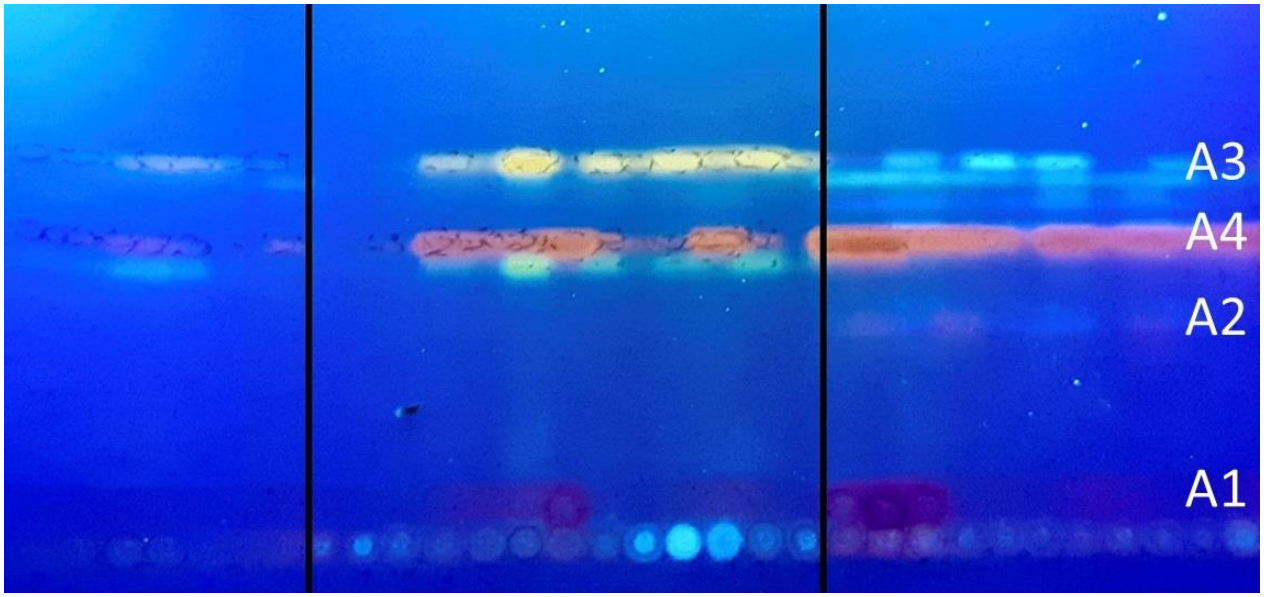

Fig. 6. Picture of a HPTLC plate under UV_{365} light before treatment with sulfuric acid and charring, showing specimens of *C. cinnabarinum* (left), *C. fallax* (middle) and *C. cuspidans* (right). The four quinoid pigments A1, A2, A3 and A4 are indicated. The additional spots have not been identified.

The morphology of 35 specimens of *A. punctiformis* s.lat. collected in Norway were studied. Of the 35 studied specimens, 16 belonged to A. *punctiformis* 1, one each to A. *punctiformis* 2 and 3, and 17 to *A. punctiformis* 4. Differences in ascospore size (Fig. 7), ascospore shape (Fig. 4D–F) and the amyloidity of the ascomatal gels were identified as useful characters for distinguishing the two main clades of *A. punctiformis* s.lat. *Arthonia punctiformis* 2 has ascospores similar to *A. punctiformis* 1, while *A. punctiformis* 3 lacks asci and ascospores. The irregularly rounded to narrowly ellipsoid to fusiform ascomata in *A. punctiformis* 1 and 4 (Fig. 8A, D) differ from the irregularly lirellate ascomata in *A. punctiformis* 2 and 3. Moreover *A. punctiformis* 2 differs from *A. punctiformis* 3 in the absence of a prominent margin and an uneven disc of the ascomata.

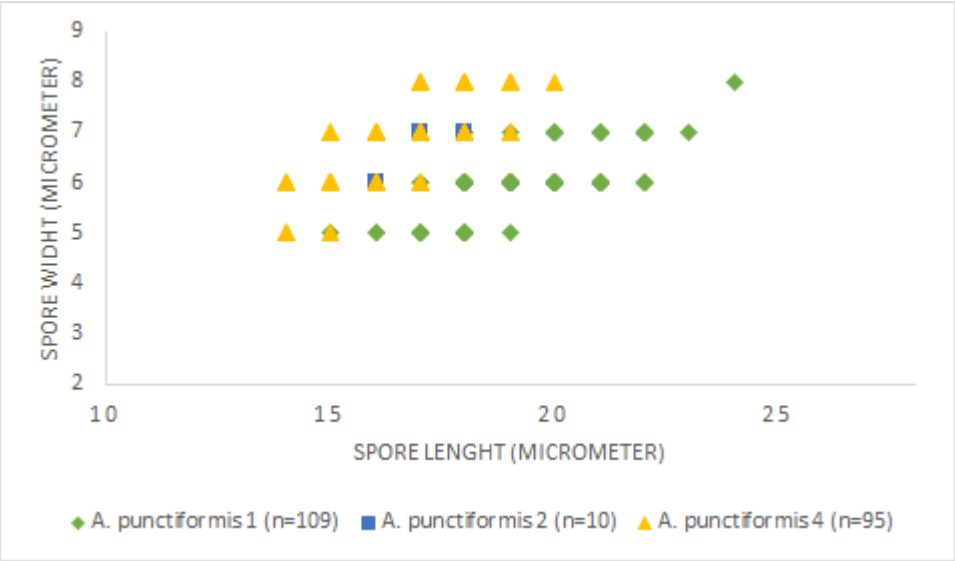

Fig. 7. Ascospore size of *Arthonia punctiformis* 1 (n= 109), *Arthonia punctiformis* 2 (n= 10) and *Arthonia punctiformis* 4 (n= 95) in Norway. Ascospores were absent in *Arthonia punctiformis* 3.

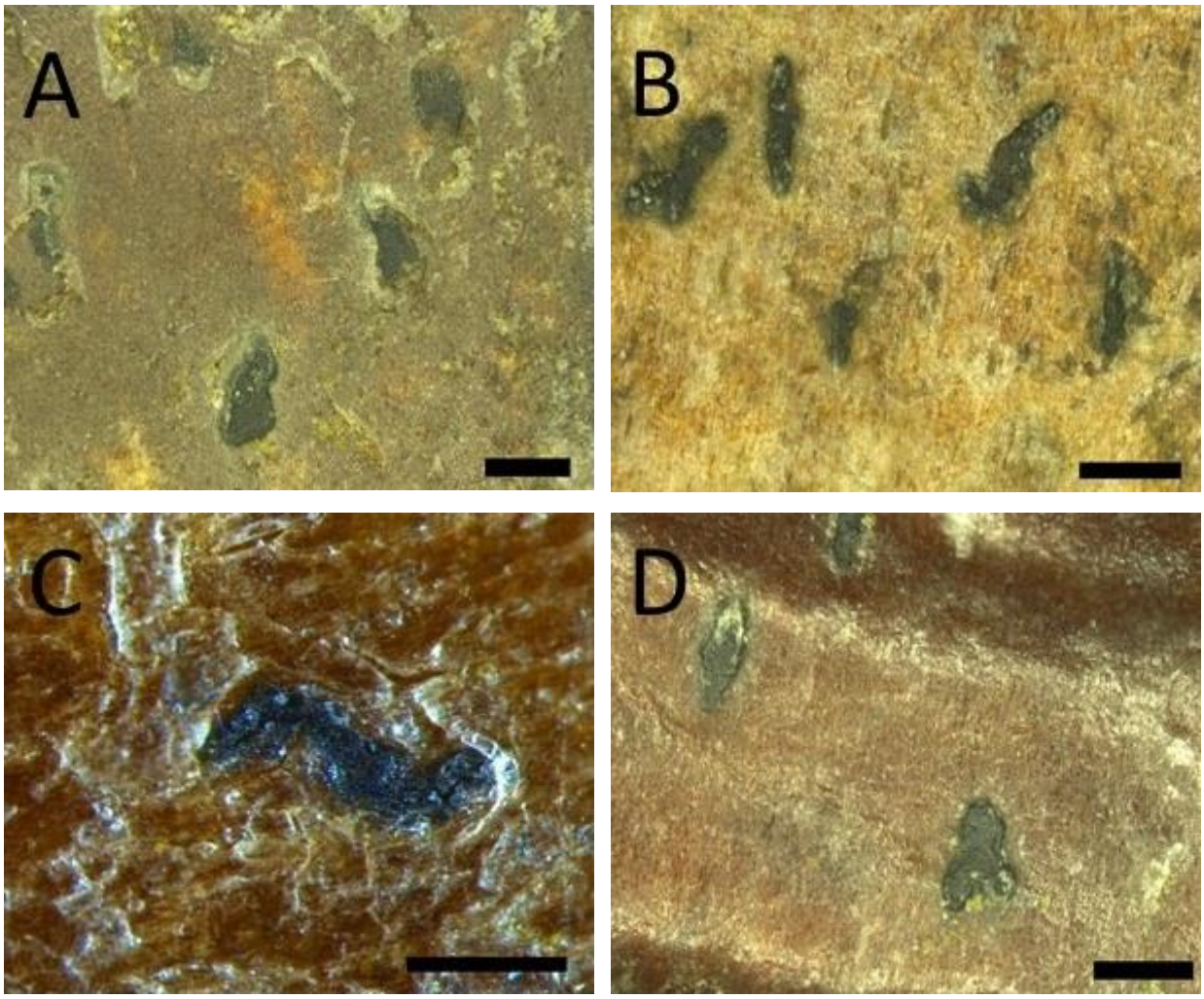

Fig. 8. Morphological diversity of *Arthonia punctiformis* s.lat. in Norway. **A** *Arthonia punctiformis* 1 on *Hippophae rhamnoides* (*Frisch 15/No2*, TRH); **B** *Arthonia punctiformis* 2 on *Corylus avellana* (*Frisch & Klepsland 18/No3*, TRH); **C** *Arthonia punctiformis* 3 on *Sorbus aucuparia* (*Frisch 15/No105*, TRH); **D** *Arthonia punctiformis* 4 on *Betula* sp. (*Frisch 18/No222*, TRH). Scale bars: A–B, D = 500 µm, C = 200 µm.

3.4 Distribution and ecology

Distribution maps based on all revised specimens of *Coniocarpon* from Scandinavia confirm *C. cinnabarinum* for Denmark, Norway and Sweden, *C. cuspidans* for Norway and *C. fallax* for Norway and Sweden (Fig. 9A–C). *Coniocarpon cinnabarinum* has been collected in Norway in the boreo-nemoral rainforests in Rogaland and Hordaland, while it occurs in other humid forests in Sweden (Skåne and Gotland) and Denmark (Sjælland and Jylland). Specimens of *C. cuspidans* have been seen in Norway from the boreo-nemoral rainforests in Vest-Agder, Rogaland and Hordaland. *Coniocarpon fallax* has been collected in Norway in the boreo-nemoral rainforests in Vest-Agder, Rogaland, Hordaland and Møre og Romsdal. Moreover, this study reports *C. fallax* from Sweden (Gotland) for the first time. Both *C. cuspidans* and *C. fallax* are confirmed for Great Britain, but their distribution is not shown in Figs. 9B, C.

Coniocarpon preferably grows on trees with smooth bark and the selected host tree species slightly follow a geographical pattern. Most collections of *C. cinnabarinum* from Norway have been made from *Corylus avellana* L., including few from *Fraxinus excelsior* L. and *Sorbus aucuparia* L. The species is collected in Denmark from *C. avellana*, *F. excelsior* and *Fagus sylvatica* L., and in Sweden from *F. excelsior*. Most specimens of *C. cuspidans* have been collected from *C. avellana*, but the species has been seen from a rather wide range of trees including *F. excelsior*, *Ilex aquifolium* L., *Quercus robur* L. and *S. aucuparia*. *Coniocarpon fallax* has mainly been collected from *F. excelsior* from Vest-Agder to Hordaland (more rarely from *C. avellana*), while all specimens from Møre og Romsdal are from *C. avellana*. The species is further collected from *F. excelsior* on Gotland.

