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Opegrapha multipuncta and *Schismatomma quercicola* (Arthoniomycetes) belong to the Lecanoromycetes

Damien ERTZ, Neil SANDERSON, Brian J. COPPINS, Jon T. KLEPSLAND and Andreas FRISCH

Abstract: *Opegrapha multipuncta* and *Schismatomma quercicola* are two sterile European lichens reproducing only vegetatively by means of soredia. RAxML and Bayesian analyses of newly generated sequence data from the mitochondrial ribosomal RNA small subunit provide clear evidence that these two species do not belong to the Arthoniomycetes, but to the Lecanoromycetes. In our phylogenetic analyses, *O. multipuncta* is nested in the genus *Porina* (*Porinaceae*) as sister to *P. austroatlantica*, while *S. quercicola* is nested in the genus *Schizotrema* (*Graphidaceae*) as sister to *S. zebrinum*. The following new combinations are introduced: *Porina multipuncta* (Coppins & P. James) Ertz, Coppins & Frisch and *Schizotrema quercicola* (Coppins & P. James) Ertz, Frisch & Sanderson. *Schizotrema quercicola* represents the first record of the genus *Schizotrema* for Europe and the first sorediate member in this genus. The species is newly recorded from Norway. The lichenicolous habit of *Arthonia invadens* is confirmed.

Key words: *Graphidaceae*, lichens, *Ostropales*, phylogeny, *Porinaceae*, *Schizotrema*, taxonomy

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Introduction

Sterile crustose lichens containing a trentepohlioid photobiont have, in recent decades, often been tentatively described in genera of *Arthoniomycetes* such as *Opegrapha* and *Schismatomma* (e.g. James 1971; Coppins & James 1989; Coppins *et al.* 1992; Øvstedal & Schaefer 2013; Diederich *et al.* 2017). However, determining the systematic position of sterile lichens is difficult using only morphological and chemical data, rendering these generic placements highly uncertain. Important progress has been made in sequencing many fungal groups allowing the taxonomic status of sterile taxa to be resolved by placing them in phylogenetic trees. For example, in the *Arthoniales*, recent molecular data were used to demonstrate that the sterile *Enterographa sorediata* Coppins & P. James is the sorediate morph of *Syncesia myrticola* (Fée) Tehler (Ertz *et al.* 2018*a*). The systematic placement of several lichenized hyphomycetes or lichens producing only pycnidia was also resolved using molecular data, with species often transferred to other, sometimes new or resurrected arthonialean genera (e.g. Ertz & Tehler 2011; Frisch *et al.* 2015; Ertz *et al.* 2018*c*).

In the framework of molecular studies of sterile *Arthoniales* described from Great Britain, fresh specimens of *Opegrapha multipuncta* Coppins & P. James and of *Schismatomma quercicola* Coppins & P. James were collected. Additional specimens of both taxa were also collected during recent surveys of crustose lichens in highly oceanic forests in western and central Norway. Sequences obtained from these specimens revealed that these two species

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do not belong to the Arthoniomycetes, but instead to the Lecanoromycetes. The present study aims to clarify their systematic position.

Materials and Methods

Voucher specimens are deposited in the herbaria BR and TRH, and the private herbarium of N. A. Sanderson. The external morphology was studied and measured using an Olympus SZX12 stereomicroscope. Macroscopic photographs were taken using a Keyence VHX-5000 digital microscope and a VH-Z20R/W/T lens. Lichen secondary metabolites were identified using thin-layer chromatography (TLC) in solvent B (Orange *et al.* 2001).

Molecular techniques

Well-preserved and freshly collected specimens lacking any visible symptoms of fungal infection were used for sequencing. A group of 4–6 soredia was used for direct PCR as described in Ertz *et al.* (2015). Amplification reactions were prepared for a 50 µl final volume containing the lichen material as explained in Ertz *et al.* (2018*c*). A targeted fragment of *c.* 0·8 kb of the mitochondrial ribosomal RNA small subunit (mtSSU) was amplified using primers mrSSU1 and mrSSU3R (Zoller *et al.* 1999). The yield of the PCRs was verified by running the products on a 1% agarose gel using ethidium bromide. Both strands were sequenced by Macrogen® using amplification primers. Sequence fragments were assembled with Sequencher v. 5.3 (Gene Codes Corporation, Ann Arbor, Michigan). Sequences were subjected to GenBank 'megablast' searches to verify their closest relatives and to detect potential contaminations.

