RESEARCH ARTICLE

A phylogenetic survey of the ascomycete genus *Arthrorhaphis* (Arthrorhaphidaceae, Lecanoromycetes) including new species in *Arthrorhaphis citrinella* sensu lato

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Abstract The genus *Arthrorhaphis* is a group of ascomycetes comprising lichenised and non-lichenised taxa from temperate to arctic-alpine regions in both hemispheres. Nine species and two infraspecific taxa are currently recognised. Their delimitation, inter-relationships, and phylogenetic placement remain poorly understood. We have used an integrative taxonomic approach to assess taxon limits, phylogenetic placement of the family, and to test the hypothesis that transition to lichenisation has happened only once. We present a first molecular phylogenetic hypothesis of all but one known *Arthrorhaphis* species based on Bayesian inference and maximum likelihood analyses of multilocus DNA sequence data. Our results support monophyly of *Arthrorhaphis*, phylogenetic placement in the Ostropomycetidae, and lichenisation having evolved from lichenicolous ancestors only once. The lichenicolous *Arthrorhaphis* species are well-defined both morphologically and genetically. The lichenised *A. alpina* s.l. and *A. citrinella* s.l., however, include multiple genetic clades that are partly supported by phenotypic data. We split *A. citrinella* s.l. into the following five species: (1) *A. bullata* sp. nov., (2) *A. catolechioides* comb. & stat. nov., (3) *A. citrinella*, (4) *A. farinosa* sp. nov., and (5) *A. vulgaris* comb. & stat. nov. A sixth phylogenetic clade from the Neotropics remains undescribed herein due to insufficient data. Five circumarctic accessions of *A. alpina* s.l. form a genetically distinct but morphologically poorly understood clade sister to the alpina-vacillans clade, which we preliminarily name "*A. septentrionalis*". Jointly, our multispecies coalescence analyses, of both single-locus (bGMYC) and multilocus (bPtP, bP&P) datasets, largely support our proposed species hypotheses in *Arthrorhaphis*.

Keywords integrative taxonomy; lichenicolous fungi; lichens; molecular phylogenetics; Ostropomycetidae; species delimitation

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Arthrorhaphis is a species-poor but morphologically and biologically diverse genus of both lichenicolous and lichenised fungi in the Lecanoromycetes. It currently includes nine species and two varieties in the monotypic family Arthrorhaphidaceae (Poelt & Hafellner, 1976; Hafellner & Obermayer, 1995) (see Appendix 1 for authorities of all taxa included in the present study). The distribution is bipolar-oreophytic (Obermayer, 1994) and centred on temperate to arctic-alpine regions of the Northern Hemisphere (e.g., Thomson, 1996; Inoue, 1997; Ihlen, 1998; Hansen & Obermayer, 1999). Few species additionally or exclusively occur in the Southern Hemisphere: *A. alpina* and *A. citrinella* in tropical-alpine and temperate regions of South America and Africa (e.g., Brusse, 1988; Marcano & al., 1996; Galloway & Quilhot, 1998; Sipman & al., 2008), Australasia (Galloway & Bartlett, 1986; Obermayer, 2001), and Antarctica (Øvstedal & Lewis Smith, 2001); *A. grisea* in Australia (Obermayer, 2001) and Brazil (Aptroot, 2002); *A. phyllobaeis* in Ecuador (Etayo, 2017); and *A. citrinella* var. *catolechioides* in Australasia (Obermayer, 2001).

Monographic treatments of *Arthrorhaphis* exist for Australia (Obermayer, 2001), Europe and Greenland (Obermayer, 1994), central Asia (Obermayer, 1996), and New Zealand (Galloway & Bartlett, 1986). In these studies, the generic circumscription of *Arthrorhaphis* is undisputed but the phylogenetic relationships among its component taxa and their delimitations remain unsettled. Moreover, the phylogenetic position of the family in the Ostropomycetidae (Wedin & al., 2005b; Miadlikowska & al., 2006; Lumbsch & al., 2007; Pino-Bodas & al., 2017) was recently questioned by Wijayawardene & al.

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(2018), who suggested a placement in the Lecideales based on results of a molecular phylogenetic study by Miadlikowska & al. (2014).

The strictly lichenicolous *Arthrorhaphis* are well circumscribed phenotypically and in their host selection (Obermayer, 1994; Santesson & Tønsberg, 1994; Kocourková & Van den Boom, 2005; Etayo, 2017) (summarized in Table 1). The delimitation of the lichenised species, on the other hand, is problematic. Notably, the widespread *A. alpina* and *A. citrinella* are highly polymorphic both in Europe, where the type specimens were collected, as well as at world level. Sterile specimens are difficult to assign to their respective taxa. In the absence of ascomata, *A. alpina* and *A. citrinella* are by some authors separated by the absence vs presence of soredia, respectively (Poelt, 1969; Poelt & Vězda, 1977; Santesson, 1984; Galloway & Bartlett, 1986; Duke & Purvis, 2009). This concept was questioned by Obermayer (1994, 1996, 2001), who rather used the presence of calcium oxalate crystals in the medulla as cardinal character for separating *A. alpina* s.l. (including *A. alpina* var. *jungens* and *A. vacillans*) from *A. citrinella* s.l. (incl. var. *catolechioides*). In addition, *A. alpina* and *A. vacillans* usually grow on at least weakly basic, Ca-influenced substrates, contrary to the acidophilic *A. citrinella* (Obermayer, 1994). Soredia are formed both in *A. alpina* s.l. and *A. citrinella* s.l. but are more common in the latter (Obermayer, 1994). The difficulties in species delimitation among the lichenised *Arthrorhaphis* species led Obermayer (1996) to conclude that the species limits in *Arthrorhaphis* may be rather unclarified.

The strictly lichenicolous *Arthrorhaphis aeruginosa*, *A. arctoparmeliae*, *A. grisea*, *A. muddii*, *A. olivaceae*, and *A. phyllobaeis* lack lichenised thalli and remain lichenicolous throughout their life cycle. All species but *A. muddii* cause visible infections and are considered to be parasites (Obermayer, 1994; Santesson & Tønsberg, 1994; Kocourková & Van den Boom, 2005; Etayo, 2017). Such infections have not been observed for *A. muddii*, which may be a parasymbiont rather than a parasite (Obermayer, 1994).