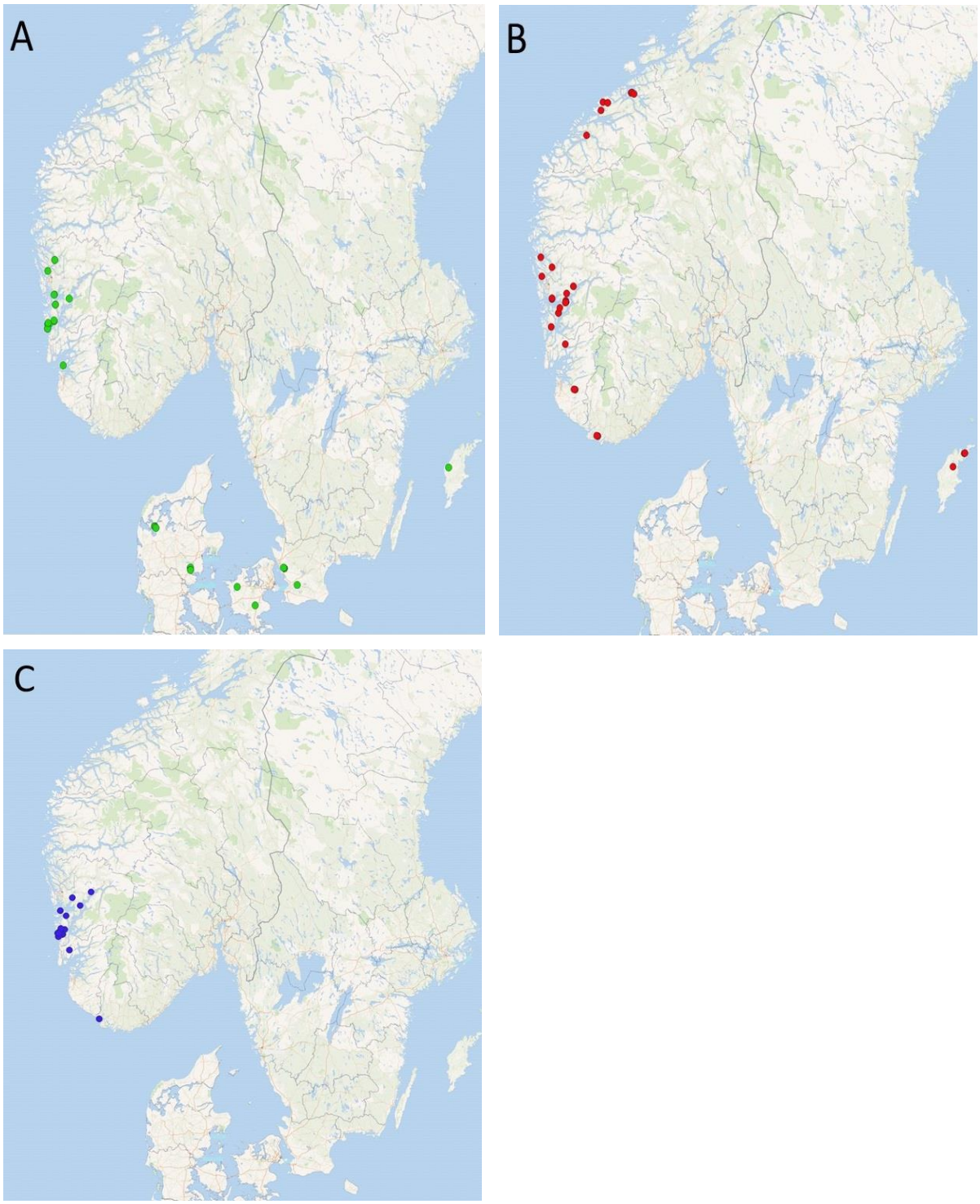

Fig 9. The distribution of 111 specimens of *Coniocarpon* in Norway, Sweden and Denmark based on material in BG, C, S, TRH and UPS. **A** *Coniocarpon cinnabarinum*; **B** *Coniocarpon fallax*; **C** *Coniocarpon cuspidans*. Single dots may represent several collections.

The distribution maps for *A. punctiformis* s.lat. show similar distribution areas for *A. punctiformis* 1 and 4 in Rogaland, Hordaland, Trøndelag, Møre og Romsdal and Nordland (Fig. 10A–B). Additionally, *A. punctiformis* 1 has been collected in Vest-Agder. *Arthonia punctiformis* 2 is known from Sogn og Fjordane and *A. punctiformis* 3 from Trøndelag. However, it needs to be remembered that the shown distributions of *A. punctiformis* s.lat. are based on the recently collected specimens for molecular analysis only and are not representative. Collections have been made in coastal shrub and heathland, boreo-nemoral and boreal rainforests, and in open agricultural landscape and parklands. *Arthonia punctiformis* 1 is known from *C. avellana*, *F. excelsior*, *H. rhamnoides*, *S. aucuparia* and *Tilia cordata* Mill. *Arthonia punctiformis* 2 has been collected from *C. avellana* and *A. punctiformis* 3 from *S. aucuparia*. *Arthonia punctiformis* 4 is known from *B. pubescens* and *S. aucuparia* in Norway, and from *B. pendula* in Sweden.

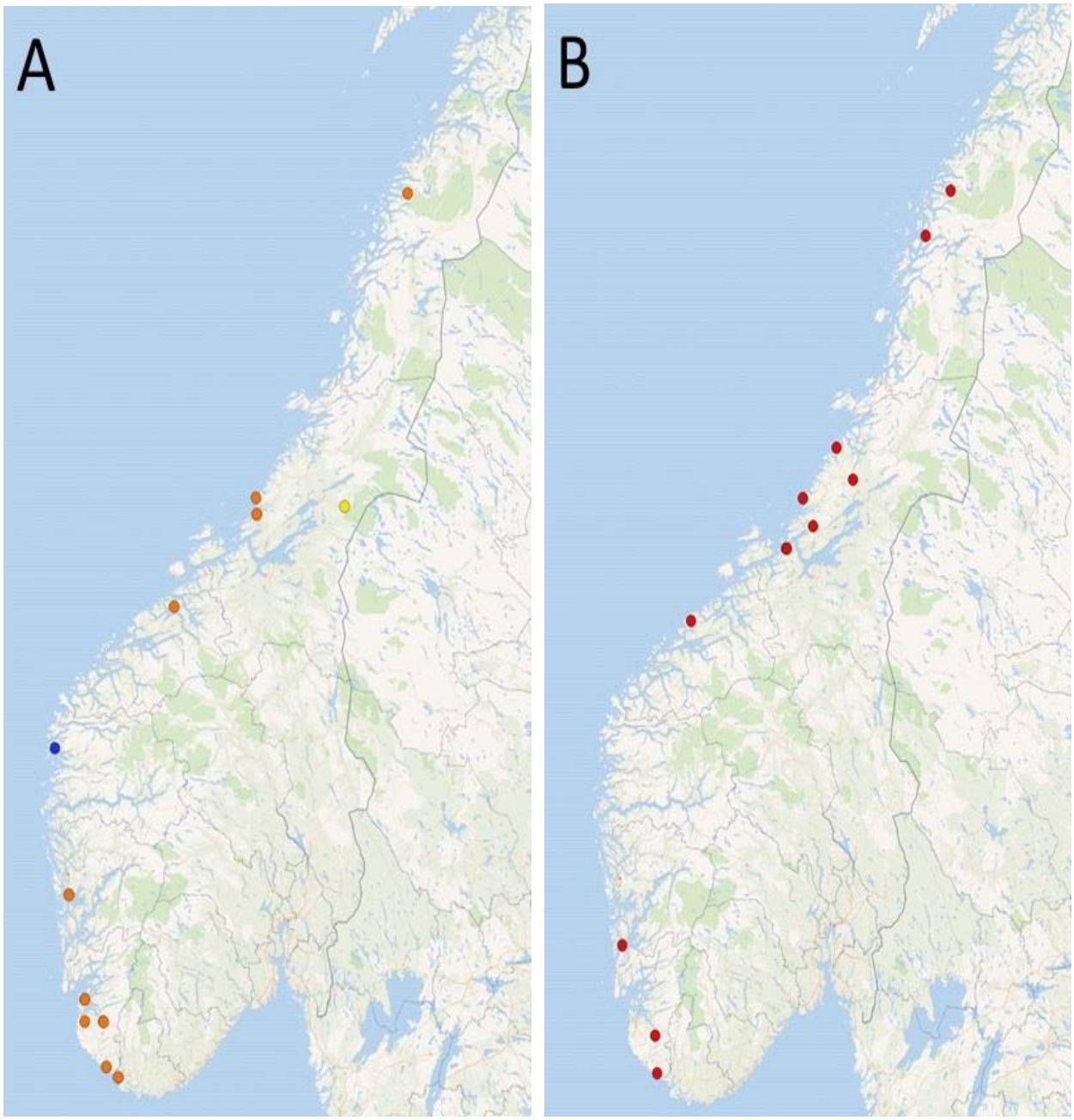

Fig 10. The distribution of 35 specimens of *Arthonia punctiformis* s.lat. in Norway based on material in TRH. **A** *Arthonia punctiformis* 1 (orange), 2 (blue) and 3 (yellow); **B** *A. punctiformis* 4 (red). Single dots may represent several collections.

4 DISCUSSION

4.1 General discussion

Species designations are hypotheses to be tested as new evidence becomes available. Recent molecular systematic studies have repeatedly revealed evolutionary lineages within phenotypically delimited lichenized fungi (e.g., Alors et al. 2016, Bendiksby et al. 2015, Boluda et al. 2019, Hawksworth & Lücking 2017, Lücking et al. 2014, Steinová et al. 2013) as well as non-lichenized fungi (e.g., Fekete et al. 2012, Hawksworth & Lücking 2017, O'Donnell et al. 1998). Whether or not such morphologically indistinguishable, or "cryptic", evolutionary lineages should be recognized at species level may have critical implications for conservation biology and other fields of biology that use species as a fundamental unit (Lumbsch & Leavitt 2011).

In general, several factors should be considered in the process of assessing species status: proper selection of genetic markers (multiple, unlinked loci and from different genomic compartments), presence of statistically supported phylogenetic lineages, sufficiently large sample size, corroborating non-molecular character variation, and thorough review of the taxonomic and nomenclatural history (Grube & Kroken 2000, Lumbsch & Leavitt 2011, Printzen 2010). The phylogenetic analyses of *Coniocarpon* are based on unlinked, multilocus DNA sequence data (mtSSU, nITS, *RPB2*) showing high statistical support for three distinct genetic lineages (Fig. 1). Re-examination of morphology against the molecular phylogeny of 26 specimens revealed that the three lineages are further supported by differences in ascospore size (Fig. 3), ascospore septation (Fig. 4A–C), distribution of pruina and ascoma shape (Fig. 5A–D). Furthermore, the three lineages differ in the amyloidity of the ascomatal gels and pigment patterns revealed by HPTLC (Fig. 6). Finally, an additional 89 specimens, for which molecular data are not available, were revised using the same morphological and/or chemical characters. As such, this study fulfills the factors recommended for assessing species status.

Evolutionary lineages that remain intact when living in sympatry with close relatives might deserve species status (Coates et al. 2018). The distribution of *Coniocarpon* in Scandinavia shows that the three distinct genetic lineages of *Coniocarpon* live in sympatry in Norway (Fig. 9A–C), providing strong indirect evidence that there are mechanisms prohibiting exchange of

genetic material among them, supporting their acceptance at species level. Hence, the integrated data gathered in this study jointly support the hypothesis of three distinct species of *Coniocarpon* in Norway, viz. *C. cinnabarinum*, *C. fallax* and *C. cuspidans*. The latter species was hidden in the extensive synonymy of *C. cinnabarinum* as *Arthonia cinnabarina* f. *cuspidans* Nyl. and is herein resurrected (see Taxonomic conclusions below).

Previously reported species distributions in *Coniocarpon* may be partly wrong due to incorrectly identified specimens. The data indicate a narrower distribution in Norway for *C. cinnabarinum* and *C. cuspidans* compared to that of *C. fallax* (Fig. 9A–C). This study reports absence of *C. cinnabarinum* in Møre og Romsdal and presence of *C. fallax* in the same county, while the preliminary distribution data in the *Norwegian Red List of Species 2015* reported the opposite observation. This suggests a current divergent understanding of the species circumscriptions in the two species. However, it needs to be remembered that not all specimens showing the preliminary distribution in Norway were revised in this study. Therefore, *C. cinnabarinum* might occur in Møre og Romsdal as well. Moreover, this study confirms the preliminary reported distribution of *C. cinnabarinum* in Denmark and Sweden, while *C. fallax* is reported from Sweden (Gotland) for the first time (Fig. 9A–B). One specimen each from S and UPS were redetermined as *C. fallax* on Gotland. The two specimens were preliminary identified as *C. cinnabarinum* suggesting preliminary divergent understanding of the species circumscriptions between the two species in Sweden.

Species diversity generally correlate with habitat preference. Most specimens of all three *Coniocarpon* species in Norway are collected from Hordaland (*C. cinnabarinum* 22, *C. cuspidans* 24, *C. fallax* 20), while for instance the number of specimens reported from Vest-Agder is distinctly lower (*C. cinnabarinum* 0, *C. cuspidans* 2, *C. fallax* 3). Hordaland is the core area of the boreo-nemoral rainforests in Norway with the highest levels of humidity and low average winter temperatures (Blom 2015, Moen 1999). In comparison, the number of studied specimens from Vest-Agder at the southern limit of the boreo-nemoral rainforests is distinctly lower, which might be explained partly by less areas with boreo-nemoral rainforests (Blom 2015). The occurrence of *C. fallax* in Møre og Romsdal indicate a wider ecological amplitude as compared to *C. cinnabarinum* and *C. cuspidans* in terms of oceanity and temperature. The distribution of *C. cuspidans* is currently unclear as the species has most likely been identified as *C. fallax* (*Arthonia*

elegans) due to similar ascospore size and the elongated ascomata. *Coniocarpon cuspidans* is currently only confirmed for the highly to markedly oceanic sections in Norway and Great Britain. However, its overall distribution is currently unclear as the species has not been distinguished from *C. fallax* (*Arthonia elegans*). *Coniocarpon cuspidans* might be widely distributed in western Europe.