Taxon selection and phylogenetic analyses

Five new mtSSU sequences were obtained for this study, three for *Opegrapha multipuncta* (MK990614, MK990615, MK990616) and two from *Schismatomma quercicola* (MK990617, MK990618). Their closest matches based on 'megablast' searches were retrieved from GenBank. For the placement of *Opegrapha multipuncta* additional species of *Porina* were selected from Grube *et al.* (2004), Baloch & Grube (2006), Nelsen *et al.* (2014) and Orange (2015). *Coenogonium luteum* (Dicks.) Kalb & Lücking, *C. pineti* (Ach.) Lücking & Lumbsch and *Gyalecta ulmi* (Sw.) Zahlbr were chosen as an outgroup based on the phylogenetic trees of Nelsen *et al.* (2014) and Orange (2015). Available sequences of mtSSU for members of the *Graphidaceae* were selected for the placement of *Schismatomma quercicola*, mainly from Frisch *et al.* (2006), Miadlikowska *et al.* (2006), Mangold *et al.* (2008), Nelsen *et al.* (2010) and Rivas Plata *et al.* (2011, 2013). *Phaeographis intricans* (Nyl.) Staiger and *Thalloloma anguinum* (Mont.) Trevis. were chosen as an outgroup based on the phylogenetic tree of Rivas Plata *et al.* (2013; selection within the 'Graphideae' clade). In total, 95 sequences were retrieved from GenBank for the two phylogenetic analyses (Figs 1 & 2). The sequences were aligned using MAFFT v. 6.814b (Katoh *et al.* 2002) within Geneious (5.1.7) (https://www.geneious.com) and improved manually using Mesquite 3.04 (Maddison & Maddison 2015). Terminal ends of sequences and ambiguously aligned regions were delimited manually and excluded from the datasets.

Bayesian analyses were carried out on the dataset using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) on the CIPRES web portal (Miller *et al.* 2010). Best-fit evolutionary models were estimated using the Akaike Information Criterion (AIC; Akaike 1973) as implemented in jModelTest2 v. 2.1.6 (Darriba *et al.* 2012). The GTR + I+G model was selected for both the '*Opegrapha multipuncta*' and the '*Schismatomma quercicola*' datasets. For each dataset, two parallel MCMCMC runs were performed, each using four independent chains and 40 million generations, sampling trees every 1000th generation. Tracer v. 1.6 (Rambaut & Drummond 2007) was used to ensure that stationarity was reached by plotting the log-likelihood values of the sample points against generation time, making sure that the ESS values were higher than 200. Convergence between runs was also verified using the PSRF (Potential Scale Reduction Factor), where all values were equal or close to 1·000. Posterior probabilities (PP) were determined by calculating a majority-rule consensus tree generated from the 60 002 post-burn-in trees of the 80 002 trees sampled by the two MCMCMC runs, using the sumt option of MrBayes for the two datasets. In addition, a maximum likelihood (ML) analysis was performed on the CIPRES web portal (Miller *et al.* 2010) using RAxML-HPC2 v.8.2.10 (Stamatakis 2014) with 1000 ML bootstrap iterations (ML-BS) and the GTRGAMMA model.

The RAxML tree did not contradict the Bayesian tree topology for the strongly supported branches. Therefore, only the RAxML tree is shown here, with the bootstrap support values added above the internal branches (Figs 1 & 2). ML-BS $\geq$ 70 and PP $\geq$ 95 were considered to be significant. Internal branches considered strongly supported by both the RAxML and Bayesian analyses are represented by thicker lines (Figs 1 & 2). Phylogenetic trees were visualized using FigTree v. 1.4.2 (Rambaut 2012).

Results

The mtSSU dataset for *Opegrapha multipuncta* consisted of 52 specimens and 597 unambiguously aligned sites, while the mtSSU dataset for *Schismatomma quercicola* consisted of 49 specimens and 756 unambiguously aligned sites.

Despite our phylogenetic analyses revealing a lack of support for the backbone of the *Porinaceae* tree (Fig. 1), several well-supported clades emerged, such as the *Porina*