The lichenised *Arthrorhaphis alpina* s.l. and *A. citrinella* s.l. may start their life cycle as juvenile parasites on *Baeomyces* spp. (less often on *Dibaeis baeomyces* and other terricolous lichens) but later form autonomous lichenised thalli containing pulvinic acid derivatives in their cortical layers (Obermayer, 1994, 1996, 2001). Individuals of these taxa showing no traces of juvenile parasitism are rather frequently observed. The initial lichenicolous stage might be obscured in such individuals, but they may as well have originated through vegetative dispersal or spore dispersal with subsequent lichenisation (Obermayer, 1994).

Species of *Arthrorhaphis* have few morphological characters on which to base taxonomic conclusions, a common challenge in fungal systematics. Various DNA sequencing technologies, generating a huge amount of neutrally evolving characters, combined with advances in molecular phylogenetics, have revolutionised studies of fungal evolution and taxonomy and revealed an extensive amount of hidden species diversity. Supplementing molecular phylogenetic species recognition in biosystematics (e.g., Taylor & al., 2000; Stewart & al., 2014), species delimitation analyses are increasingly used for testing species hypotheses (Carstens & al., 2013).

In the present study, we use an integrative taxonomic approach, combining molecular phylogenetics with studies of morphology and chemistry, to study both freshly collected and fungarium specimens of all except one species currently assigned to *Arthrorhaphis*. We use Bayesian inference (BI) and maximum likelihood (ML) phylogenetic analyses of multilocus DNA sequence data to test current species hypotheses, re-examine the phylogenetic position of the genus within the Lecanoromycetes, and assess the phylogenetic position of the strictly parasitic *Arthrorhaphis* species in relation to the finally lichenised taxa. Following recommendations by Carstens & al. (2013), we apply several independent species delimitations methods, including bGMYC on single-locus- and both bPtP and bP&P on multilocus datasets, to test our revised species hypotheses in *Arthrorhaphis*.

■ MATERIALS AND METHODS

Taxon sampling. — The 338 *Arthrorhaphis* specimens examined in the present study are placed in the lichen collections in ASU, BC, BG, C, E, G, H, LD, M, MIN, NY, PRH, PRM, O, S, TNS, TRH, and UPS, or were collected by the authors. Our taxon sampling is centred on the main distribution area of the genus in the Holarctic, supplemented by accessions from Central and South America (Chile, Costa Rica, Peru, Venezuela), East and South Africa (Republic of South Africa, Tanzania), the southern Indian Ocean (Kerguelen Islands, Réunion), and New Zealand. In addition to new DNA sequences produced

Table 1. Strictly lichenicolous species of *Arthrorhaphis* with their host lichens and references.

Taxon	Hosts	References
Arthrorhaphis aeruginosa	*Cladonia* spp. squamules, rarely podetia	Santesson & Tønsberg, 1994
Arthrorhaphis arctoparmeliae	*Arctoparmelia incurva*	Kocourková & Van den Boom, 2005
Arthrorhaphis grisea	*Baeomyces rufus*, *B. placophyllus*	Obermayer, 1994
Arthrorhaphis muddii	*Dibaeis baeomyces*	Obermayer, 1994
Arthrorhaphis olivaceae	*Melanohalea olivacea*	Santesson & Tønsberg, 1994
Arthrorhaphis phyllobaeis	*Phyllobaeis imbricata*	Etayo, 2017

for 157 *Arthrorhaphis* specimens in the present study, we retrieved 65 mrSSU, 63 nrLSU, and 53 *RPB1* sequences from GenBank for 2 specimens of *A. citrinella* and for the outgroup (Appendix 1).

DNA extraction, PCR amplification and Sanger sequencing. — Thallus and/or apothecia of 194 *Arthrorhaphis* specimens were crushed using a Retsch TissueLyser II. Total genomic DNA was extracted using the E.Z.N.A. SP Plant DNA Mini Kit (Omega Bio-tek, Norcross, Georgia, U.S.A.) following the manufacturer's instructions. The following four DNA-regions were PCR amplified and sequenced: the mitochondrial ribosomal small subunit (mrSSU), the nuclear ribosomal large subunit (nrLSU), the internal transcribed spacer (nrITS) and the DNA-directed RNA polymerase II subunit (*RPB1*). The PuRe Taq Ready-To-Go PCR beads (GE Healthcare Life Sciences, Little Chalfont, U.K.) were used for most PCR amplifications. For the lichenicolous *A. aeruginosa*, three apothecia per specimen were extracted using the Thermo Scientific Phire Plant Direct PCR Kit (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.) using the dilution protocol of the manufacturer. The following primer pairs were used: (1) mrSSU: mrSSU1 and mrSSU3R (Zoller & al., 1999), (2) nrLSU: LIC24R (Miadlikowska & Lutzoni, 2000) and LSU-hypR2 (Bendiksby & Timdal, 2013), (3) nrITS: ITS4 and ITS1f/ITS5 (White & al., 1990), and (4) *RPB1*: our newly designed primers RPB1-arthrF (AGGCTTCATCAATAAGATCA) and RPB1-arthrR (TGCGCGAATGATATCTCCAA). In older specimens, higher PCR success was achieved by amplifying shorter fragments using the following internal primers designed by Bendiksby & Timdal (2013): (1) mrSSU: mrSSU-hypF and mrSSU-hypR and (2) nrITS: ITS-lichF and ITS-lichR.

For nrITS and nrLSU, the samples were run on a BIO RAD T100 Thermal Cycler with the following settings: initial denaturation at 95°C for 7 min, 13 cycles at 95°C for 30 s, 62°C lowered by 0.5°C in each cycle for 30 s and 72°C for 45 s, followed by 30 cycles at 95°C for 30 s, 56°C for 30 s and 72°C for 45 s, and a final extension at 72°C for 7 min. For mrSSU and *RPB1*, the only modification was that the annealing temperatures started at 60°C and were lowered to 54°C. For the Thermo Scientific Phire Plant Direct PCR Kit, the following cycler settings were used: denaturation for 5 min at 98°C, followed by 40 cycles for 5 s at 98°C, 5 s at 59°C (mrSSU, nrITS) or 57°C (nrLSU, *RPB1*) and 30 s at 72°C, and a final extension of 1 min at 72°C. All PCR products were visualized through electrophoresis on a 1% agarose gel. The PCR products were purified with the ExoProStar 1-step Enzymatic PCR and Sequence Reaction Clean-up Kit (GE Healthcare Life Sciences) and sent for sequencing to Eurofins Genomics (Ebersberg, Germany) with the same primers for sequencing as the ones used for the PCRs.