The study of *A. punctiformis* s.lat. investigated a molecular phylogeny of totally 33 sequenced specimens based on unlinked, multilocus data (mtSSU, ITS2, nLSU, *RPB2*). The molecular phylogeny of *A. punctiformis* s.lat. show the presence of two well-supported main lineages (*A. punctiformis* 1 and 4) and two additional genetically distinct specimens (*A. punctiformis* 2 and 3) forming a clade with *A. punctiformis* 1 (Fig. 2). The lineage representing the true *A. punctiformis* is uncertain as the typification remains. The combination of several life strategies (e.g., lichized, lichenicolous) within the same clade has been confirmed also for other groups within the Arthoniaceae, such as the *A. radiata* and *Bryostigma* clades (Frisch et al. 2014). The molecular phylogeny recovers *A. punctiformis* s.lat. as paraphyletic by including *A. dispersa* which is lichenized with a trentepohlioid photobiont, suggesting several different life strategies (i.e., lichenized, non- lichenized and saprotrophic fungi) within this clade as well.

In the process of assessing species status, there is no general definition of a sufficiently large sample size that applies to all situations. However, at least two representatives from each taxon is recommended (Grube & Kroken 2000). This criterion is not fulfilled in the study of *A. punctiformis* s.lat. as *A. punctiformis* 2 and 3 are represented by single specimens only, respectively. Therefore, this study is unable to clarify whether *A. punctiformis* 2 and 3 represent two independent phylogenetic lineages. On the other side, *A. punctiformis* 1 (n= 14) and *A. punctiformis* 4 (n= 17) represent two well-supported lineages with a sufficiently large sample size. As morphological, chemical and ecological differences correspond to the molecular results, the results strongly suggest that *A. punctiformis* 1 and 4 represent two different species. Although *A. punctiformis* 1 and 4 share the same irregularly rounded ascomata (8A, D), they differ in ascospore size (Fig. 7), ascospore shape (Fig. 4D, F) and the amyloidity of the ascomatal gels. Moreover, this study hypothesizes that *A. punctiformis* 2 and 3 may be confirmed as independent phylogenetic lineages with extended taxon sampling. Also *A. punctiformis* 2 and 3 share the same irregularly lirellate ascomata (Fig. 8B, C), but *A. punctiformis* 2 differ from *A. punctiformis* 3 by

its absence of prominent exciple and uneven disc. On the molecular side, *A. punctiformis* 2 (with mtSSU, ITS2, nLSU and *RPB2* sequence data) and *A. punctiformis* 3 (with mtSSU and nLSU sequence data) are genetically distinct from a largely homogenous *A. punctiformis* 1.

Collection data are commonly used to determine species distributions (e.g., McCarthy 1998, Prendergast et al. 1993). However, such data can be compromised, for instance by biased sampling and collecting gaps in space and time (Ponder et al. 2000). The specimens of *A. punctiformis* s.lat. used for this study were mainly collected in coastal areas along the west-coast of Norway and are not representative for the entire distribution area of the species in Norway (Timdal 2019). This sampling bias towards coastal areas is reflected in the distribution maps for the species (Fig. 10A–B) showing more restricted distributions than provided by Timdal (2019). Nevertheless, the limited distribution data in this study might indicate that *A. punctiformis* 1 and 4 have similar distributions in coastal Norway, but that *A. punctiformis* 1 might be more abundant in southern Norway due to the more southerly distribution of some of the host trees.

Lichenized fungi living as epiphytes on the bark of trees are known to differ in their tree species preference (Johansson & Ehrlèn 2003, Uliczka & Angelstam 1999). *Coniocarpon* were collected from *C. avellana*, *F. sylvatica*, *F. excelsior*, *I. aquifolium*, *S. aucuparia* and young trees of *Q. robur*, confirming the preference of smooth bark as reported by Blom et al. (2015). Moreover, the host tree preference differs between the habitat types. Most specimens of *C. cinnabarinum* and *C. cuspidans* in the boreo-nemoral rainforests in Norway are collected from *C. avellana* while *C. fallax* has mainly been collected from *F. excelsior* except for the most northern localities where it was collected only from *C. avellana*. The latter might be caused by the fact that *F. excelsior* is not a common member of the rainforest communities in the collected areas of Møre og Romsdal. Outside the boreo-nemoral rainforests, *C. cinnbarinum* is collected from *F. excelsior* in Denmark and Sweden as well as from *F. sylvatica* which naturally does not occur in the boreo-nemoral rainforests.

Non-lichenized fungi like *A. punctiformis* s.lat. differ from lichenized fungi in their relationship to the host tree species, as they get energy from it, while lichenized fungi are purely epiphytic (Lamit et al. 2011). However, the nutritional relationship of *A. punctiformis* s.lat. to the host trees is poorly understood. The species is often described as saprophytic (Frisch et al. 2014), but it is growing on living branches/twigs and not obviously damaging the tree, suggesting some kind of a

commensalistic/parasitic relationship as an alternative. A possible explanation of the observed host tree preferences by *A. punctiformis* 1 and 4 might be differences in bark traits such as chemistry and pH. At Stokkøya in Åfjord, *A. punctiformis* 1 and 4 grow side by side on three different species; *A. punctiformis* 1 grows on *H. rhamnoides*, whereas A. *punctiformis* 4 grows on *B. pubescens* and *S. aucuparia*. This observation of sympatric life of the two genetic lineages suggest they are evolving independently (limited or no geneflow). *Arthonia punctiformis* 1 and 4 differ in the preferred host tree species (Fig. 2), except for the occurrence of *S. aucuparia* in both clades. The broad range of host trees in *A. punctiformis* 1 as compared to *A. punctiformis* 4 is observed through a wide geographical space.

This study identified previously unrecognized evolutionary lineages within the genus *Coniocarpon* and *A. punctiformis* s.lat., which might raise the question of possible cryptic diversity. The existence of several inconsistent definitions of the term "cryptic species" is complicating the process of correctly giving cryptic species status for taxa (e.g., Bickford et al. 2006, Fišer et al. 2017, Struck et al. 2017). Some have regarded phylogenetic lineages as cryptic species when incongruent with morphological and/or chemical data (e.g., Steinová et al. 2013). However, our results show morphological and chemical variation that corroborate the molecular phylogeny, suggesting cryptic species status should be avoided.

This study provides a further step in the process of improving the biodiversity conservation in Norway by applying an integrative taxonomic approach for delimiting taxa in *Coniocarpon* and *A. punctiformis* s.lat. *Coniocarpon cinnabarinum* and *C. fallax* are designated as vulnerable (VU) in the latest version of the *Norwegian Red List for Species* (Henriksen & Hilmo 2015). It is likely that the same status applies to *C. cuspidans*, growing with similar abundance in the boreo-nemoral rainforests as the other species of *Coniocarpon*. Moreover, all three species are facing the same threats such as algae growth on trees which is inhibiting the establishment and growth of lichens (Blom 2018). On the other hand, *Arthonia punctiformis* s.lat. was designated as least concern (LC). *Arthonia punctiformis* s.lat. is a pioneer taxon and therefore unlikely to be endangered. A natural progression of this work is to analyze a sufficiently large sample size of all genotypes of *A. punctiformis* s.lat. collected from variable localities and tree-species in Norway. Moreover, the typification of *A. punctiformis* s.lat. and clarification of the nomenclature should

be done. Another possible area of future research would be investigating whether host tree specificity is a local or global phenomenon in *A. punctiformis* s.lat.

4.2 Taxonomic conclusions

4.2.2 *Coniocarpon* DC.

In Lamarck & de Candolle, Flore française 2: 323 (1805) [MB 1208]. Lectotype (selected in Santesson, Symbolae Botanicae Upsalienses 12(1): 68, 1952): *Coniocarpon cinnabarinum* DC., in Lamarck & de Candolle, Flore française 2: 323 (1805).

Key to *Coniocarpon* in Norway

1 Ascospores mostly > 20 µm long; ascomata typically rounded to weakly lobate, rarely lirellate; orange-red pruina present ..... *C. cinnabarinum*

1' Ascomata mostly ≤ 20 µm long; ascomata typically irregularly lirellate; orange-red pruina present or absent 2

2 Orange-red pruina present; ascospores (15–)17–20(–22) × (6–)7–9(–10) µm, (1–)3–4(–5) transversely septate ..... *C. fallax*

2' Orange-red pruina absent; ascospores (15–)16–18(–20) × (6–)7–8(–9) µm, (2–)3(–4) transversely septate ..... *C. cuspidans*

Coniocarpon cinnabarinum DC.

In Lamarck & de Candolle, Flore française 2: 323 (1805). Type: St. Sever. Leon Dufour (PC 0735925!).

= *Spiloma* ? *tumidulum* Ach., Methodus qua omnes detectos lichenes: 11 (1803) [MB 405550]. Type: Hispania, Schousboe (H-Ach. 3 c!, holotype).

= *Spiloma tumidulum* var. *rubrum* Ach., Lichenographia universalis: 137 (1810) – nom. illegit. Type: Gallia (H-Ach. 2 c!).

[MB 383614]

Figs. 3, 4A, 5A–B, 6, 9A.

THALLUS pale olive grey to brown, weakly glossy to matt, smooth, endophloeodal to partly epiphloedal, continuous; *prothallus line* dark grey to brown, sometimes present when in contact with other lichens; *photobiont* trentepohlioid, the cells rounded to elliptical, 7–12 × 4–8 µm, forming short chains. ASCOMATA irregularly rounded to elliptical to weakly lobed, rarely distinctly lirellate, with steep flanks, emergent from thallus, 0.1–0.4 × 0.1–0.3 mm, 95–140 µm tall, solitary or forming loose to dense aggregations of 3–15 ascomata, (0.3–)0.5–2.0(–3.5) × 0.3–1.6 mm; *disc* dark purple black, flat to weakly convex, matt to weakly glossy, white pruinose, a layer of orange-red pruina sometimes present above the white pruina; old ascomata sometimes epruinose; *margins* level with the disc, typically orange-red pruinose, sometimes with additional patches of white pruina; *proper exciple* brown, 8–15 µm wide, composed of compressed and vertically oriented paraphysoidal hyphae, the hyphae 1–2 µm thick, branched and netted, often forming short hairs up to 15 µm long at the outer margin; old bark cells often attached to the exciple; *epithecium* brown, 10–25 µm tall, conglutinated only in the lower parts, composed of branched tips of the paraphysoidal hyphae extending horizontally above the asci; the tips slightly widened to 3(–4) µm, sometimes extending from the epithecium as sparsely branched anticlinal hairs up to 22 µm long; *hymenium* hyaline, strongly conglutinated, (45–)65–90 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline, conglutinated,

20–35 µm tall, formed of irregular prosoplectenchymatic hyphae 1–2 µm diam.; *crystals* common in epithecium and proper exciple, of two types: hyaline, leafy crystals, 1–5(–8) µm, and orange, red or purple, granular crystals, 1–2(–4) µm; a weak amorphous, red to purple pigmentation present in exciple, epithecium and patchily distributed in the hymenium. ASCI of the *Arthonia*-type, long obpyriform to clavate, 62–84 µm × 24–35 µm (n=34), 8-spored, the ascospores stacked; tholus 8–11 µm thick, lateral ascospore wall 1–2 µm thick. ASCOSPORES hyaline, (3–)4–5(–8) transversely septate, (19–)23–28(–30) × (8–)10–11(–12) µm (l: mean=25.7, STD=2.3; w: mean=10.5, STD=0.9; n=132), obovate, with enlarged apical cell, getting pale brown with granular ornamentation in the epispore at late maturity; development macrocephalic.

Chemistry. Pigments A1 (major), A2 (absent), A3 (major), A4 (minor) in solvents C detected by HPTLC. *Proper exciple* I_{dil}+ blue, I+ blue, KI+ blue; *epithecium* I_{dil}+ blue, I+ blue, KI+ blue; *hymenium* I_{dil}+ red, I+ red, KI+ blue; *hypothecium* I_{dil}+ red, I+ red, KI+ blue. A hemiamyloid ring present in the tholus of the asci. Hyaline crystals dissolve in K. Orange, red and purple crystals dissolve in K with a clear, fleeting, purplish solution.