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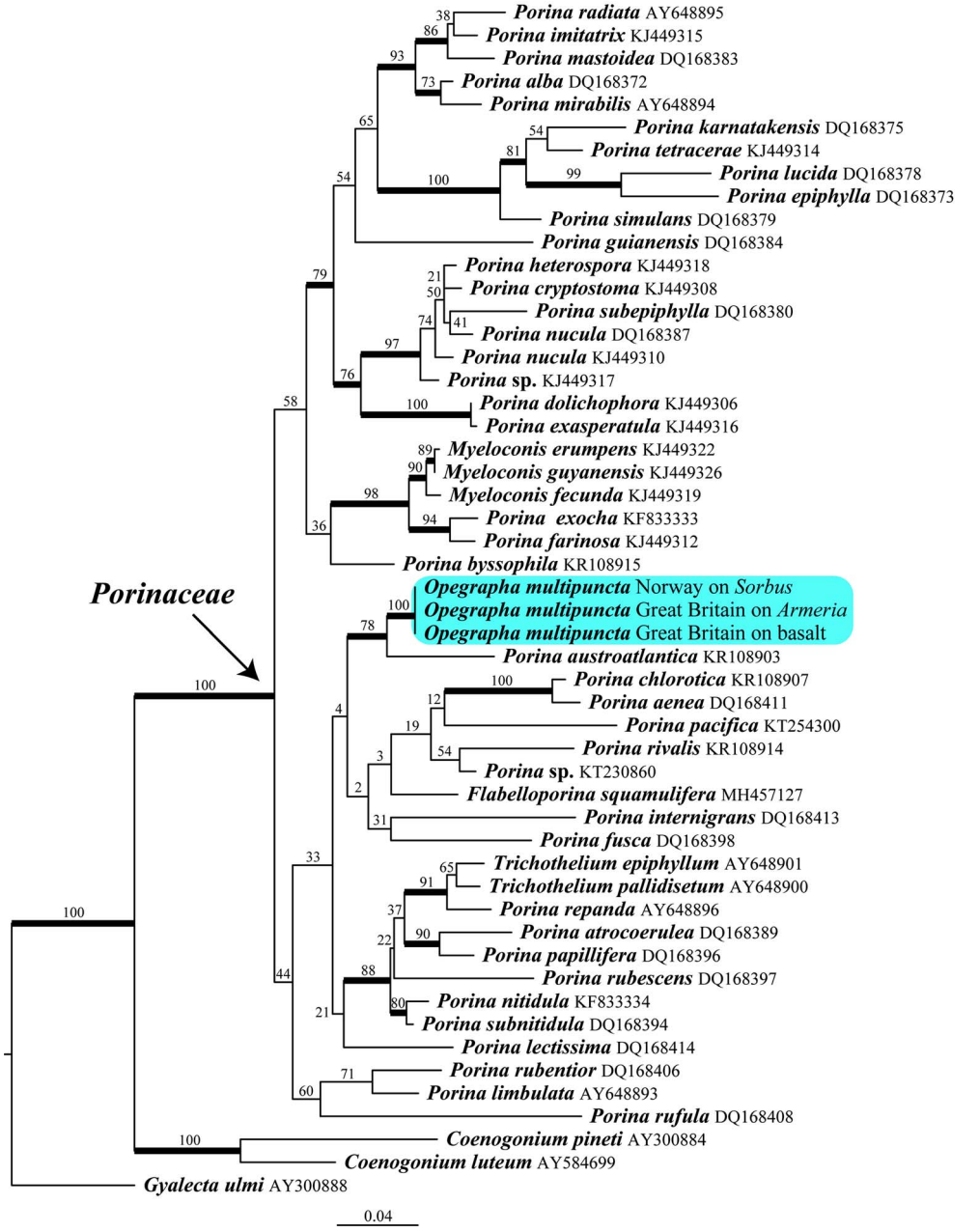

FIG. 1. Phylogeny of *Porinaceae* based on a dataset of mtSSU sequences obtained from a RAxML analysis. Maximum likelihood bootstrap values are shown above or near internal branches. Internal branches, considered strongly supported by both the RAxML and Bayesian analyses, are represented by thicker lines. The newly sequenced samples of *Porina* ('*Opegrapha*') *multipuncta* are highlighted. The outgroup consists of *Coenogonium luteum*, *C. pineti* and *Gyalecta ulmi*. In colour online.