Multiple sequence alignments and phylogenetic analyses. — Two concatenated four-locus multiple-sequence-alignments (MSAs), both comprising 159 *Arthrorhaphis* accessions but with different outgroups, were established and analysed phylogenetically (http://purl.org/phylo/treebase/phylows/study/TB2:S29606). MSA-1 (224 accessions) includes additional 62 Lecanoromycete outgroup taxa and 3 accessions of the Leotiomycetes as operational outgroup. These accessions were selected based on results from previous studies (Wedin & al., 2005b; Miadlikowska & al., 2006; Lumbsch & al., 2007; Pino-Bodas & al., 2017). MSA-2 (160 accessions) comprises only the *Arthrorhaphis* accessions and *Anzina carneonivea* as the operational outgroup. In MSA-1, the nrITS and four short regions of the mrSSU (alignment positions 55–73, 450–464, 612–622, 701–783) were excluded from the outgroup taxa prior to final analyses due to highly ambiguous alignment. Furthermore, nrITS sequences were not available from GenBank for most of the outgroup taxa. For both MSA-1 and MSA-2, sequences were aligned using the general MAFFT settings as implemented in the Guidance Web Server (Penn & al., 2010) and manually corrected. The faster *6mer* pairwise alignment was used for *RPB1*, while *genafpair* was applied for mrSSU, nrLSU and nrITS. Prior to concatenation, all four single-gene alignments were tested for conflicting tree topologies. The BI and ML phylogenetic analyses were performed using the same settings for the single-gene alignments as for the concatenated four-gene MSAs (suppl. Figs. S1–S7). Serious conflict was assumed when deviant tree topologies were supported by ≥70% bootstrap values (ML BS) and ≥0.95 posterior probabilities (BPP).

A partitioned dataset was used for the final phylogenetic analyses of the four-gene MSAs to enable independent parameter estimation for each partition. The following eight pre-set partitions (= subset) were evaluated for MSA-1 and MSA-2 separately using PartitionFinder 2 (Lanfear & al., 2012): (1) mrSSU, (2) nrLSU, (3) nrITS1, (4) nr5.8S, (5) nrITS2, (6) *RPB1* exon 1, (7) *RPB1* intron 1, and (8) *RPB1* exon 2. The coding regions (partitions 6 and 8) of *RPB1* were further partitioned according to codon positions to allow for the higher evolutionary rate of the 3rd codon position. The PartitionFinder settings were as follows: branchlengths = linked, models = mrbayes, and model_selection = BIC. The following partitioning schemes were used for both the BI and ML analyses: MSA-1 [subset 1 = 1, 4, 6(pos. 2); subset 2 = 2, 6(1); subset 3 = 3, 5; subset 4 = 6(3), 8(3); subset 5 = 7; subset 6 = 8(1), 8(2)]; and MSA-2 [subset 1 = 1, 4, 6(2); subset 2 = 2, 6(1), 8(1); subset 3 = 3, 5, 6(3), 7, 8(3); subset 4 = 8(2)].

The BI and ML phylogenetic analyses were performed for both alignments on the CIPRES Science Gateway (Miller & al., 2010). For the BI, we used MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003). The analysis was run for 10 million generations in eight chains and every 200th generation was sampled. Tracer v.1.5 (Rambaut & Drummond, 2009) was used to assess if chains had converged. We considered that convergence had been reached if effective sample size (ESS) values were above 200 for all sampled parameters. The first 50% of trees were discarded as burn-in and the posterior probabilities (BPPs) summarised on a 50% majority-rule consensus tree. For the ML analysis, we used the RAxML-HPC black box with rapid bootstrapping and full ML analysis under the GTR+GAMMA approximation (i.e., not allowing for a proportion of invariable sites, I). The analysis was automatically stopped

after 504 bootstrap replicates using the bootstrapping option implemented in RAxML v.3.2.7 (Pattengale & al., 2009).

Species delimitation. — Molecular species delimitation analyses were performed on MSA-2 using bGMYC v.1.0.2 (Reid & Carstens, 2012; Fujisawa & Barraclough, 2013) and bPtP v.051 (Zhang & al., 2013), and evaluated by bP&P v.4.3 (Yang & Rannala, 2010; Flouri & al., 2020). For bGMYC, the three loci mrSSU, *RPB1* and nrITS were analysed independently. The nrLSU was excluded from the analysis due to the low phylogenetic signal from this conserved locus. The nrITS was partitioned into nrITS1, nr5.8S, and nrITS2. The *RPB1* was partitioned in exons 1 + 2 and intron 1, with the exons further partitioned into codon positions. The model selection for tree inference with BEAST v.2.6.3 (Bouckaert & al., 2014) was guided by the models of sequence evolution estimated for the phylogenetic analyses. Single-gene phylogenies were inferred relying on an uncorrelated lognormal relaxed clock and a coalescent tree prior. All BI analyses were run for 20 million generations, and trees and parameters were sampled every 1000th generation. Three independent BI analyses were performed for each of the three gene loci to confirm consistency between runs. Tracer v.1.7.1 (Rambaut & al., 2018) was used to assess if runs had reached a stationary phase and converged on model parameters. We considered that convergence had been reached if ESS values were above 200 for all sampled parameters. After removing 25% of trees as burn-in, the remaining trees were summarized in TreeAnnotator (as part of the BEAST v.2.6.3 package) for generating a single ultrametric tree for each gene locus. The bGMYC analyses with a single threshold model were performed in R (http://www.R-project.org) under the splits package v.1.0-20 using the gmyc function (http://r-forge.r-project.org/projects/splits/). The single-threshold model of bGMYC was preferred since it has been demonstrated to outperform the multiple-threshold model (Fujisawa & Barraclough, 2013; Talavera & al., 2013).

The best-scoring ML tree from the phylogenetic analysis of MSA-2 was used for the bPtP-ML analysis as implemented in the bPtP web server at https://species.h-its.org/ under default parameters.