Notes. *Coniocarpon cinnabarinum* differs from the other *Coniocarpon* species in Norway by its larger ascospores and in ascospore septation (*C. cinnabarinum*: (19–)23–28(–30) × (8–)10–11(–12) µm, (3–)4–5(–8) transversely septate vs *C. cuspidans*: (15–)16–18(–20) × (6–)7–8(–9) µm, (2–)3(–4) transversely septate vs *C. fallax*: (15–)17–20(–22) × (6–)7–9(–10) µm, (1–)3–4(–5) transversely septate). Further, *C. cinnabarinum* separates from *C. cuspidans* and *C. fallax* by its ascomata shape (*C. cinnabarinum*: rounded to elliptical ascomata, rarely distinctly lirellate vs *C. cuspidans* and *C. fallax*: weakly elongated to irregularly lirellate to stellate). Moreover, *C. cinnabarinum* differs from the other *Coniocarpon* species by the thick layer of white pruina on the ascomatal disc which may be overlaid by an orange-red pruina, and an orange-red pruinose margin (*C. cuspidans*: disc and margin epruinose or patchily covered by white pruina, orange-red pruina is always absent; *C. fallax*: disc epruinose or orange-red pruinose, sometimes with additional patches of white pruina). Additionally, *C. cinnabarinum* differs in the reaction of the proper exciple and epithecium to iodine (*C. cinnabarinum*: I_{dil}+ blue, I+ blue *C. cuspidans*: I_{dil}+ red, I+ red vs *C. fallax*: I_{dil}+ blue, I+ dark blue) and secondary compounds revealed by HPTLC (*C. cinnabarinum*: A1 major, A2 absent, A3 major, A4 minor vs *C. cuspidans*: A1 major to minor, A2 minor to trace, A3 absent, A4 major vs *C. fallax*: A1 minor to trace, A2 absent, A3

major, A4 major). In all three species, red/purple pigments are sometimes present on the thallus close to the ascomata and/or in the middle of the thallus. The former might be caused by rain, wind and/or disturbance by insects, mites or snails. The latter may be due to the growth of new ascomata.

Specimens examined. NORWAY, ROGALAND: Rennesøy, Berge (59°05'52.10"N, 05°42'19.20"E), on *C. avellana*, 30–40 m a.s.l., 1/12/2008, *J. I. Johnsen* (BG-L-86128). HORDALAND: Askøy, close to Ask farm, on *S. aucuparia*, 10–30 m a.s.l. 8/31/1909, *J. J. Havaas* (UPS-L-277202); Bømlo, Børøy, Storavatnet (59°42'56.52"N, 05°15'46.08"E), on *C. avellana*, 4/30/2018, *G. Gaarder* (TRH-L-18030), ibid., Lykling (59°42'40.68"N, 05°12'21.24"E), on *C. avellana*, 4/30/2018, *G. Gaarder* (TRH-L-18036); ibid., S of Liarnuten, on *C. avellana*, 6/21/1997, *T. Knutsson* (UPS-L-737333); ibid., Skogafjellet (59°38'48.7"N, 05°12'05.9"E), on *C. avellana*, 35 m a.s.l., 7/19/2017, *A. Frisch 17/No39* (TRH); ibid., (59°38'49.1"N, 05°12'04.9"E), on *C. avellana*, 10 m a.s.l., 7/19/2017, *A. Frisch S06-1-Ca2-3, S06-1-Ca3-1, S06-1-Ca5-1* (TRH); ibid., on *F. excelsior*, *A. Frisch S06-1-Fe1-7* (TRH); ibid., (59°38'50.0"N, 05°12'09.2"E), on *C. avellana*, 50 m a.s.l., 7/19/2017, *A. Frisch 17/No42, 17/No46* (TRH); Kvam, Gravdal SW, Geitaknottane Nat. Reserve, NE of Lønningshaugen (60°06'41.41"N, 05°51'04.13"E), on *C. avellana*, 150–250 m a.s.l. 8/28/1997, *P. G. Ihlen* (BG-L-35863); Lindås, Kvalvika-Røyldalane (60°38'20.3"N, 05°26'15.5"E), on *C. avellana*, 35 m a.s.l., 5/14/2018, *A. Frisch S12-2-Ca3-1, S12-2-Ca3-2, S12-2-Ca3-3* (TRH); Os, Innerøya, Halhjem (60°08'30.12"N, 05°24'51.12"E), on *S. aucuparia*, 5/10/2018, *G. Gaarder* (TRH-L-18042); ibid., (60°08'35.52"N, 05°25'20.64"E), on *C. avellana*, 5/10/2018 *G. Gaarder* (TRH-L-18043); Stord, Digernes, Geitåsen (59°45'24.12"N, 05°25'5.52"E), on *Corylus avellana*, 4/28/2018, *G. Gaarder* (TRH-L-18033); ibid., Valavåg, Nes-Åsen (59°46'4.44"N, 05°24'48.24"E), on *C. avellana*, 4/27/2018, *G. Gaarder & U. Hanssen* (TRH-*L-18087*); Tysnes, Beltestad, Beltestadknappen (59°59'53.0"N, 05°27'32.6"E), on *C. avellana*, 13 m a.s.l., 5/9/2018, *A. Frisch 18/No11, 18/No28* (TRH); ibid., (59°59'54.0"N, 05°27'33.3"E), on *C. avellana*, 5 m a.s.l., 5/9/2018, *A. Frisch 18/No70* (TRH). SWEDEN, GOTLAND: Stenkumla, Myrsö, 1869, *Laurer* (UPS-L-002825); SKÅNE: Dalby, Dalby Söderskog, on *F. excelsior*, 7/23/1947, *R. Santesson* (UPS-L-118296); ibid., Ottarp, Bälteberga, on *F. excelsior*, 8/29/1946, *O. Almborn* (S-F-71116, UPS-L-60625), ibid., 9/16/1959, *G. Degelius* & *O. Almborn* (UPS-L-60624). DENMARK, JYLLAND: Horsens, Elling Skov, on *F. excelsior*, 3/26/1887, *J. Jeppesen* (C-L-28996); ibid., on *F.*

sylvatica, 3/26/1887 *J. Jeppesen* (C-L-28993); ibid., on *F. excelsior*, 2/26/1887, *J. Jeppesen* (S-F-71202, C-L-28992); ibid., on *F. excelsior*, 2/20/1887, *J. P. Pedersen* (C-L-28991, C-L-28994); ibid., Hansted Skov, on *F. excelsior*, 12/5/1886, *J. Jeppesen* (C-L-29000); ibid., 2/1/1887, *J. Jeppesen* (C-L-28999); ibid., on *F. sylvatica*, 3/6/1887, *J. Jeppesen* (C-L-28998); Lihme, W of Skive, on *C. avellana*, 5/25/1976, *M. S. Christansen* (C-L-28990). Lihme, Kås skov, on *C. avellana*, 8/6/1979, *G. Thor* (UPS-L-165392); ibid., on *F. excelsior*, 5/25/1976, *S. Svane* (C-L-28997, C-L-28988); ibid., Bringsbjerg Krat (56°37′7.78″N, 08°41′25.40″E), on *C. avellana*, 10/21/2002, *R. S. Larsen* (C-L-17076). SJÆLLAND: Haslev, 7/29/1887, *Taussieng* (C-L-28995), ibid., Skarresø, 11/4/1870, *C. Grönlund* (UPS-L-002896).

Coniocarpon cuspidans (Nyl.) Moen, Frisch & Grube

Arthonia cinnabarina f. *cuspidans* Nyl., Flora 59: 310 (1876) [MB 372360]. Type: Hibernia, n. 6, Dough, 1875, Larbalestier (H-Nyl 5607!).

[MB #####]

Figs. 3, 4C, 5D, 6, 9C.

THALLUS pale brown to pale fawn to off white, matt to weakly glossy, smooth, endophloeodal to partially epiphloeodal, continuous*; prothallus line* dark grey to brown to black, sometimes present when in contact with other lichens*; photobio*nt trentepohlioid, the cells rounded to elliptical, 6–13 × 5–11 µm forming short chains. ASCOMATA weakly elongate to irregularly lirellate, with steep flanks, emergent from thallus, 0.2–0.6 × 0.1–0.2 mm, 60–105 µm tall, typically forming loose to dense aggregations of 3–15 ascomata, weakly elongated to irregularly lirellate to stellate, 0.4–1.8(–2.5) × (0.1)0.3–1.0(–2.0) mm; *disc* black to dark purple black, flat to weakly convex, weakly glossy to matt, epruinose, rarely with patches of a thin white pruina; *margins* level with the disc, epruinose, rarely with patches of a thin white pruina; *proper exciple* brown, 7–20 µm wide, composed of compressed and vertically oriented paraphysoidal hyphae, the hyphae 1–2 µm thick, branched and netted, sometimes forming short hairs up to 16 µm long at the outer margin; old bark cells sometimes attached to the exciple; *epithecium* brown, 8–20 µm tall, conglutinated only in the lower parts, composed of branched tips of the paraphysoidal hyphae extending horizontally above the asci; the tips slightly widened to 3(–4) µm, sometimes extending from the epithecium as sparsely branched anticlinal hairs up to 12 µm long; h*ymenium* hyaline, strongly conglutinated, 41–73 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline, conglutinated, 15–30 µm tall, formed of irregular prosoplectenchymatic hyphae 1–2 µm diam.; *crystals* common in epithecium and proper exciple, of two types: hyaline, leafy crystals, 1–5 µm, and red or purple granular crystals, 1–3 µm; a weak amorphous, red to purple pigmentation present in exciple, epithecium and patchily distributed in the hymenium. ASCI of the *Arthonia*-type, long obpyriform to clavate, 45–70 × 19–28 µm (n=31), 8-spored, the ascospores stacked; tholus 4–8 µm thick, lateral ascospore wall 1–2 µm

thick. ASCOSPORES hyaline, (2–)3(–4) transversely septate, (15–)16–18(–20) × (6–)7–8(–9) µm (l: mean=17.4, STD=1.2; w: mean=7.5, STD=0.7; n=100), obovate, with enlarged apical cell, getting pale brown with granular ornamentation in the epispore at late maturity; development macrocephalic.

Chemistry. Pigments A1 (major to minor), A2 (minor to trace), A3 (absent), A4 (major) in solvents C detected by HPTLC. *Proper exciple* I_{dil}+ red, I+ red, KI+ blue; *epithecium* I_{dil}+ red, I+ red, KI+ blue; *hymenium* I_{dil}+ red, K+ red, KI+ blue; *hypothecium* I_{dil}+ red, I+ red, KI+ blue. A hemiamyloid ring in the tholus of the asci not observed. Hyaline crystals dissolve in K. Purple crystals dissolve in K with hyaline solution. Red and purple crystals dissolve in K with purplish solution.

Notes. *Coniocarpon cuspidans* differs from the other species in *Coniocarpon* by the lack of an orange-red pruina on the ascomata. The species superficially resembles *C. fallax* due to the weakly elongate to irregularly lirellate ascomata and overlapping ascospore size. The disc of *C. cuspidans* is epruinose, rarely showing patches of a thin white pruina. On the other hand, the disc of *C. fallax* is epruinose to covered in a thin layer of white pruina. *Coniocarpon cuspidans* slightly differs from *C. fallax* in ascospore septation (*C. cuspidans*: (2–)3(–4) transversely septate vs *C. fallax*: (1–)3–4(–5) transversely septate). Moreover, it differs from that species in the reaction of proper exciple, epithecium and hypothecium to iodine (*C. cuspidans*: I_{dil}+ red, I+ red vs *C. fallax*: I_{dil}+ blue, I+ dark blue). Further, the two species differ in the HPTLC results (*C. cuspidans*: A1 major to minor, A2 minor to trace, A3 absent, A4 major vs *C. fallax*: A1 minor to trace, A2 absent, A3 major, A4 major). The quinoid pigment A4 is present in all species except *C. cuspidans*. A possible explanation is that A4 corresponds to the orange pigment crystals observed in microscopical preparations of *C. cinnabarinum* and *C. fallax* but not in *C. cuspidans*, which are located in the pruina of the ascomatal margin and disc. The amyloid ring in the tholus of the asci were checked in 3 specimens with well-developed asci, but it was not observed.