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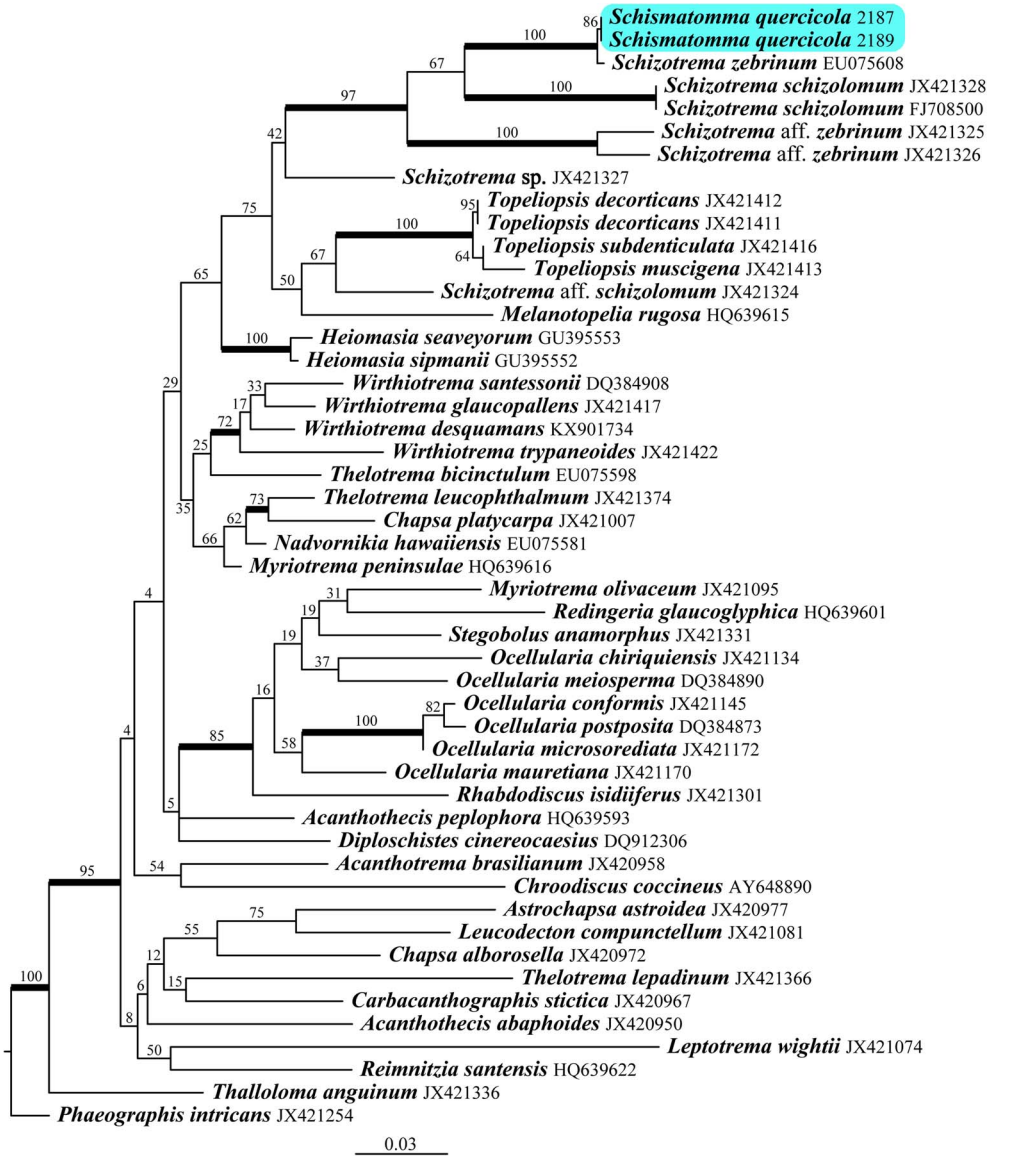

FIG. 2. Phylogeny of *Graphidaceae* based on a dataset of mtSSU sequences obtained from a RAxML analysis. Maximum likelihood bootstrap values are shown above or near internal branches. Internal branches, considered strongly supported by both the RAxML and Bayesian analyses, are represented by thicker lines. The newly sequenced samples of *Schizotrema* ('*Schismatomma*') *quercicola* are highlighted. The outgroup consists of *Phaeographis intricans* and *Thalloloma anguinum*. In colour online.

subnitidula to *Trichothelium epiphyllum* clade, the *P. aenea-chlorotica* clade, the *Porina farinosa* to *Myeloconis erumpens* clade (all with muriform ascospores), and the *P. exasperatula* to *P. radiata* clade (including the generic type *P. nucula* and three well-supported subclades). Our three specimens of *Opegrapha multipuncta* growing on three different substrata (basalt rock, dead stem of *Armeria maritima* and trunk of *Sorbus*) have identical mtSSU

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sequences and form a well-supported clade with *Porina austroatlantica* P. M. McCarthy & Fryday, a saxicolous species recently described from the Falkland Islands (McCarthy & Fryday 2009). Therefore, *Opegrapha multipuncta* is newly combined below in the genus *Porina*.

In our phylogenetic tree of the *Graphidaceae* (Fig. 2), only a small number of clades are strongly supported by both analyses, corresponding to the genera *Heiomasia*, *Topeliopsis* and *Wirthiotrema*, and the *Rhabdodiscus isidiiferus* to *Myriotrema olivaceum* clade, the *Chapsa platycarpa* and *Thelotrema leucophthalmum* clade, and the *Schizotrema* aff. *zebrinum* to *Schismatomma quercicola* clade. *Schismatomma quercicola* is closely related to *Schizotrema zebrinum* Mangold, the type species of *Schizotrema*. Therefore, *Schismatomma quercicola* is newly combined below in the genus *Schizotrema*.

Taxonomy

Porina multipuncta (Coppins & P. James) Ertz, Coppins & Frisch comb. nov.