Species hypotheses obtained from the bGMYC and bPtP analyses, the molecular phylogenetic analyses and the morphological data were evaluated with bP&P under two scenarios: a conservative 15-species scenario (14 *Arthrorhaphis* + the outgroup, *Anzina carneonivea*) and a 22-species scenario (21 *Arthrorhaphis* + the outgroup). For the 15-species scenario, all species delimited by at least two gene loci in the bGMYC analysis and/or by bPtP were grouped as species. This included all accepted species based on the molecular phylogeny and morphological data. The different clades recovered in *A. alpina* s.l. (incl. var. *jungens*) were treated as a single taxon, except for "*A. septentrionalis*". For the 22-species scenario, all those clades were additionally grouped as species. For each scenario, we ran three independent bP&P analyses (method A11) for 100,000 generations, sampling every 2nd generation, with a burn-in of 10%. We used the rjMCMC algorithm 1 with fine-tune parameters $\alpha = 2$ and $m = 1$. After several test analyses for optimizing the results, we assigned two (a and b) combinations of diffuse gamma priors to the multispecies coalescent (MSC) model: (a) $\theta = 0.0001$ (3, 0.0002) and $\tau = 0.00015$ (3, 0.0003), and (b) $\theta = 0.001$ (3, 0.002) and $\tau = 0.0015$ (3, 0.003). We allowed for the automatic adjustment of the fine-tune variables (MCMC step lengths) in the proposal for the MCMC algorithm (Yang & Rannala, 2010; Flouri & al., 2020). Posterior probabilities ≥0.95 were considered highly supported.

Morphological investigations and thin-layer chromatography. — Morphology and anatomy were studied for all specimens of *Arthrorhaphis alpina* s.l. and *A. citrinella* s.l. included in the phylogenetic analyses. For the taxa of *A. citrinella* s.l. treated in the Taxonomy section, additional available specimens were investigated. Anatomical details were studied on hand sections and on squashed preparations in water, 10% KOH, 1% Lugol's iodine solution, and cotton blue in lactic acid (LCB). Measurements of the hymenium include the epihymenium, which was also measured separately. Ascospore size is given as $\bar{x}$ – SD [minimum value]–$\bar{x}$ + SD [maximum value] when more than 20 ascospores were measured ($\bar{x}$ = mean; SD = standard deviation; n = number of ascospores). All measurements were made on preparations mounted in water.

Secondary lichen compounds were identified for selected samples of all major clades in the phylogeny by thin-layer chromatography (Orange & al., 2010) using solvent B'. The pigment in the epihymenium was tested with 60% nitric acid. Calcium oxalate crystals were identified by applying 10% sulphuric acid to squashed preparations of thallus samples, resulting in fine straight crystal needles of gypsum.

■ RESULTS

MSAs and phylogenetic analyses. — New DNA sequences could be generated for 157 of the 194 extracted individuals of *Arthrorhaphis* (144 mrSSU, 139 nrLSU, 147 nrITS [147 5.8S + ITS2, 62 ITS1], and 125 *RPB1*), representing all currently accepted taxa of the genus except for the recently described *A. phyllobaeis*. Sequences could be generated from specimens up to 45 years since collection. MSA-1 (extensive outgroup), comprising 224 accessions, consists of 2590 nucleotide positions (828 mrSSU, 572 nrLSU, 600 nrITS, 590 *RPB1*). Of these, 1325 are variable (454, 296, 128, 447) and 1184 parsimony informative (428, 245, 108, 403). MSA-2 (single-taxon outgroup), comprising 160 accessions, consists of 2607 nucleotide positions (830 mrSSU, 574 nrLSU, 603 nrITS, 600 *RPB1*). Of these, 387 are variable (105, 57, 135, 90) and 309 parsimony informative (82, 50, 114, 63). Substitution models for the BI analyses were for MSA-1: GTR+Γ+I (subsets 1, 2, and 6), HKY+Γ (subset 3), SYM+I+Γ (subset 4), and K80+Γ (subset 5), and for MSA-2: GTR+Γ (subsets 2, 3), HKY+Γ (subset 1) and JC (subset 4).

Separate BI and ML analyses for the mrSSU, nrLSU, and *RPB1* gene loci of MSA-1 (suppl. Figs. S1–S3) revealed one relevant conflict in the *RPB1* gene locus, where *Lecidoma*

demissum grouped as sister taxon to *Arthrorhaphis* instead in Lecanoromycetidae (suppl. Fig. S3). Since the respective sequence was obtained from GenBank and could not be evaluated, it was removed from the four-gene MSA-1 prior to the final analyses. The nrITS gene locus was not tested separately due to the large amount of missing data in the outgroup taxa (Appendix 1).

After concatenation, *Arthrorhaphis* is supported as monophyletic by BI and ML analyses of MSA-1 (Fig. 1). The genus is accommodated in a well-supported clade (clade 1) together with *Anzina carneonivea*, *Protothelenella corrosa,* and *P. sphinctrinoidella*. The placement of clade 1, sister to the Ostropales (clade 2), receives support by BPP only, while its inclusion in the Ostropomycetidae (clade 3) is supported by both the BI and ML analyses.

Separate BI and ML analyses for the mrSSU, nrLSU, nrITS, and *RPB1* gene loci of MSA-2 (suppl. Figs. S4–S7) show varying resolution of the *Arthrorhaphis* phylogeny for the different gene loci as well as differing support for several taxa including, e.g., *A. farinosa*, "*A. septentrionalis*", *A. vacillans*, alpina 1, and alpina 3. The highest resolution is observed