Specimens examined. NORWAY, VEST-AGDER: Flekkefjord, Hidra, Høgåsen (58°13'35.1"N, 06°33'22.2"E), on *S. aucuparia*, 35 m a.s.l., 7/15/2017, *J. Klepsland 17/No65* (TRH); ibid., Nonfjell (58°13'26.7"N, 06°33'33.0"E) 5–25 m. a.s.l., 7/15/2017, *A. Frisch S01-1-Ca2-1* (TRH). ROGALAND: Tysvær, Svinali W (59°25'5.88"N, 05°34'6.24"E), on *C. avellana*, 10/19/2017, *G. Gaarder* (TRH-L-18034). HORDALAND: Austevoll, Huftaøy, Bjelland farm NE

(60°05'00.0"N, 05°16'00.0"E), on *C. avellana*, 0–40 m a.s.l. 6/6/1996, *T. Tønsberg* (BG-L-L-32077, BG-L-34115). Bømlo, Børøy, Masterhaugane nord (59°42'50.4"N, 05°15'30.24"E), on *S. aucuparia*, 4/30/2018 *G. Gaarder* (TRH-L-18038, TRH-L-18078); ibid., (59°42'38.52"N, 05°15'21.24"E), on *C. avellana*, 4/30/2018, *G. Gaarder* (TRH-L-18040); ibid., (59°38'48.7"N, 05°12'05.9"E), on *C. avellana*, 35 m a.s.l., 7/19/2017, *A. Frisch 17/No38, 17/No40* (TRH); ibid., (59°38'49.1"N, 05°12'04.9"E), on *C. avellana*, 10 m a.s.l., 7/19/2017, *A. Frisch S06-1-Ca1-6* (TRH); ibid., on *S. aucuparia*, 10 m a.s.l., 7/19/2017, *A. Frisch S06-1-Sa3-2* (TRH); ibid., (59°38'58.3"N, 05°12'25.9"E), on *C. avellana*, 12 m a.s.l., 7/19/2017, *A. Frisch S06-2-Ca1-1*, *S06-2-Ca1-2* (TRH); ibid., Kuhillerdalen (59°45'21.94"N, 05°16'49.67"E), on *C. avellana*, 70 m a.s.l., 5/11/2015, *J. B. Jordal & H. H. Blom* (TRH-L-16794); ibid., Lykling, Lyklingfjorden N (59°42'19.31"N, 05°10'34.18"E) on *C. avellana*, 10–20 m a.s.l., 5/13/1996, *T. Tønsberg* (BG-L-31539); ibid., (59°42'18.0"N, 05°10'36.0"E), on *C. avellana*, 40-60 m a.s.l., 6/1/1997, *S. Ekman* (BG-L-38200); ibid., Skogafjellet (59°38'50.0"N, 05°12'09.2"E), on *C. avellana*, 50 m a.s.l, 7/19/2017, *A. Frisch 17/No43* (TRH); ibid., S of Totlandstjørna (59°41'10.32"N, 05°20'56.4"E), on *C. avellana*, 6/28/2017, *G. Gaarder* (TRH-L-18035); ibid., Totsida (59°40'49.08"N, 05°19'33.24"E), on *I. aquifolium*, 6/27/2017, *G. Gaarder & M. Lorentzen* (TRH-L-18037); ibid., Våge (59°43'37.56"N, 05°13'30.36"E), on *C. avellana*, 4/30/2018, *G. Gaarder* (TRH-L-18031). Fusa, Holmefjord, Eikhaugen (60°17'57.1"N, 05°39'52.0"E), on *Q. robur*, 30 m a.s.l., 5/8/2018, *A. Frisch 18/No24* (TRH). Kvam, Nes N (60°10'05.1"N, 05°55'32.1"E) on *F. excelsior*, 6/4/2018, *G. Gaarder* (TRH-L-18608). Stord, Åsen SW of Sagvåg (59°46'02.6"N, 05°24'35.6"E), on *C. avellana*, 50 m a.s.l., 4/28/2018, *A. Frisch, 18/No124* (TRH); ibid., (59°46'05.3"N, 05°24'45.4"E), on *C. avellana*, 33 m a.s.l., 4/28/2018, *A. Frisch 18/No125* (TRH). Sund, Steinsland (60°12'11.96"N, 05°04'55.78"E) on *C. avellana*, 20–40 m a.s.l., 3/9/1997, *T. Tønsberg* (BG-L-34117). Tysnes, Beltestad, Beltestadknappen (59°59'53.0"N, 05°27'32.6"E), on *C. avellana*, 13 m a.s.l., 5/9/2018, *A. Frisch 18/No12* (TRH).

Additional examined specimens. GREAT BRITAIN, SCOTLAND: Argyll, Appin, Glen Stockdale (N56°34'23" W005°21'35"), on *C. avellana*, 65–90 m a.s.l., 6/5/2018, *A. Acton, J. Malíček* & *Z. Palice* 25146 (PRA); ibid., Westerness Locli Surnart, Reripole Ravine, on *Corylus* sp., 3/10/1983, *B. J. Coppins* (BG-L-58163).

Coniocarpon fallax (Ach.) Grube

In Frisch et al., Taxon 63: 737 (2014). *Spiloma fallax* Ach., Methodus qua omnes dectectos lichenes: 10 (1803) [MB 405518]. Type: Germania (H-Ach.!, lectotype, selected in Frisch et al., Taxon 63: 737, 2014).

= *Spiloma elegans* Ach., Lichenographia universalis: 135 (1810) [MB 405516]. *Coniocarpon elegans* (Ach.) Duby, Aug. Pyrami de Candolle Botanicon Gallicum: 675 (1830) [MB 383617]. *Lichen elegans* (Ach.) Lam. in Lamarck & Poiret, Encyclopédie méthodique, botanique, suppl. 3(1): 352 (1813) [MB 122540]. *Arthonia elegans* (Ach.) Almq., Kongliga Svenska vetenskaps-akademiens handlingar 17(6): 19 (1880) [MB#118959]. Type: Schleicher, Plantae Cryptogamicae Helvetiae exsiccatae, centuria5 no. 54 (S, lectotype, selected in Van den Broeck et al., Plant Ecology and Evolution 151: 346, 2018).

[MB 808766]

Figs. 3, 4B, 5C, 6, 9B.

THALLUS pale fawn to grey brown, weakly glossy to matt, smooth, endophloeodal to partly epiphloedal, continuous; *prothallus line* dark grey to brown, sometimes present when in contact with other lichens; *photobiont* trentepohlioid, the cells rounded to elliptical, 8–13 × 5–10 µm, forming short chains. ASCOMATA weakly elongate to irregularly lirellate, with steep flanks, emergent from thallus, 0.2–0.4 mm × 0.1–0.2 mm, 65–110 µm tall, typically forming loose to dense aggregations of 3–15 ascomata, weakly elongated to irregularly lirellate to stellate, 0.2–1.5(–2.3) × 0.1–1.8 mm; *disc* black to dark purple black, flat to weakly convex, weakly glossy to matt, epruinose or with a thin layer of white pruina; *margins* level with the disc, orange-red pruinose, sometimes with additional patches of white pruina; *proper exciple* brown, 7–20 µm wide, composed of compressed and vertically oriented paraphysoidal hyphae, the hyphae 1–2 µm thick, branched and netted, often forming short hairs up to 17 µm long at the outer margin; old bark cells sometimes attached to the exciple; *epithecium* brown, 10–20 µm tall, conglutinated only in the lower parts, composed of branched tips of the paraphysoidal hyphae extending horizontally above the asci; the tips slightly widened to 3(–4) µm, sometimes extending from the

epithecium as sparsely branched anticlinal hairs up to 24 µm long; h*ymenium* hyaline, strongly conglutinated, 35–70 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline, conglutinated, 15–30 µm tall, formed of irregular prosoplectenchymatic hyphae 1–2 µm diam.; *crystals* common in epithecium and proper exciple, of two types: hyaline, leafy crystals, 1–5(–7) µm, and orange, red or purple granular crystals, 1–2(–4) µm; a weak amorphous, red to purple pigmentation present in exciple, epithecium and patchily distributed in the hymenium. ASCI of the *Arthonia*-type, long obpyriform to clavate, 50–75 × 20–32 µm (n=33), 8-spored, the ascospores stacked; tholus 5–8 µm thick, lateral ascospore wall 1–2 µm thick. ASCOSPORES hyaline, (1–)3–4(–5) transversely septate, (15–)17–20(–22) × (6–)7–9(–10) µm (l: mean=18.5, STD=1.9; w: mean=8.2, STD=0.9; n=191), obovate, with enlarged apical cell, getting pale brown with granular ornamentation in the epispore at late maturity; development macrocephalic.

Chemistry. Pigments A1 (minor to trace), A2 (absent), A3 (major), A4 (major) in solvents C detected by HPTLC. *Proper exciple* I_{dil}+ blue, I+ dark blue, KI+ dark blue; *epithecium* I_{dil}+ blue, I+ dark blue, KI+ dark blue; *hymenium* I_{dil}+ red, I+ red brown, KI+ dark blue; *hypothecium* I_{dil}+ blue, I+ dark blue, KI+ dark blue. Ahemiamyloid ring present in the tholus of the asci. Hyaline, crystals dissolve in K. Orange, red and purple crystals dissolve in K with purplish solution.

Notes. *Coniocarpon fallax* superficially resembles *C. cinnabarinum* by ascomata that are covered in an orange-red and white pruina. The ascomatal margin in both species is typically covered in an orange-red pruina with sometimes additional patches of white pruina. The distribution of pruina on the disk differs between the two species. The disc of *C. fallax* is epruinose to covered in a thin layer of white pruina. On the other hand, the disc of *C. cinnabarinum* is covered in a thick layer of white pruina, sometimes overlaid by orange-red pruina. The ascomata of *C. fallax* are slightly elongate to clearly lirellate as compared to the irregularly rounded to elliptical to weakly lobed ascomata in *C. cinnabarinum* which are only raley distinctly lirellate. The ascospores of *C. fallax* are distinctly smaller and with less septa (*C. fallax*: (15–)17–20(–22) × (6–)7–9(–10) µm, (1–)3–4(–5) transversely septate vs C. *cinnabarinum*: (19–)23–28(–30) × (8–)10–11(–12) µm, (3–)4–5(–8) transversely septate). Mature, apparently well-developed elliptical ascospores with only a single septum were found in one specimen (TRH L-17089) of *C. fallax*. The reaction of the hypothecium to iodine differs

between the two species (*C. fallax*: I_{dil}+ blue, I+ dark blue vs *C. cinnabarinum*: I_{dil}+ red, I+ red). Moreover, the HPTLC results differs (*C. fallax*: A1 minor to trace, A2 absent, A3 major, A4 major vs *C. cinnabarinum*: A1 major, A2 absent, A3 major, A4 minor).

Specimens examined. NORWAY, VEST-AGDER: Lyngdalsfjord, on *F. excelsior*, 4/8/1905, *A. H. Magnusson* (S-F-71115); ibid., 1925, *A. H. Magnusson* (S-F-71114); ibid., on *F. excelsior*, 1/25/1939, *A. H. Magnusson* (UPS-L-002899). ROGALAND: Gjesdal, Dirdal, on *F. excelsior*, 10/6/1984, *S. Hultengren* (UPS-L-654296); ibid., (58°49'48.6"N, 06°11'58.2"E), on *F. excelsior*, 160 m a.s.l., 7/12/2017, *A. Frisch S04-2-Fe2-7, 17/No23* (TRH). HORDALAND: Askøy, on *C. avellana* and *F. excelsior*, 1909, *J. J. Havaas* (UPS-L-137313). Fusa, Tveitane, 13 km S of Mundheim (60°03'00.0"N, 05°52'00.0"E), on *C. avellana*, 150 m a.s.l., 8/18/1995, *A. Nordin* (UPS-L-61739); ibid., Øvre Hålandsdalen, W of Orra (60°15'30.39"N, 05°55'8.22"E), on *F. excelsior*, 120 m a.s.l., 2/24/2015, *S. Vatne* (TRH-L-16793). Kvam, Daleelva N (60°07'27.2"N, 05°52'43.3"E), on *F. excelsior*, 6/10/2018, *G. Gaarder* (TRH-L-18605); ibid., (60°07'40.1"N, 05°52'53.9"E), on *F. excelsior*, 6/13/2018, *G. Gaarder* (TRH-L-18606); ibid., Furhovda (60°09'14.6"N, 05°53'54.6"E), on *F. excelsior*, 6/5/2018, *G. Gaarder* & *M. Lorentzen* (TRH-L-18604); ibid., Hovden (60°13'44.1"N, 05°59'38.0"E), on *F. excelsior*, 6/11/2018, *G. Gaarder* (TRH-L-18607). Lindås, Helltveit W (60°37'52.33"N, 05°26'04.82"E), on *F. excelsior*, 7/24/1980, T. Tønsberg (BG-L-26222); ibid., Kvalvika-Røyldalane (60°38'14.7"N, 05°26'20.7"E), on *F. excelsior*, 35 m a.s.l., 5/14/2018, *A. Frisch & J. Klepsland 18/No95* (TRH). Os, Li (60°10'23"N, 05°26'27"E), on *F. excelsior*, 60–120 m a.s.l., 7/22/1979, *T. Tønsberg* (BG-L-26221, BG-L-26221). Stord, Valavåg, Nes-Åsen (59°46'6.96"N, 05°24'39.6"E), on *F. excelsior*, 4/27/2018, *G. Gaarder & U. Hanssen* (TRH-L-18041). Tysnes: Skardnipa near Teigen (59°58'21.6"N, 05°39'00.5"E), on *F. excelsior*, 23 m a.s.l., 5/9/2018, *A. Frisch & J. Klepsland, 18/No64* (TRH); ibid., (59°58'21.7"N, 05°39'01.4"E), on *F. excelsior*, 19 m a.s.l., 5/9/2018, *A. Frisch & J. Klepsland 18/No77, 18/No83* (TRH); ibid., (59°58'21.0"N, 05°38'59.5"E), on *F. excelsior*, 24 m a.s.l., 5/9/2018, *A. Frisch & J. Klepsland, 18/No86* (TRH); ibid., Sunde, Loksund, on *F. excelsior*, 8/27/1910, *J. J. Havaas* (UPS-L-137512). Tysnesøy, N of Onarheim (59°58'22.6"N, 05°39'02.8"E), on *F. excelsior*, 30 m a.s.l., 7/21/2017, *A. Frisch & J. Klepsland 17/No49, 17/No53* (TRH). MØRE OG ROMSDAL: Fræna, S of Hustad, Lunheim (62°55'23.23"N, 07°06'53.5"E), on *C. avellana*, 60 m a.s.l., 4/15/2016, *H. Holien* (TRH-L-17089); ibid., Nordmark E (62°54'59.91"N, 07°07'04.07"E), on *C. avellana*, 80 m a.s.l.,