MycoBank No.: MB 831216

Opegrapha multipuncta Coppins & P. James, in Coppins *et al.*, *Lichenologist* **24:** 365 (1992); type: Great Britain, Scotland ['Caledonia'], Zetlandia (V.C.112), Mainland, between Voe and Gonfirth, HU/374618, abundant on *Salix aurita* by small stream, June 1980, *P. W. James & W. Syratt* (BM—holotype).

(Fig. 3A–D)

Descriptions. See Coppins *et al.* (1992), Pentecost & James (2009), and Tønsberg (1992).

Distribution and ecology. Known from the Azores (Aptroot & Rodrigues 2005), France (Aptroot *et al.* 2007; Bricaux 2007), Great Britain (Coppins *et al.* 1992), Italy (Tretiach 2004) and Norway (Tønsberg 1992), where it grows on various trees (e.g. *Callistemon*, *Juglans*, *Malus*, *Populus*, *Pyrus*, *Quercus*), shrubs, rocks and stems of plants (e.g. *Armeria*) in areas characterized by intense precipitation and high air humidity.

Notes. 1) Our phylogenetic results place *Opegrapha multipuncta* in the genus *Porina*. 2) *Porina multipunctata* G. Merr. ex R. Sant. is a name based on a different type and a synonym of *Strigula multipunctata* (G. Merr. ex R. Sant.) R. C. Harris, a foliicolous lichen. The species name '*multipunctata*' is similar to that of the new combination ('*multipuncta*'). Therefore, the name of the new combination might have to be treated as a homonym following Art. 53.2. However, we consider that the two species names are sufficiently different not to be confused so we prefer to introduce a new combination rather than a new name. 3) *Opegrapha multipuncta* is characterized by a thin, dull or dark red-brown thallus with bright orange soralia and an absence of lichen secondary products. The species name was first published in an identification key to the genus *Opegrapha* in Great Britain as *O. multipuncta* Coppins & P. James (*ined.*) (Pentecost & Coppins 1983), and later recorded from the Faroe Islands (Alstrup & Alstrup 1989) before being validly published in Coppins *et al.* (1992).

Sequenced specimens. **Great Britain**: *Scotland*: **V.C. 82,** East Lothian, Tyninghame, Baldred's Cradle, Grid NT637813, 10 m, on dead stems of *Armeria maritima* on cliff top, 21 viii 2017, *Coppins* s. n. (E; GenBank no MK990615); *ibid.*, on E-facing, basalt sea-cliff, 21 viii 2017, *Coppins* s. n. (E; GenBank no MK990616).—**Norway**: *Trøndelag*: Åfjord, Lauføya, Plassahaugen, 63°55·883′N, 09°56·681′E, on the trunk of *Sorbus aucuparia*, 14 m, 2015, *Frisch* 15/No17 (TRH; GenBank no MK990614).

Schizotrema quercicola (Coppins & P. James) Ertz, Frisch & Sanderson comb. nov.

MycoBank No.: MB 831217

Schismatomma quercicola Coppins & P. James, *Lichenologist* **21:** 237 (1989); type: Great Britain, England, V.C.11, Hampshire, New Forest, *c.* 500 m NE of Rufus Stone, Grid 41/274.127, on *Quercus*, 3 December 1979 (published as '3 Iulius 1978'), *F. Rose* (BM—holotype; E, UPS—isotypes).

(Fig. 3E & F)

Descriptions. See Coppins & James (1989) and Wolseley & Hawksworth (2009).