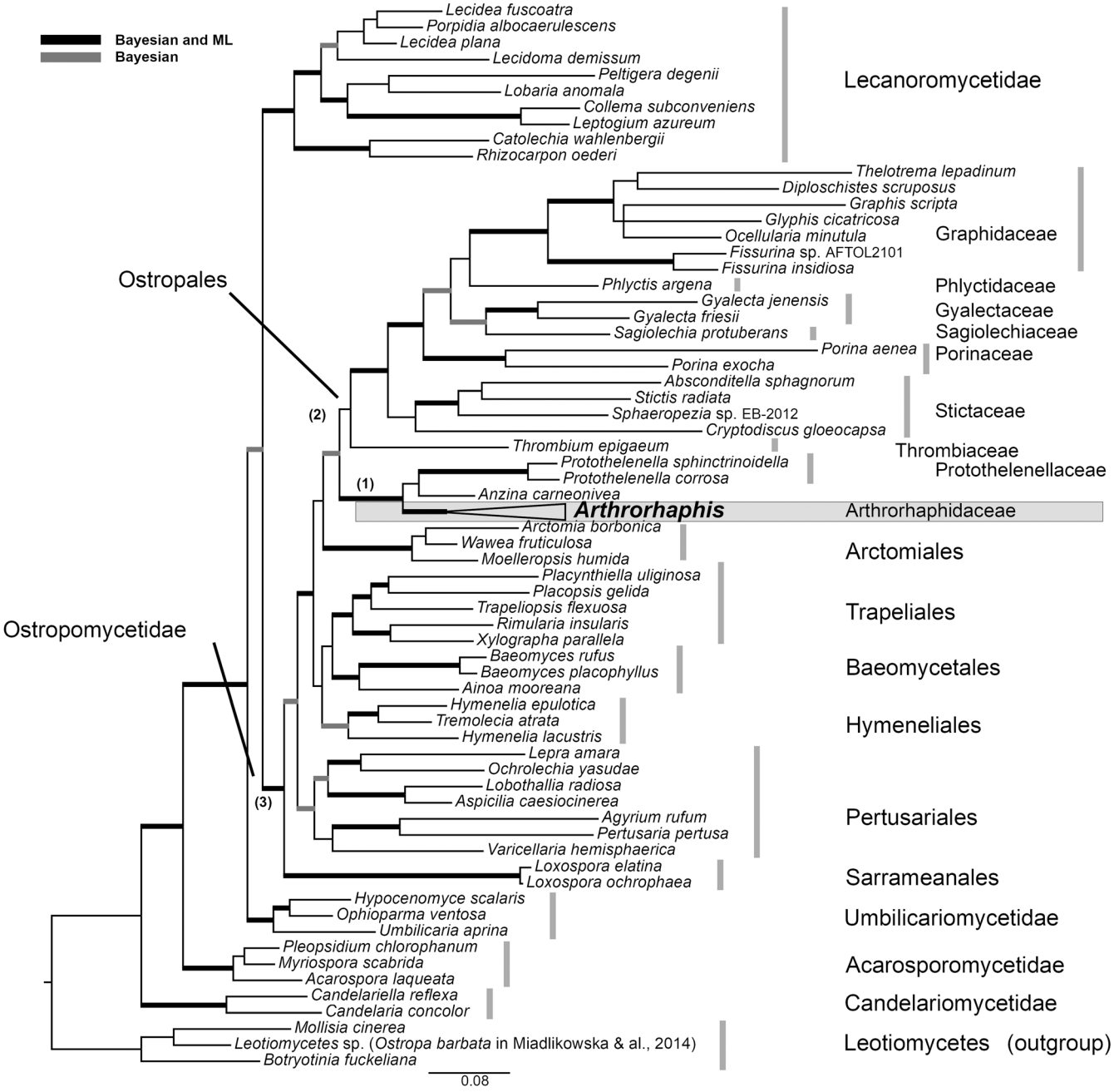

Fig. 1. Bayesian 50% majority-rule consensus tree from analysis of MSA-1, showing the placement of *Arthrorhaphis* as sister to Ostropales, Ostropomycetidae. Branches supported by BPP ≥ 0.95 and ML BS ≥ 70% are indicated by bold black lines; branches supported only by BPP ≥ 0.95 are indicated by bold grey lines. Numbers in brackets represent clades discussed in the text.

in the mrSSU (suppl. Fig. S4) and the *RPB1* (suppl. Fig. S6) gene loci, while lower resolution is observed in both the conservative nrLSU (suppl. Fig. S5) and the variable nrITS (suppl. Fig. S7). With few relevant exceptions, however, none of the deviating tree topologies receive support by BPP and ML BS. Examples for supported conflicts include the position of *A. arctoparmeliae* sister to all other included *Arthrorhaphis* accessions (mrSSU: suppl. Fig. S4; nrITS: suppl. Fig. S7) or between *A. aeruginosa* and the remaining *Arthrorhaphis* accessions (mrSSU: suppl. Fig. S4); and the position of *A.* sp. 1 and *A. catolechioides* either in the *A. citrinella* s.l. clade (mrSSU, nLSU, nrITS: suppl. Figs. S4, S5, S7) or sister to the *A. alpina* s.l. clade (*RPB1*, ML BS only: suppl. Fig. S6). None of these conflicts were considered critical enough for preventing concatenation of the four single gene loci.

In the final phylogenetic hypothesis derived from BI and ML analyses of the concatenated four-gene MSA-2 (Fig. 2), *Arthrorhaphis aeruginosa* and *A. olivaceae* (clade 1) form a strongly supported sister to the remaining *Arthrorhaphis* (clade 2). Depicted sister-relations in the latter clade receive significant support by the BI analysis only, including the sister-relation between *A. grisea* and the lichenised taxa (clade 3). The lichenised taxa (clade 4) receive strong support in all analyses and consist of two strongly supported subclades: the alpina s.l. clade and the citrinella s.l. clade.

In the alpina s.l. clade (Fig. 3), "*A. septentrionalis*" (clade 1) is sister to a large polytomy (clade 2), accommodating all remaining accessions of *Arthrorhaphis alpina* in addition to multiple accessions of both *A. alpina* var. *jungens* and *A. vacillans*. Three supported, largely geographically defined clades of *A. alpina* accessions are evident in the polytomy: alpina 1 (clade 3), accommodating accessions from eastern and southern Africa, the south Indian Ocean, and a single accession from China (ML BS support only); alpina 2 (clade 6) accommodating accessions from Japan and eastern Russia; and alpina 3 (clade 7), accommodating accessions from the Neotropics. All specimens of *A. vacillans* in the analyses form a strongly supported monophyletic group (clade 4). This clade consists of two well-supported subclades, one accommodating accessions from China (Sichuan, Tibet), the other from Austria and north-eastern Russia (Severnaya Zemlya Archipelago, Yakutia). Monophyly is neither supported nor rejected for the accessions of *A. alpina* var. *jungens*. All *A. alpina* var. *jungens* accessions group with at least one of its own, resulting in four clades: jungens 1 (clade 5; China, Nepal, Pakistan; ML BS support only), jungens 2 (clade 8; China), jungens 3 (clade 9; China, including an isotype specimen [T]), and jungens 4 (clade 10; Kalb, Lichenes neotropici 577 [GZU, M], Venezuela).