4/26/1998, *G. Gaarder* (BG-L-39619); ibid., Tverrfjell, N of Stormyra (62°54'52.3"N, 07°16'14.6"E), on *C. avellana*, 60 m a.s.l., 7/5/2017, *A. Frisch S19-1-Ca2-1*, *17/No56* (TRH); Skodje, Igletjønna (62°28'39.39"N, 06°34'29.07"E), on *C. avellana*, 4/20/2014, *G. Gaarder & P. Larsen* (TRH-L-16791). Tingvoll, Kamsvågtrøa (63°01'53.99"N, 08°08'8.99"E), on *C. avellana*, 2/16/2014, *G. Gaarder* (TRH-L-15366); ibid., Langvatnet NE (63°02'56.76"N, 08°04'18.12"E), on *C. avellana*, 11/8/2014, *G. Gaarder* (TRH-L-16792); ibid., Skjelberget (63°03'12.24"N, 08°03'51.84"E), on *C. avellana*, 4/25/2014, *G. Gaarder* (TRH-L-16789); ibid., Årøyvatnet (63°02'49.92"N, 08°02'23.64"E), on *C. avellana*, 11/8/2014, *G. Gaarder* (TRH-L-16790). SWEDEN, GOTLAND: Bunge, 1 km from Bunge church, (57°51'0"N, 19°00'0"E) on *F. excelsior*, 15 m a.s.l., 4/27/1996, *A. Nordin* (UPS-L-74225); ibid., *G. Westling* (S-L-52399); Bäl, 1 km E of Bäl church (57°39'00.0"N, 18°40'00.0"E), on *F. excelsior*, 11/25/1996, *P. Johanson* (UPS-L-98398).

Additional examined specimens. AUSTRIA, UPPER AUSTRIA: Totes Gebirge, Lake Almsee SSE (47°44'36.0"N, 13°57'24.0"E), on *F. excelsior*, 600 m a.s.l., 5/31/1998, *T. Tønsberg* (BG-L-66299). TURKEY, TRABZON: Trabazon Vilayet, Uzungöl c. 14 km SSE of Caykara (40°36'52.2"N, 40°18'51.0"E), on *Picea orientalis*, 6/24/2001, *C. Printzen* & *B. Kanz* (BG-L-77481).

4.2.2 *Arthonia punctiformis* Ach. s.lat.

Kongliga vetenskaps academiens nya handlingar 29: 130 (1808) [MB 241025]. Type: Suecica (H-ACH 32A lectotype, selected in Sundin & Tehler, The Lichenologist 30: 399, 1998; UPS-ACH isotype).

Nomenclatural note. The extensive synonymy of *A. punctiformis* in Europe could not be solved in this project, partly due to the inaccessibility of important type specimens. The observed phylogenetic lineages are named *A. punctiformis* 1 to 4 until the nomenclature of *A. punctiformis* s.lat. has been clarified. *Arthonia punctiformis* 2 and 3 are represented by single collections only and their taxonomic status needs further evaluation.

Key to *Arthonia punctiformis* s.lat. in Norway

1 Ascomata irregularly rounded to elliptical to shortly elongate 2

1' Ascomata irregularly lirellate 3

2 Ascospores (17–)18–21(–24) × 5–7(–8) µm, narrowly oblanceolate (length/width ratio 2.6–3.7×); hymenium I+ blue; growing on the twigs of *Betula* sp. or *S. aucuparia* ..... *A. punctiformis* 4

2' Ascospores (14–)15–18(–20) × (5–)6–7(–8) µm, oblanceolate (length/width ratio 2.1–2.8×); hymenium I+ red mottled with blue or I+ blue; growing on the twigs of *C. avellana*, *F. excelsior*, *H. rhamnoides*, *S. aucuparia* or *T. cordata* ..... *A. punctiformis* 1

3 Disc uneven; margins prominent to level with the disc ..... *A. punctiformis* 3

3' Disc flat to weakly convex; margins level with the disc ..... *A. punctiformis* 2

Arthonia punctiformis 1

Figs. 4D, 7, 8A, 10A.

THALLUS indistinct, endophloeodal; *prothallus line* dark grey to brown, sometimes present when in contact with other lichens; *photobiont* absent. ASCOMATA irregularly rounded to narrowly ellipsoid to fusiform, rarely distinctly lobed, with mild to steep flanks, immersed in the host bark, slightly emergent, 0.3–1.0(–1.2) × 0.1–0.6(–0.7) mm, 50–70(–80) µm tall, solitary; *disc* black, erumpent, flat to weakly convex, matt to weakly glossy, epruinose, sometimes partially covered with thin remnants of bark tissue; *margins* level with the disc, epruinose, mostly covered by a thin layer of bark tissue; *proper exciple* olivaceous brown to blackish, 8–12 µm wide, composed of compacted paraphysoidal hyphae, the hyphae 1–2 µm thick, densely branched and netted; *epithecium* olivaceous brown to blackish, 6–10 µm tall, conglutinated only in the lower parts, composed of densely branched tips of the paraphysoidal hyphae extending vertically to slightly horizontally above the asci; the tips slightly widened to 2(–3) µm, sometimes with dark pigment cups; *hymenium* hyaline, strongly conglutinated, 30–35(–40) µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline to slightly greyish, conglutinated, 8–15 µm tall, formed of irregular prosoplectenchymatic hyphae, hyphae 1 µm diam.; *crystals* absent. ASCI of the *Arthonia*-type, ovoid to subglobose, 35–43 µm × 18–24 µm (n=6), 8-spored; tholus 3–7 µm thick, lateral ascospore wall 1–2 µm thick. ASCOSPORES hyaline, 3(–4) transversely septate, (14–)15–18(–20) × (5–)6–7(–8) µm (l: mean=16.3, STD=1.4; w: mean=6.8, STD=0.8; n=95), oblanceolate (length/width ratio 2.1–2.8×), without enlarged apical cell; older ascospores pale brownish, with constricted septa and with a brownish granular ornamentation in the ascospore wall; development microcephalic.

Chemistry. *Proper exciple* I_{dil}+ blue, I+ blue, KI+ blue; *epithecium* I_{dil}+ blue, I+ blue, KI+ blue; *hymenium* I_{dil} blue, I+ red mottled with blue or entirely blue, KI+ blue; *hypothecium* I_{dil}+ blue, I+ blue, KI+ blue. *Asci* with hemiamyloid ring in the tholus. *Ascospore wall* I_{dil}+ pale red, I+ pale red, KI+ pale blue.

Notes. The ascomata of *A. punctiformis* 1 resemble those of *A. punctiformis* 4. *Arthonia punctiformis* 1 differs from *A. punctiformis* 4 in ascospores size and shape (*A. punctiformis* 1: (14–)15–18(–20) × (5–)6–7(–8) µm, oblanceolate vs *A. punctiformis* 4: (15–)18–21(–24) × 5–7(–8) µm, narrowly oblanceolate) and in their preference of host tree species. *Arthonia punctiformis*

1 has been collected from a rather broad range of host trees including *C. avellana*, *F. excelsior*, *H. rhamnoides*, *S. aucuparia* and *T. cordata*, while *A. punctiformis* 4 was collected from *B. pendula* in Sweden and *B. pubescens* and *S. aucuparia* in Norway. *Arthonia punctiformis* 1 is similar in ascospore shape and size to *A. punctiformis* 2. It differs by the irregularly rounded to narrowly ellipsoid to fusiform vs irregularly lirellate ascomata. *Arthonia punctiformis* 3 lacks asci and ascospores but differs from *A. punctiformis* 1 by ascoma shape (*A. punctiformis* 1: irregularly rounded to narrowly ellipsoid to fusiform vs *A. punctiformis* 3: irregularly lirellate). The hymenium's reaction to iodine in *A. punctiformis* 1 was I+ red mottled with blue in most investigated specimens. However, in some specimens it was entirely blue. Moreover, the I+ red mottled with blue hymenium was observed in *A. punctiformis* 2 and 3 as well, while the hymenium of *A. punctiformis* 4 was I+ blue in all investigated specimens.

Specimens examined. VEST-AGDER: Flekkefjord, Hidra, Høgåsen (58°13'35.1"N, 06°33'22.2"E), on *C. avellana*, 20–50 m a.s.l., 7/15/2017, *A. Frisch S01-2-Ca2-1*, 17/No71 (TRH). ROGALAND: Gjesdal, Dirdal NE (58°49'48.6"N, 06°11'58.2"E), on *T. cordata*, 145–175 m a.s.l., 7/12/2017, *A. Frisch S04-2-Tc1-6* (TRH); ibid., (58°50'02.7"N, 06°11'29.1"E), on *C. avellana*, 15–30 m a.s.l., 7/12/2017, *A. Frisch S04-1-Ca1-8* (TRH); ibid., (58°50'03"N, 06°11'29"E), on *T. cordata*, 160 m a.s.l., 7/12/2017, *A. Frisch S04-1-Tc1-2* (TRH). Rennesøy, Hodnafjellet (59°04' 26.2"N, 05°44'09.6"E), on *C. avellana*, 25–50 m a.s.l. 7/13/2017, *A. Frisch S06-1-Ca1-11* (TRH); ibid., on *F. excelsior*, *A. Frisch S06-1-Fe3-5* (TRH). Sokndal, Skåras (58°20'24.5"N, 06°15'51.5"E), on *C. avellana*, 110–135 m a.s.l., 7/14/2017, *A. Frisch S03-1-Ca1-2* (TRH); ibid (58°20'30.2"N, 06°15'54.9"E), on *C. avellana*, 70–110 m a.s.l., 7/14/2017, *A. Frisch S03-2-Ca1-1* (TRH). HORDALAND: Os, Strøno, Svensvikmyrane (60°10'43.4"N, 05°20'52.3"E), on *S. aucuparia*, 20–50 m a.s.l., 5/12/2018, *A. Frisch 18/No48* (TRH); ibid., (60°10'39.0"N, 05°20'58.6"E), on *C. avellana*, 35–50 m a.s.l., 5/12/2018, *A. Frisch 18/No23* (TRH). MØRE OG ROMSDAL: Tingvoll, Aspøya, Sterdalen, Sallaupen E (63°02'14.9"N, 07°55'55.7"E), on *C. avellana*, 7/6/2017, *A. Frisch S21-2-Ca2-1* (TRH). TRØNDELAG: Åfjord, Selnes, Prestnaustet (63°54'02.9"N, 09°58'01.9"E), on *H. rhamnoides*, 10 m a.s.l., 6/12/2015 *A. Frisch 15/No2, 15/No3* (TRH); ibid; Stokkøya, Hosnavika (64°03'04.2"N, 09°56'45.7"E), on *H. rhamnoides*, 10 m a.s.l., 6/22/2017, *A. Frisch 17/No136* (TRH). NORDLAND: Meløy, Holandsfjorden, Fonndalen, Fonndal W (66°41'53.8"N, 13°40' 36.1"E), on *S. aucuparia*, 10–25 m a.s.l., 7/1/2018, *A. Frisch N13-1-Sa2-2* (TRH).

Arthonia punctiformis 2

Figs. 4E, 7, 8B, 10A.

THALLUS indistinct, endophloeodal; *prothallus line* pale brown, sometimes present when in contact with other lichens; *photobiont* absent. ASCOMATA irregularly lirellate, with mild to steep flanks, immersed in the host bark, slightly emergent, 0.2–1.4 × 0.1–0.2(–4) mm, 45–65 µm tall, typically solitary, sometimes 2–3 grouped together; *disc* black, erumpent, flat to weakly convex, matt to weakly glossy, epruinose; *margins* level with the disc, epruinose, sometimes partially covered with thin remnants of bark tissue; *proper exciple* olivaceous brown to blackish, 7–10 µm wide, composed of compacted paraphysoidal hyphae, the hyphae 1–2 µm thick, densely branched and netted; *epithecium* olivaceous brown to blackish, 7–10 µm tall, conglutinated only in the lower parts, composed of densely branched tips of the paraphysoidal hyphae extending vertically to slightly horizontally above the asci; the tips slightly widened to 2(–3) µm, sometimes with dark pigment cups; *hymenium* hyaline, strongly conglutinated, 20–30 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline to slightly greyish, conglutinated, 8–10 µm tall, formed of irregular prosoplectenchymatic hyphae, hyphae 1 µm diam.; *crystals* absent. ASCI of the *Arthonia*-type, ovoid subglobose, 35–40 µm × 20–23 µm (n=3), 8-spored; tholus 5–7 µm thick, lateral ascospore wall 1–2 µm thick. ASCOSPORES hyaline, 3 transversely septate, 16–18 × 6–7 µm (n=10), oblanceolate, without enlarged apical cell; older ascospores pale brownish, with constricted septa and with a brownish granular ornamentation in the ascospore wall; development microcephalic.