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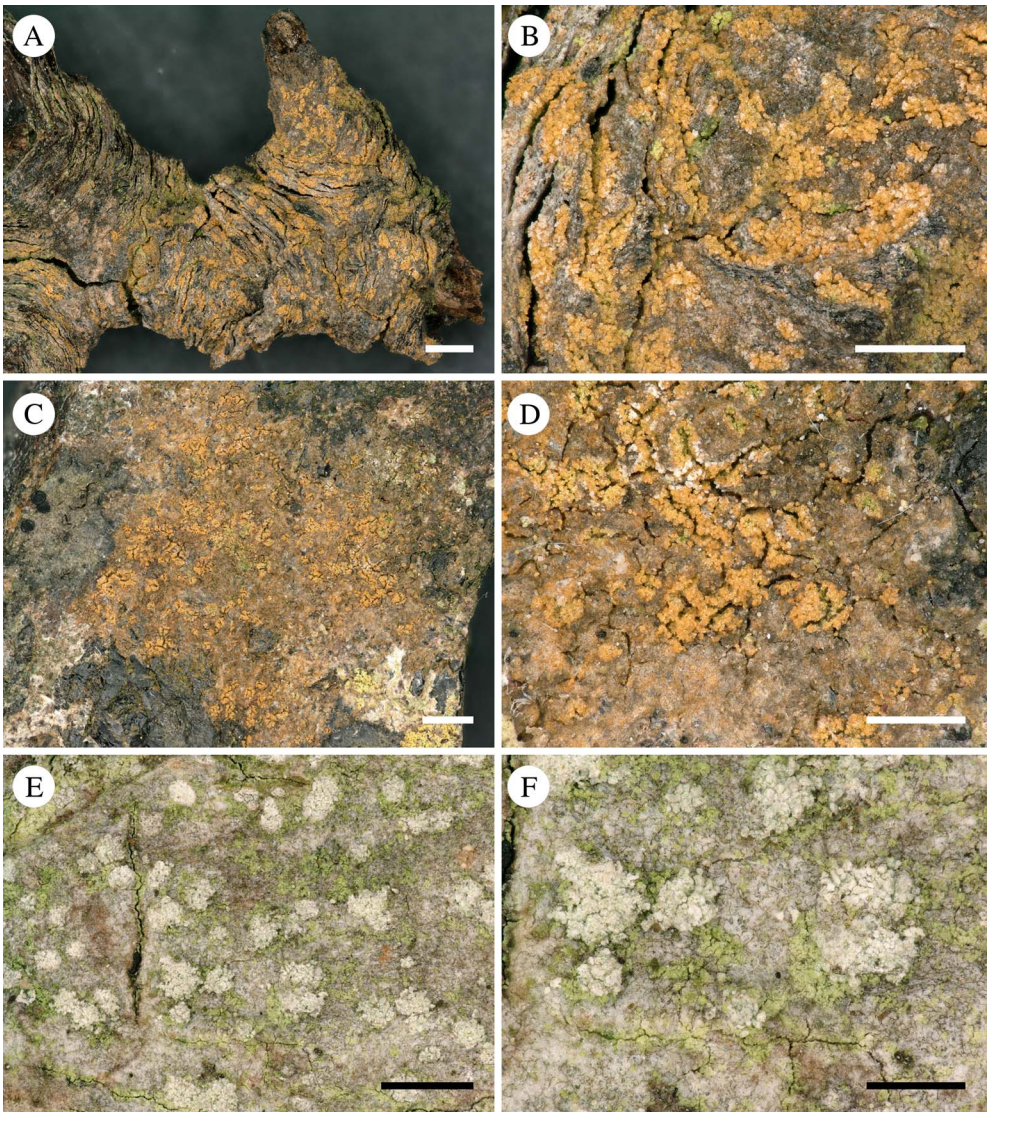

FIG. 3. Sequenced specimens of *Opegrapha multipuncta* (A–D) and *Schismatomma quercicola* (E & F). A & B, fresh thallus of *O. multipuncta* with bright orange soralia on dead stem of *Armeria maritima* (*Coppins* s. n.); C & D, fresh thallus of *O. multipuncta* with bright orange soralia on basalt sea-cliff (*Coppins* s. n.). E & F, thallus of *S. quercicola* with pale greyish soralia on bark of *Quercus petraea* (*Sanderson* 2187). Scales: A, C & E = 1 mm; B, D & F = 500 μm. In colour online.

Distribution and ecology. Known from Great Britain (Coppins & James 1989) and France (Roux 2014), and recorded here as new to Norway from five localities in Hordaland and Sogn og Fjordane. In Great Britain, it grows most frequently on the acid bark of mature *Quercus* trees. The species can, however, also be locally common on *Alnus*, *Ilex*, *Betula* and *Fagus*, and can occasionally colonize other phorophytes such as *Castanea*, *Corylus*, *Crataegus*, *Larix*, *Pinus sylvestris*, *Prunus padus*, *Salix* and *Sorbus aucuparia* (Coppins & James 1989; British Lichen Society 2019). Occasionally it has been found on

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Quercus lignum. In Great Britain, it is essentially a species of ancient or old-growth woodland and is used as an indicator of ecological continuity (Sanderson *et al.* 2018). It is most frequent in the extensive old-growth woodlands of the New Forest (Hampshire, England), where it has also been noted colonizing adjacent, more disturbed woods. Here Sanderson (2001) recorded it on 60 and 69 trees per hectare in two sampled little disturbed old-growth stands, and on 17–30 trees per hectare within three 19th century oak plantations. The obligate lichenicolous fungus *Arthonia invadens* Coppins was recorded growing on *Schizotrema quercicola* only in the sites with 60 or more occupied trees per hectare, where the parasite occurred on 3–5 trees per hectare. Beyond the New Forest, *Schizotrema quercicola* is a much less frequently encountered species in Britain. In Norway, the species was mainly found on Scots pine in highly oceanic, coastal pine forests but also at the base of an old oak in agricultural landscape.