In the citrinella s.l. clade (Fig. 4), two accessions named *Arthrorhaphis* sp. 1 (Mexico, Peru) form a well-supported clade sister to *A. catolechioides*. This well-supported group (clade 1) is sister to the remaining accessions of *A. citrinella* s.l. from the Holarctic (clade 2). Specimens from East Asia occur in two

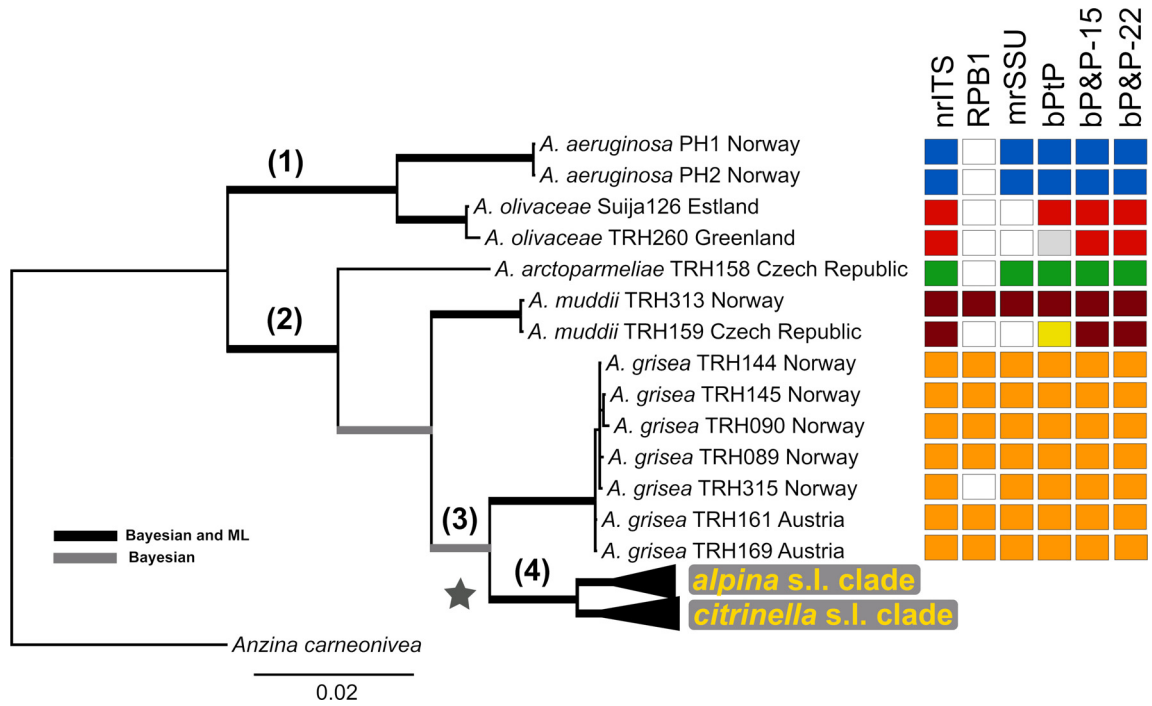

Fig. 2. Bayesian 50% majority-rule consensus tree from analysis of MSA-2, showing the basal position of the exclusively parasitic species in *Arthrorhaphis*. The evolution of lichenised thalli containing pulvinic acid derivatives in the *A. alpina*- and the *A. citrinella* s.l. clades is indicated by an asterisk. Branches supported by BPP ≥ 0.95 and ML BS ≥ 70% are indicated by bold black lines; branches supported only by BPP ≥ 0.95 are indicated by bold grey lines. Numbers in brackets represent clades discussed in the text. Graphical representation of species delimitations in bGMYC, bPtP and bP&P: Colours represent delimited species for each species delimitation analysis independently, but have been selected to highlight delimitations congruent across analyses. White represents missing data. The colouring scheme applies only to the current figure.

clades (clades 3 + 5), of which one (clade 5) includes accessions from a narrow area of north-western Dalarna in Sweden. *Arthrorhaphis citrinella* s.str. (clade 4) accommodates accessions from northern and western Europe and Iceland, while the majority of *A. citrinella* s.l. accessions from throughout the Holarctic fall in a separate clade (clade 6). Except for clade 1 being sister to clade 2, the inferred phylogenetic relationships among the main clades within *A. citrinella* s.l. (clades 3–6) are not supported.

Species delimitation. — The bGMYC model is favoured over the null model for all three gene loci (Table 2). The number of inferred entities varies from 15 (mrSSU, *RPB1*) to 19 (nrITS). The bGMYC entities are largely congruent to our delimitations based on the molecular phylogenetic results