Chemistry. *Proper exciple* I_{dil}+ blue, I+ blue, KI+ blue; *epithecium* I_{dil}+ blue, I+ blue, KI+ blue; *hymenium* I_{dil} blue, I+ red mottled with blue, KI+ blue; *hypothecium* I_{dil}+ blue, I+ blue, KI+ blue. *Asci* with hemiamyloid ring in the tholus. *Ascospore wall* I_{dil}+ pale red, I+ pale red, KI+ pale blue.

Notes. *Arthonia punctiformis* 2 separates from *A. punctiformis* 1 and 4 by its ascoma shape (*A. punctiformis* 2: irregularly lirellate vs *A. punctiformis* 1 and 4: irregularly rounded to narrowly ellipsoid to fusiform). The single specimen of *A. punctiformis* 2 is growing on the twigs of *C. avellana* and this host tree species is also present in *A. punctiformis* 1. *Arthonia punctiformis* 2 superficially resembles *A. punctiformis* 3 due to similar ascoma shape, but it separates by

differences of the margin and disc (*A. punctiformis* 2: disc flat to weakly convex; margins level with the disc vs *A. punctiformis* 3: disc uneven; *margins* prominent to level with the disc).

Specimens examined. NORWAY, SOGN OG FJORDANE: Florø, Storefjellet NW (61°40'00.5"N, 05°00'02.2"E), on *C. avellana*, 35–70 m a.s.l., 5/17/2018, *A. Frisch & J. Klepsland 18/No3* (TRH).

Arthonia punctiformis 3

Figs. 7, 8C, 10A.

THALLUS indistinct, endophloeodal; *prothallus line* dark grey, sometimes present when in contact with other lichens; *photobiont* absent. ASCOMATA irregularly lirellate, with mild to steep flanks, immersed in the host bark, slightly emergent, 0.2–0.4 × 0.1–0.2 mm, 50–70 µm tall, typically solitary, sometimes 2–3 grouped together; *disc* black, erumpent, uneven, matt to weakly glossy, epruinose; *margins* prominent to level with the disc, epruinose, sometimes partially covered with thin remnants of bark tissue; *proper exciple* olivaceous brown to blackish, 7–10 µm wide, composed of compacted paraphysoidal hyphae, the hyphae 1–2 µm thick, densely branched and netted; *epithecium* olivaceous brown to blackish, 7–10 µm tall, conglutinated only in the lower parts, composed of densely branched tips of the paraphysoidal hyphae extending vertically to slightly horizontally above the asci; the tips slightly widened to 2(–3) µm, sometimes with dark pigment cups; *hymenium* hyaline, strongly conglutinated, 25–30 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline to slightly greyish, conglutinated, 8–10 µm tall, formed of irregular prosoplectenchymatic hyphae, hyphae 1 µm diam.; *crystals* absent.

Chemistry. *Proper exciple* I_{dil}+ blue, I+ blue, KI+ blue; *epithecium* I_{dil}+ blue, I+ blue, KI+ blue; *hymenium* I_{dil} blue, I+ red mottled with blue, KI+ blue; *hypothecium* I_{dil}+ blue, I+ blue, KI+ blue.

Notes. The single specimen of *Arthonia punctiformis* 3 lacks asci and ascospores. *Arthonia punctiformis* 3 resembles *A. punctiformis* 2, and the difference between the two is described in detail under *A. punctiformis* 2. *Arthonia punctiformis* 3 differs from *A. punctiformis* 1 and 4 by its ascoma shape (*A. punctiformis* 3: irregularly lirellate vs *A. punctiformis* 1 and 4: irregularly rounded to narrowly ellipsoid to fusiform). *Arthonia punctiformis* 3 is collected from *S. aucuparia* which also is a host species in *A. punctiformis* 1 and 4.

Specimens examined. NORWAY, TRØNDELAG: Steinkjer, Mokk farm (63°58'19.5"N, 12°07'37.0"E), on *S. aucuparia*, 358 m a.s.l., 08/04/2015, *Frisch 15/No105* (TRH).

Arthonia punctiformis 4

Figs. 4F, 7, 8D, 10B.

THALLUS indistinct, endophloeodal; *prothallus line* dark grey, rarely present when in contact with other lichens; *photobiont* absent. ASCOMATA irregularly rounded to narrowly ellipsoid to fusiform, with mild to steep flanks, immersed in the host bark, slightly emergent, 0.2–1.0(–1.4) × 0.1–0.5(–0.8) mm, 50–70 µm tall, solitary; *disc* black, erumpent, flat to weakly convex, matt to weakly glossy, epruinose; sometimes partially covered with thin remnants of bark tissue; *margins* level with the disc, epruinose; mostly covered by a thin layer of bark tissue; *proper exciple* olivaceous brown to blackish, 5–10 µm wide, composed of compacted paraphysoidal hyphae, the hyphae 1–2 µm thick, densely branched and netted; *epithecium* olivaceous brown to blackish, 7–15 µm tall, conglutinated only in the lower parts, composed of densely branched tips of the paraphysoidal hyphae extending vertically to slightly horizontally above the asci; the tips slightly widened to 2(–3) µm, sometimes with dark pigment cups; *hymenium* hyaline, strongly conglutinated, 20–35 µm tall, paraphysoids densely branched and netted, 1–2 µm thick; *hypothecium* hyaline to slightly greyish, conglutinated, 8–15 µm tall, formed of irregular prosoplectenchymatic hyphae, 1 µm diam.; *crystals* absent. ASCI of the *Arthonia*-type, ovoid subglobose, 35–40 × 18–22 µm (n=10), 8-spored; tholus 3–7 µm thick, lateral ascospore wall 1–2 µm thick. ASCOSPORES hyaline, 3(–4) transversely septate, (15–)18–21(–24) × 5–7(–8) µm (l: mean=19.4, STD=1.7; w: mean=6.1, STD=0.6; n=109), narrowly oblanceolate (length/width ratio 2.6–3.7×), without enlarged apical cell; older ascospores pale brownish, with constricted septa and with a brownish granular ornamentation in the ascospore wall; development microcephalic.

Chemistry. *Proper exciple* I_{dil}+ blue, I+ blue, KI+ blue; *epithecium* I_{dil}+ blue, I+ blue, KI+ blue; *hymenium* I_{dil}+ blue, I+ blue, KI+ blue; *hypothecium* I_{dil}+ blue, I+ blue, KI+ blue. *Asci* with hemiamyloid ring in the tholus. *Ascospore wall* I_{dil}+ pale red, I+ pale red, KI+ pale blue.

Notes. *Arthonia punctiformis* 4 is collected from the twigs of *B. pendula* in Sweden and *B. pubescens* and *S. aucuparia* in Norway. *Arthonia punctiformis* 4 resembles *A. punctiformis* 1. The differences between the two are described in detail under of *A. punctiformis* 1. *Arthonia punctiformis* 4 separates from *A. punctiformis* 2 and 3 by its irregularly rounded to narrowly ellipsoid to fusiform ascomata (not clearly lirellate) and the reaction of the hymenium to iodine

(*A. punctiformis* 4: I+ blue vs *A. punctiformis* 2 and 3: red mottled with blue). Moreover, it differs from *A. punctiformis* 2 by its ascospore size and shape (*A. punctiformis* 4: (15–)18–21(–24) × 5–7(–8) µm, narrowly oblanceolate vs *A. punctiformis* 2: 16–18 × 6–7 µm, oblanceolate).

Specimens examined. ROGALAND: Berkreim, Vinjavatnet (58°44'48.2"N, 06°12'56.0"E), on *B. pubescens*, 190 m a.s.l., 7/12/2017, *A. Frisch 17/No70* (TRH). Sokndal, Skåras (58°20'24.5"N, 06°15'51.5"E), on *S. aucuparia*, 110–135 m a.s.l., 07/14/2017, *A. Frisch S03-1-Sa3-1* (TRH). HORDALAND: Bømlo, Moster, Mosterhamn E (59°42'07.1"N, 05°23'09.2"E), on *Sorbus* sp., 9 m a.s.l., 4/29/2018, *A. Frisch 18/No127* (TRH). MØRE OG ROMSDAL: Fræna, Lunheim E (62°55'08.6"N, 07°07'13.8"E), on *S. aucuparia*, 80–120 m a.sl., 7/4/2017, *A. Frisch S20-1-Sa2-2* (TRH). TRØNDELAG: Agdenes, Slettvika (63°35'32"N, 09°32'19"E), on *B. pubescens*, 15 m. a.s.l., 11/14/2018, *A. Frisch 18/No240*, *18/No239* (TRH); ibid., (63°35'28"N, 09°32'22"E), on *B. pubescens*, 20 m a.s.l., 11/14/2018, *A. Frisch, 18/No238* (TRH); ibid., (63°35'29.0"N, 09°32'18.0"E), on *S. aucuparia*, 20 m a.s.l., 11/14/2018, *A. Frisch 18/No237* (TRH); ibid., Stavøya (63°35'32"N, 09°31'18"E), on *S. aucuparia*, 3 m. a.s.l., 11/14/2018, *A. Frisch 18/No241* (TRH). Flatanger, Einvikfjellet W (64°30'14.8"N, 10°47'38.7"E), on *Betula pubescens*, 25 m a.s.l., 8/5/2015, *A. Frisch 15/No98* (TRH). Fosen, Rissa, Nordelva Nat. Reserve (63°47'51"N, 10°12'10"E), on *B. pubescens*, 100 m a.s.l., 03.05.2017, *A. Frisch 17/No135* (TRH). Namdalseid, Namdalseid church (64°13'05.9"N, 11°12'35.9"E), on *Betula* sp., 96 m a.s.l., 8/9/2018, *A. Frisch 18/No222* (TRH). Åfjord, Stokkøya, Hosnavika (64°03'04.2"N, 09°56'45.7"E), on *S. aucuparia*, 10 m a.s.l., 6/22/2017, *A. Frisch 17/No137* (TRH); ibid., on *B. pubescens*, 10 m a.s.l., 6/22/2017, *A. Frisch 17/No138, 17/No142* (TRH). NORDLAND: Lurøy, Stokkvågen, Varpa (66°19'32.8"N, 13°02'47.3"E), on *B. pubescens*, 16 m a.s.l., 6/30/2018, *A. Frisch 18/No142* (TRH). Meløy, Holandsfjorden, Fonndalen, Fondal W (66°41'53.8"N, 13°40'36.1"E), on *S. aucuparia*, 10–25 m a.s.l., 7/1/2018, *A. Frisch N13-1-Sa9-1* (TRH).

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APPENDIX A

Table A1. Vouchers and their GenBank accession numbers for specimens included in the phylogeny of *Coniocarpon*. New sequences * and missing sequences –.