Notes. 1) The species was tentatively described in the genus *Schismatomma* based on its morphological resemblance to *S. decolorans* (Erichsen) Clauzade & Vězda (Coppins & James 1989). *Schismatomma quercicola* is characterized by a thin, pale brownish grey to greyish white, crustose thallus with scattered, discrete, pink-grey soralia when fresh, becoming whitish in the herbarium, and a chemistry with fumarprotocetraric acid, ±protocetraric acid and an unidentified substance (soralia Pd+ orange). Our phylogenetic results, based on material sequenced from the type locality (New Forest), prove that *S. quercicola* is a member of the genus *Schizotrema*. 2) In the original description of *Schismatomma quercicola* (Coppins & James 1989), the holotype specimen from BM is dated '3 Iulius 1978', but the collection date of the holotype specimen on JSTOR (specimen BM000975908) is '3 December 1979'. We consider that there was an error in the original publication. 3) *Arthonia invadens* is an obligate lichenicolous fungus on *Schizotrema quercicola*, endemic to Great Britain and Ireland. However, because its host lichen is known only as a sterile crust, the lichenicolous habit of *A. invadens* was questioned in the original description since it is possible that its ascomata could be those of the host (Coppins 1989). Our phylogenetic results showing the placement of '*Schismatomma*' *quercicola* in the family *Graphidaceae*-genus *Schizotrema*, definitively prove that the arthonioid ascomata belong to a lichenicolous fungus. Moreover, sequences of *A. invadens* obtained recently from the type locality (New Forest) place the species in the *Coniocarpon-Reichlingia* clade (as defined by Van den Broeck *et al.* 2018) in the *Arthoniaceae*, where several other lichenicolous fungi confined to *Graphidaceae* hosts occur (D. Ertz, unpublished data).

Sequenced specimens. **Great Britain:** *England*: **V.C.11,** New Forest, Sunny Bushes, Grid Ref SU25946 14250, Grid2 41 21, *Quercus-Fagus-Ilex* pasture woodland, acid bark on old *Quercus petraea*, 2016, *Sanderson* 2187 (hb. Sanderson; GenBank no MK990617); *ibid.*, Coppice of Linwood, Grid Ref SU25418 14222, Grid2 41 21, *Quercus-Fagus-Ilex* pasture woodland, acid bark on old *Quercus petraea*, 2016, *Sanderson* 2189 (hb. Sanderson; GenBank no MK990618).

New localities. **Norway:** *Hordaland*: Fusa, Holmefjord, Eikhaugen, 60°17·922′N, 05°39·847′E, at the base of an old oak, 37 m, 2018, *Frisch* 18/No60 (TRH); Os, Strøno, Svensvikmyrane, 60°10′39·0″N, 05°20′58·6″E, on *Pinus sylvestris* in coastal pine forest, 35–50 m, 2018, *Frisch* 18/No56 & *Klepsland* (TRH). *Sogn og Fjordane*: Gulen, Sygnefest nordøst, 61°04′16·6″N, 05°06′23·3″E, on *Pinus sylvestris* in coastal pine forest, 20–50 m, 2018, *Frisch* TSD S13-2-Ps4-2 & *Klepsland* (TRH); Florø, Svanøya, Vågsfjellet nord, 61°29′23·0″N, 05°04′56·7″E, on *Pinus sylvestris* in coastal pine forest, 25–50 m, 2018, *Frisch* TSD S14-1-Ps2-1 & *Klepsland* (TRH); *ibid.*, on *Sorbus aucuparia*, 25–50 m, 2018, *Frisch* TSD S14-1-Sa2-7 & *Klepsland* (TRH); *ibid.*, Storefjellet nordvest, 61° 40′00·5″N, 05°00′02·2″E, on *Pinus sylvestris* in coastal pine forest, 35–70 m, 2018, *Frisch* 18/No96 & *Klepsland* (TRH).

Discussion

Our molecular data using mtSSU sequences prove that *Opegrapha multipuncta* and *Schismatomma quercicola* do not belong to the Arthoniomycetes, where these species were originally described, but to the Lecanoromycetes (Figs 1 & 2). The sequencing of sterile *Arthoniales* usually changes the generic or family position within the order (e.g.

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Schismatomma cretaceum was moved from the *Roccellaceae* to the *Arthoniaceae*; Frisch *et al.* 2015), but examples where sterile taxa have been transferred from one class to another are rare. Among them, *Herpothallon antillarum* (Vain.) Aptroot *et al.* and *H. sipmanii* (Aptroot *et al.*) Nelsen *et al.* (Arthoniomycetes: *Arthoniaceae*) were placed in *Diorygma* and *Heiomasia* (Lecanoromycetes: *Graphidaceae*) respectively (Nelsen *et al.* 2010, 2012), while *Buellia violaceofusca* (Lecanoromycetes: *Caliciaceae*) was shown to represent the trebouxioid photomorph of *Lecanographa amylacea* (Arthoniomycetes: *Lecanographaceae*) (Ertz *et al.* 2018*b*).