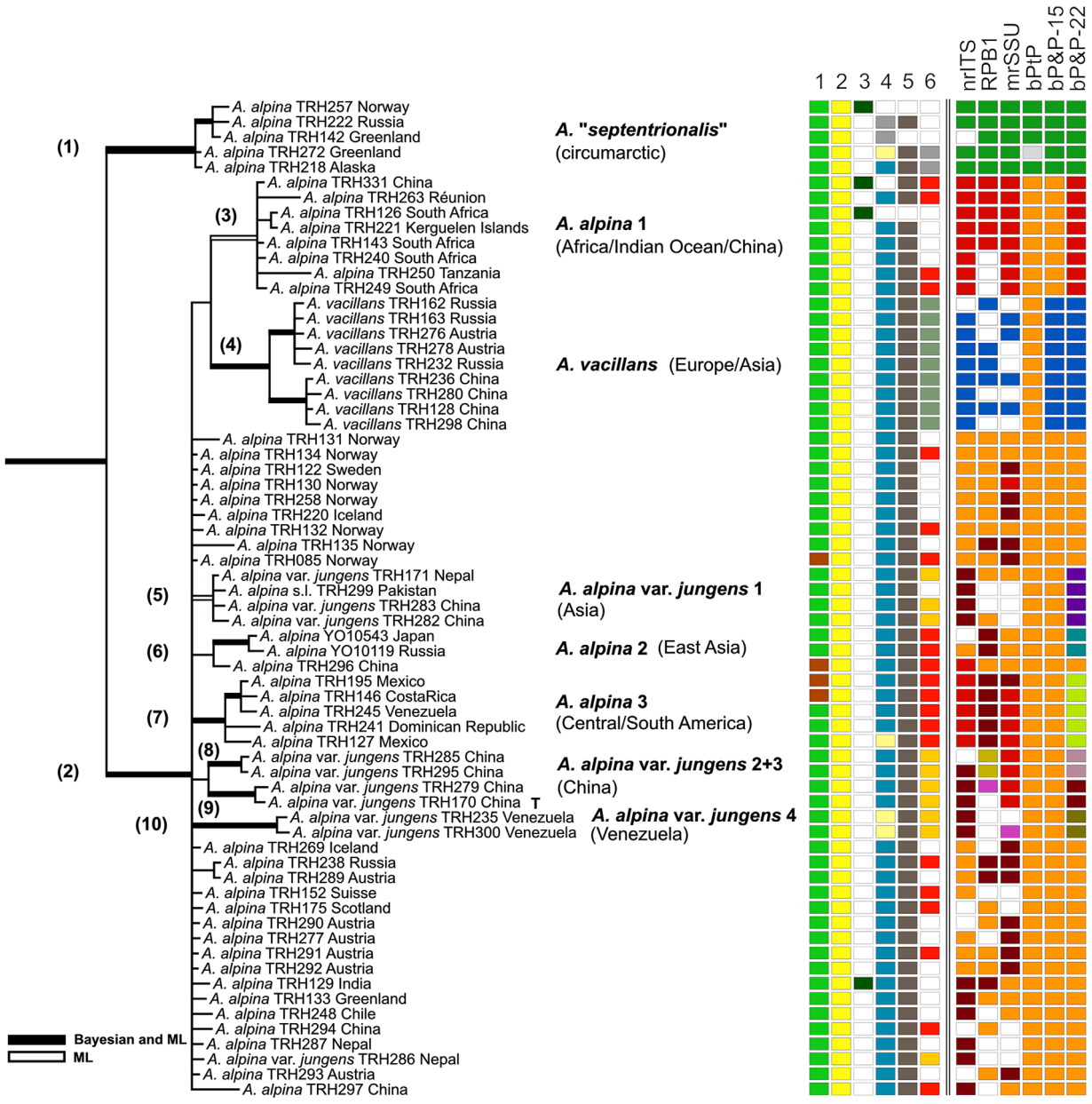

Fig. 3. Partial representation of the Bayesian 50% majority-rule consensus tree from analysis of MSA-2, showing the *Arthrorhaphis alpina* s.l. clade. Branches supported by BPP ≥ 0.95 and ML BS ≥ 70% are indicated by bold black lines; branches supported only by ML BS ≥ 70% are indicated by thin double lines. Numbers in brackets represent clades discussed in the text. "T" indicates an isotype specimen of *A. alpina* var. *jungens*. Character states: **1** Life form: juvenile parasitism absent (light green), present (reddish brown). **2** Thallus areolae: present (yellow); **3** Soredia: present (dark green), absent (white); **4** Medulla: pale yellow (yellow), white (blue), cavity (grey), absent (white); **5** Ca-oxalate crystals: present (dark brown), absent (white); **6** Ascospores: alpina type (red), jungens type (light orange), vacillans type (dark olive), 'septentrionalis type' (grey), absent (white). Graphical representation of species delimitations in bGMYC, bPtP, and bP&P: Colours represent delimited species for each species delimitation analysis independently, but have been selected to highlight delimitations congruent across analyses. White represents missing data. The colouring scheme applies only to the current figure.