Specimens	**Voucher**	**mtSSU**	***RPB2***	**nITS**
Arthonia didyma	Belgium; *Ertz 7587* (BR)	EU704047	EU704010	–
Arthonia granithophlia	Sweden; *Frisch 10/Se74* (UPS)	KJ850981	KJ851107	–
Arthonia physcidiicola	Uganda; *Frisch 11/Ug318* (UPS)	KF707646	KF707657	–
Coniocarpon cinnabarinum 1	Norway; *Frisch S06-1-Fe1-7* (TRH)	*	*	*
Coniocarpon cinnabarinum 2	Norway; *Frisch 17/No39* (TRH)	*	*	*
Coniocarpon cinnabarinum 3	Norway; *Frisch 17/No46* (TRH)	*	*	*
Coniocarpon cinnabarinum 4	Norway; *Johnsen 111003* (UPS)	KJ850976	KJ851103	–
Coniocarpon cinnabarinum 5	Norway; *Frisch S06-1-Ca5-1* (TRH)	*	*	*
Coniocarpon cinnabarinum 6	Norway; *Frisch 17/No42* (TRH)	*	*	*
Coniocarpon cinnabarinum 7	Uganda; *Frisch 11/Ug297* (UPS)	KJ850977	KJ851104	–
Coniocarpon cinnabarinum 8	Uganda; *Frisch 11/Ug296* (UPS)	KP870158	KP870170	–
Coniocarpon cinnabarinum 9	Rwanda; *Ertz 8730* (BR)	EU704046	EU704009	–
Coniocarpon cinnabarinum 10	Japan; *Frisch 13/Jp128* (TNS)	MG201840	–	–
Coniocarpon cinnabarinum 11	Japan; *Frisch 13/Jp127* (TNS)	MG201841	–	–
Coniocarpon fallax 1	Norway; *Wågström 111123* (UPS)	MG201842	MG201850	–
Coniocarpon fallax 2	Norway; *Frisch 17/No56* (TRH)	*	*	*
Coniocarpon fallax 3	Norway; *Gaarder & Larsen* (TRH-L-16791)	*	*	*
Coniocarpon fallax 4	Norway; *Frisch S19-1-Ca2-1* (TRH)	*		*
Coniocarpon fallax 5	Norway; *Gaarder* (TRH-L-16790)	*	*	*
Coniocarpon fallax 6	Norway; *Gaarder* (TRH-L-16792)	*	*	*
Coniocarpon fallax 7	Norway; *Gaarder* (TRH-L-16789)	*	*	*
Coniocarpon fallax 8	Norway; *Gaarder* (TRH-L-15366)	*	*	*
Coniocarpon fallax 9	Norway; *Frisch & Klepsland 17/No53* (TRH)	*	*	*

Coniocarpon fallax 10	Great Britain; L10175	KJ850979	KJ851101	–
Coniocarpon fallax 11	Norway; *Frisch & Klepsland 17/No49* (TRH)	*	*	*
Coniocarpon fallax 12	Norway; *Frisch S04-2–Fed-7* (TRH)	*	–	*
Coniocarpon fallax 13	Norway; *Frisch 17/No23* (TRH)	*	*	*
Coniocarpon cuspidans 1	Norway; *Frisch S06-2-Ca1-2* (TRH)	*	*	*
Coniocarpon cuspidans 2	Great Britain; *Acton, Malíček & Palice 25146* (PRA)	*	*	–
Coniocarpon cuspidans 3	Norway; *Frisch 17/No38* (TRH)	*	*	*
Coniocarpon cuspidans 4	Norway; *Frisch S06-2-Ca1-1* (TRH)	*	*	*
Coniocarpon *cuspidans* 5	Norway; *Frisch 17/No40* (TRH)	*	*	*
Coniocarpon cuspidans 6	Norway; *Klepsland 17/No65* (TRH)	*	*	*
Coniocarpon cuspidans 7	Norway; *Frisch S01-1-Ca2-1* (TRH)	*	*	*
Coniocarpon cuspidans 8	Norway; *Frisch 17/No43* (TRH)	*	*	*
Coniocarpon cuspidans 9	Norway; *Frisch S06-1-Ca1-6* (TRH)	*	–	*
Coniocarpon cuspidans 10	Norway; *Frisch S06-1-Sa3-2* (TRH)	*	–	*
Reichlingia leopoldii	Belgium; *Ertz 13293* (BR)	JF830773	HQ454722	–
Reichlingia syncesioides	Uganda; *Frisch 11/Ug14* (UPS)	KF707651	KF707656	–
Reichlingia zwackhii	Sweden; *Thor 26800* (UPS)	KF707652	KF707662	–
Synarthonia aurantiacopruinsa	DR Congo; *Van den Broeck 5764* (BR)	MH251874	MH271697	–
Synarthonia inconspicua	Uganda; *Van den Broeck 6325* (BR)	MH251880	MH271701	–
Synarthonia muriformis	Madagascar; *Ertz 19344* (BR)	MH251877	MH271699	–

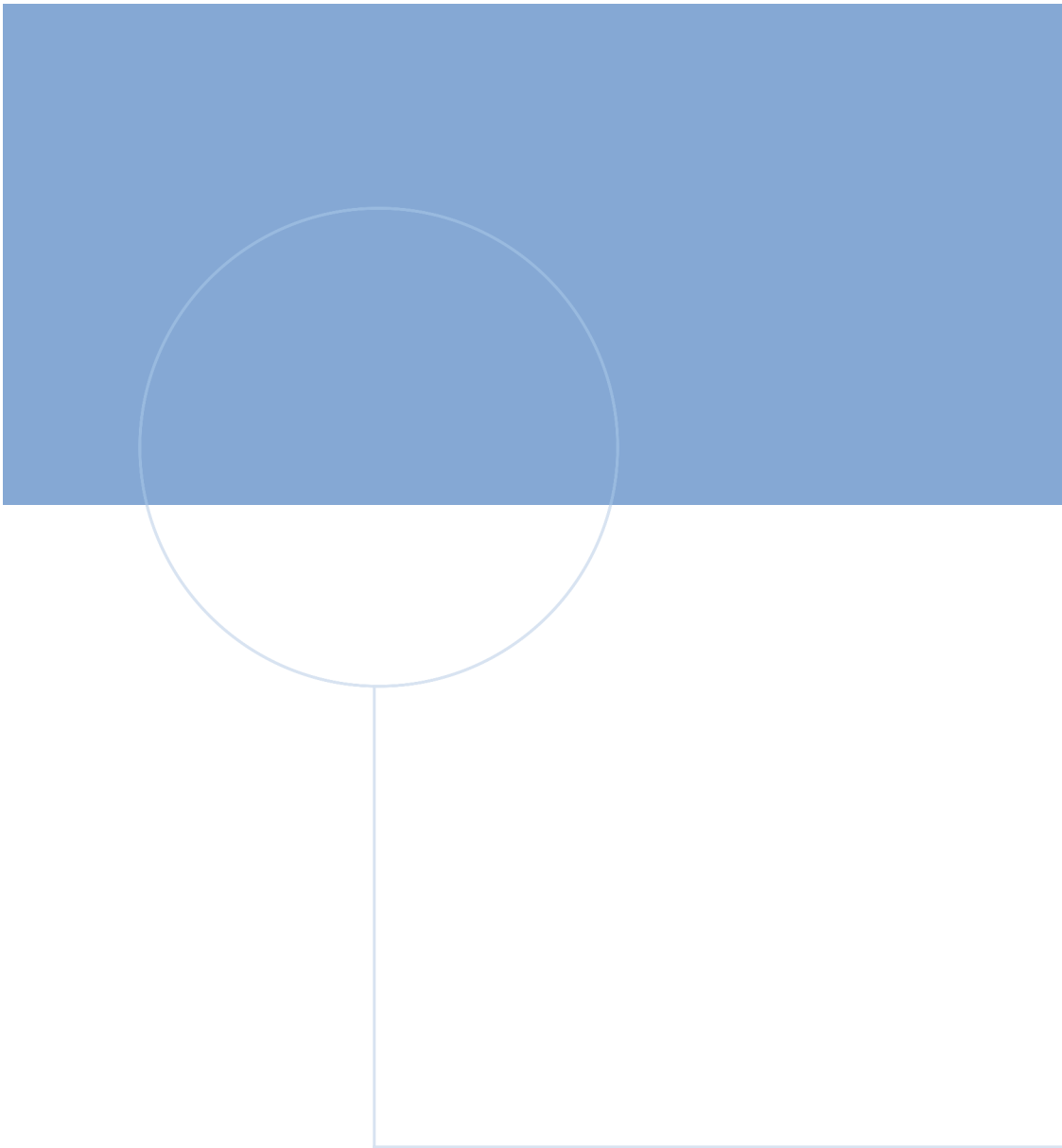
APPENDIX B

Table B1. Vouchers and their GenBank accession numbers for specimens included in the phylogeny of the *A. punctiformis* species complex. New sequences * and missing sequences –.

Specimens	**Voucher**	**mtSSU**	**nLSU**	***RPB2***	**ITS2**
Arthonia anglica	Florida; *Ertz 9090* (BR)	EU704050	–	EU704013	–
Arthonia apotheciorum	Sweden; *Frisch 11/Se23* (UPS)	KJ850970	–	KJ851148	–
Arthonia atra 1	Norway; *Frisch S06-1-Ca2-4* (TRH)	*	*	*	–
Arthonia atra 2	Norway; *Frisch S05-2-Sa3-1* (TRH)	*	*	*	–
Arthonia calcarea	France; *Ertz 7539* (BR)	EU704064	–	EU704028	–
Arthonia dispersa 1	Sweden; *Holm s.n.* (UPS)	AY571383	AY571381	–	–
Arthonia dispersa 2	Information not available	AY350570	AY350578	–	–
Arthonia excipienda 1	Norway; *Klepsland JK16-471* (O)	*	*	*	–
Arthonia excipienda 2	Norway; *Frisch S21-2-Ca1-3* (TRH)	*	*	*	–
Arthonia graphidicola	Japan; *Frisch 10/Jp102* (UPS)	KJ850980	KJ851034	–	–
Arthonia punctiformis 1	Norway; *Frisch N13-1-Sa2-2* (TRH)	*	*	*	–
Arthonia punctiformis 2	Norway; *Frisch S06-1-Ca1-11* (TRH)	*	*	*	–
Arthonia punctiformis 3	Norway; *Frisch 17/No71* (TRH)	*	*	*	–
Arthonia punctiformis 4	Norway; *Frisch S04-1-Tc1-2* (TRH)	*	*	*	–
Arthonia punctiformis 5	Norway; *Frisch S04-2-Tc1-6* (TRH)	*	*	–	–
Arthonia punctiformis 6	Norway; *Frisch S06-1-Fe3-5* (TRH)	*	*	–	*
Arthonia punctiformis 7	Norway; *Frisch S04-1-Ca1-8* (TRH)	*	*	*	*
Arthonia punctiformis 8	Norway; *Frisch S03-2-Ca1-1* (TRH)	*	*	*	*
Arthonia punctiformis 9	Norway; *Frisch S03-1-Ca1-2* (TRH)	*	*	*	*
Arthonia punctiformis 10	Norway; *Frisch 17/No136* (TRH)	*	*	*	–
Arthonia punctiformis 11	Norway; *Frisch S21-2-Ca2-1* (TRH)	*	*	*	–
Arthonia punctiformis 12	Norway; *Frisch 15/No2* (TRH)	*	–	*	–
Arthonia punctiformis 13	Norway; *Frisch S01-2–Ca2-1* (TRH)	*	*	*	–

Arthonia punctiformis 14	Norway; *Frisch 18/No23* (TRH)	*	*	*	–
Arthonia punctiformis 15	Norway; *Frisch & Klepsland 18/No3* (TRH)	*	*	*	*
Arthonia punctiformis 16	Norway; *Frisch 15/No105* (TRH)	*	*	–	–
Arthonia punctiformis 17	Norway; *Frisch S03-1–Sa3-1* (TRH)	*	*	*	*
Arthonia punctiformis 18	Norway; *Frisch 18/No241* (TRH)	*	*	*	–
Arthonia punctiformis 19	Norway; *Frisch 18/No222* (TRH)	*	*	*	*
Arthonia punctiformis 20	Norway; *Frisch 18/No237* (TRH)	*	*	*	*
Arthonia punctiformis 21	Norway; *Frisch 17/No135* (TRH)	*	*	*	*
Arthonia punctiformis 22	Norway; *Frisch 17/No70* (TRH)	*	*	*	*
Arthonia punctiformis 23	Norway; *Frisch S20-1-Sa2-2* (TRH)	*	*	*	*
Arthonia punctiformis 24	Norway; *Frisch 17/No137* (TRH)	*	*	*	*
Arthonia punctiformis 25	Norway; *Frisch 17/No138* (TRH)	*	*	*	*
Arthonia punctiformis 26	Norway; *Frisch 18/No239* (TRH)	*	*	*	*
Arthonia punctiformis 27	Sweden; *Thor 26158* (UPS)	KJ850973	KJ851044	KJ851113	–
Arthonia punctiformis 28	Norway; *Frisch N13-1-Sa9-1* (TRH)	*	*	*	*
Arthonia punctiformis 29	Norway; *Frisch 15/No98* (TRH)	*	–	*	*
Arthonia punctiformis 30	Norway; *Frisch 18/No238* (TRH)	*	*	*	*
Arthonia punctiformis 31	Norway; *Frisch 18/No240* (TRH)	*	*	*	–
Arthonia punctiformis 32	Norway; *Frisch 18/No142* (TRH)	*	*	*	*
Arthonia punctiformis 33	Norway; *Frisch 17/No142* (TRH)	*	–	*	*
Arthonia punctiformis 34	Norway; *Frisch 18/No127* (TRH)	*	*	*	*
Arthonia aff. *punctiformis*	Japan; *Thor 24702* (UPS)	KJ850975	KJ851043	–	–
Arthonia physcidiicola	Uganda; *Frisch 11/Ug318* (UPS)	KF707646	–	KF707657	–
Arthonia radiata 1	Norway; *Frisch S01-2-Ca1-4* (TRH)	*	*	*	*
Arthonia radiata 2	Norway; *Frisch 18/No210* (TRH)	*	*	*	*
Arthonia subfuscicola	Sweden; *Frisch 11/Se15* (UPS)	KJ850972	–	KJ851111	–
Coniocarpon cinnabarinum 6	Norway; *Frisch 17/No42* (TRH)	*	–	*	*

Coniocarpon fallax 8	Norway; *Gaarder* (TRH-L-15366)	*	–	*	*
Coniocarpon cuspidans 3	Norway; *Frisch 17/No38* (TRH)	*	–	*	*
Reichlingia leopoldii	Belgium; *Ertz 13293* (BR)	JF830773	–	HQ454722	–
Reichlingia syncesioides	Uganda; *Frisch 11/Ug14* (UPS)	KF707651	KF707636	KF707656	–



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