Our phylogenetic analyses prove that *Opegrapha multipuncta* belongs to the *Porinaceae* (*Ostropales*), with *P. austroatlantica* being the closest relative (Fig. 1). As a consequence, we combined this species in *Porina* (see Results). However, the generic placement remains somewhat uncertain because *Porina* is a paraphyletic genus. Indeed, phylogenetic analyses placed the genera *Myeloconis* (Nelsen *et al.* 2014), *Flabelloporina* (Sobreira *et al.* 2018) and *Trichothelium* (Baloch & Grube 2006) within *Porina*, rendering the generic delimitations within *Porinaceae* unclear. This is also evident in our phylogenetic analyses with species of *Trichothelium* being sister to *Porina repanda* and species of *Myeloconis* sister to *Porina exocha* + *P. farinosa*, while *Flabelloporina squamulifera* is included in the clade *Porina fusca*-*P. chlorotica* despite this latter position being weakly supported (Fig. 1). There is little evidence for a splitting of the genus *Porina* because recent phylogenies recovered several proposed segregate genera of *Porina* as non-monophyletic (Baloch & Grube 2006; Nelsen *et al.* 2014), but a larger sampling and the sequencing of more genes are needed to re-evaluate the status of *Porina* s. lat. *Porina multipuncta* is distantly related to the type species of *Porina* (*P. nucula*). Its closest known relative, *P. austroatlantica*, is a saxicolous species recently described from the Falkland Islands and characterized by a thin, rimose to sparingly areolate, off-white to pale greenish, esorediate thallus, brownish black to black, prominent perithecia with a variably developed reddish brown involucrellum and small 3-septate ascospores (McCarthy & Fryday 2009). Our phylogenetic analyses confirm that *Porina multipuncta* is distinct from all the other sequenced species of the genus (Fig. 1). Therefore, *P. multipuncta* does not appear to represent a sorediate morph of another known *Porina*, at least with the molecular data available. The species disperses strictly by means of soredia. A strictly sterile dispersal strategy is rare in the family *Porinaceae*, an example being *Porina distans* Vězda & Vivant that disperses by means of isidia (Vězda 1994), but the status of this species is still unclear as it might represent the sterile isidioid morph of another, usually fertile species (Lücking 2008). Within *Porinaceae*, some species of the tropical genus *Myeloconis* are also known to form brightly coloured soralia (McCarthy & Elix 1996). However, these lichens are all known to be fertile, despite *M. erumpens* P. M. McCarthy & Elix usually being sterile. Their medulla and soralia contain bright yellow or orange pigments (viz. leucomyeloconone, myeloconone and myelocoterpene), while *P. multipuncta* is not known to contain secondary metabolites.

In contrast with *Opegrapha multipuncta*, the new generic position of *Schismatomma quercicola* leaves no doubt. Our molecular data clearly place *S. quercicola* in the genus *Schizotrema*, close to its type species *S. zebrinum* (Fig. 2). The two mtSSU sequences of *S. quercicola* are identical and very similar (3 different nucleotides) to that of *S. zebrinum*, a corticolous species endemic to south-east Australia (Australian mainland, Tasmania and Lord Howe Island) and New Zealand, where it occurs in temperate and subtropical rainforests (Mangold *et al.* 2009; Lumbsch *et al.* 2010; McCarthy 2018). *Schizotrema zebrinum* is characterized by an almost endophloeodal, smooth, greyish thallus lacking vegetative propagules, perithecioid to indistinctly apothecioid ascomata with a layered margin and moderately large, transversely septate ascospores. Some specimens have a secondary chemistry of the protocetraric acid chemosyndrome, thus similar to the chemistry of *Schismatomma quercicola*. Others have the stictic acid chemosyndrome or

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produce acids of both chemosyndromes. Except for the mode of reproduction, the thallus and the chemistry of some specimens of *S. zebrinum* are thus similar to those of *S. quercicola*. A larger sampling and ITS sequences would be needed to verify if *S. zebrinum* might represent the fertile morph of *S. quercicola* (in that case, *S. zebrinum* would become a synonym of *S. quercicola*), but this is unlikely considering their disjunct distribution in Europe and Australasia. With the new systematic position of *S. quercicola*, the genus *Schizotrema* is newly reported from Europe, the other species of the genus being so far known only from the Southern Hemisphere, China and the Caribbean (Mangold *et al.* 2009; Zefeng & Lücking 2019). A strictly sterile dispersal strategy is known from different taxa in the family *Graphidaceae* (e.g. the genus *Heiomasia* and the species *Diorygma antillarum*, *Myriotrema frondosolucens* Lücking and *M. maroense* Lücking), and might be more widespread because sterile trentepohlioid lichens are frequent in tropical regions but are still poorly studied.

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