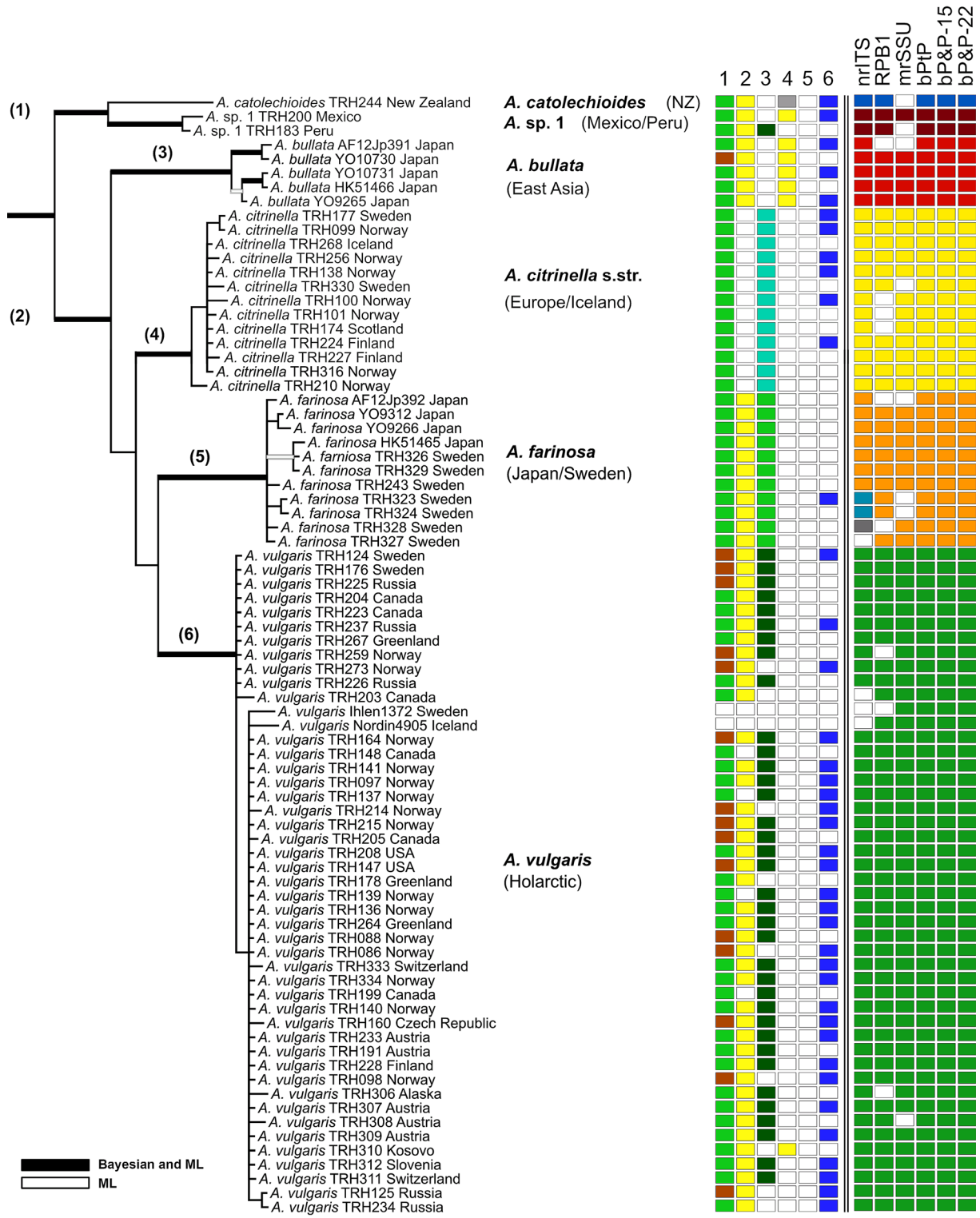

Fig. 4. Partial representation of the Bayesian 50% majority-rule consensus tree from analysis of MSA-2, showing the *Arthrorhaphis citrinella* s.l. clade. Branches supported by BPP ≥ 0.95 and ML BS ≥ 70% are indicated by bold black lines; branches supported only by ML BS ≥ 70% are indicated by thin double lines. Numbers in brackets represent clades discussed in the text. Character states: **1** Life form: juvenile parasitism absent (light green), present (reddish brown), missing data (white). **2** Thallus areolae: present (yellow), absent (white); **3** Soredia: citrinella type (turquoise), farinosa type (light green), vulgaris type (dark green), absent (white); **4** Medulla: pale yellow (yellow), cavity (grey), absent (white); **5** Ca-oxalate crystals: absent (white); **6** Ascospores: citrinella type (blue), absent (white). Graphical representation of species delimitations in bGMYC, bPtP, and bP&P: Colours represent delimited species for each species delimitation analysis independently, but have been selected to highlight delimitations congruent across analyses. White represents missing data. The colouring scheme applies only to the current figure.

and morphological considerations for the strictly parasitic species and the taxa of the *Arthrorhaphis citrinella* s.l. clade (Figs. 2, 4). Only *A. farinosa* is delimited as three entities for the nrITS (Fig. 4; Table 3). In the *A. alpina* s.l. clade (Fig. 3), *A. vacillans* and "*A. septentrionalis*" are delimited as discrete entities, except that the latter is not distinguished from *A. alpina* for the mrSSU. *Arthrorhaphis alpina* s.l. (incl. var. *jungens*) splits in three (nrITS), four (mrSSU), and five (*RPB1*) entities, respectively (Table 3). None of these entities are congruent with the supported clades (3, 5–10) on the phylogenetic tree (Fig. 3). Except for alpina_TRH195_Mexico (clade alpina 3, mrSSU), however, all specimens of a particular phylogenetic clade are assigned to the same bGMYC species in all three gene loci.

A total of 16 *Arthrorhaphis* species are delimited by bPtP. In contrast to bGMYC, *A. alpina* s.l. (incl. var. *jungens*) is delimited as a single species that additionally includes *A. vacillans*, while *A. muddii*, *A. olivaceae, and* "*A. septentrionalis*" split in two species each (Figs. 2, 3; Table 3).

The bP&P analyses overwhelmingly support a 21 (+ outgroup)-species scenario for *Arthrorhaphis*, highly consistent with our delimitations based on the molecular phylogeny and morphological considerations. Applying diffuse gamma priors of $\theta = 0.0001$ and $\tau = 0.00015$, the most species-rich

Table 2. Results from the bGMYC analyses for mrSSU, nrITS, and *RPB1* gene loci.

	mrSSU	nrITS	*RPB1*
Likelihood null model	1231.294	1199.214	1160.623
Maximum likelihood GMYC model	1264.052	1230.614	1180.092
Likelihood ratio	65.51679	62.80141	38.93693
Result of likelihood ratio test	5.884182e-15***	2.309264e-14***	3.507144e-09***
Number of maximum likelihood clusters with confidence interval in brackets	10 (9–10)	15 (15–15)	12 (12–20)
Number of maximum likelihood entities with confidence interval in brackets	15 (14–15)	19 (19–20)	15 (15–30)
Threshold time	–0.002228722	–0.007533381	–0.002175746

***denotes $P < 0.001$.

Table 3. Summary of species delimitations from the bGMYC, bPtP, and bP&P analyses.

	bGMYC			bPtP	bP&P	
	mrSSU	nrITS	*RPB1*		15	22
A. aeruginosa	1	1	–	1	1	1
A. alpina s.l. (incl. var. *jungens*)	4	3	5	1	1	8
A. arctoparmeliae	1	1	–	1	1	1
A. bullata	1	1	1	1	1	1
A. catolechioides	–	1	1	1	1	1
A. citrinella	1	1	1	1	1	1
A. farinosa	1	3	1	1	1	1
A. grisea	1	1	1	1	1	1
A. muddii	1	1	1	2	1	1
A. olivaceae	–	1	–	2	1	1
"*A. septentrionalis*"	0	1	1	2	1	1
A. sp. 1	1	1	1	1	1	1
A. vulgaris	1	1	1	1	1	1
A. vacillans	1	1	1	0	1	1
Anzina carneonivea (outgroup)	1	1	–	1	1	1
Sum	15	19	15	17	15	22

A "0" indicates species not recovered by the species delimitation analysis. An en-dash indicates missing data. For bP&P, species delimitations are given for the 15- and 22-species scenarios.

model receives the highest support in both the 15-species and the 22-species scenarios, and all species delimitations are supported using a 0.95 BPP threshold (Figs. 3, 4; suppl. Tables S1A, S2A). A 24-species scenario that was further explored for this study (suppl. Table S3A), using the same settings as for the 15- and 22-species scenarios, receives only low support for delimiting 22 or 23 species depending on the run. Two runs support a 22-species scenario, delimiting *A. farinosa* (A3, A24) as one species, while delimiting two species in *A. bullata* (A4, A23; not shown). The third run delimits all 23 *Arthrorhaphis* clades albeit with low support of the variously delimited species A3, A4, A23, A24, A24A3, and A23A4 (suppl. Table S3A).

Applying diffuse gamma priors of θ = 0.001 and τ = 0.0015 for the 15-species scenario, a 15-species model (BPP 0.52–0.56) is only slightly favoured over a 14-species model (BPP 0.44–0.48; Figs. 3, 4; suppl. Table S1B). In the 14-species model, *Arthrorhaphis catolechioides* and *A.* sp. 1 are delimited as one species. In the 22- and 24-species scenarios, a 20- or a 21-species model receive the highest, albeit low, support depending on the run (Figs. 3, 4; suppl. Tables S2B, S3B). All additional clades in *A. alpina* s.l. are delimited with low BPP support (<0.95), while in the 24-species scenario, *A. bullata* and *A. farinosa* are additionally delimited as uniform species. The remaining *A. alpina* s.l. receives only low support (BPP 0.87–0.95) in the 24-species scenario.

Morphology. — In the present study, juvenile parasitism is most prevalent in investigated specimens of *Arthrorhaphis vulgaris*, with *Baeomyces rufus* and *B. placophyllus* (only in TRH259) as the host taxa. Molecular differences among accessions parasitizing different host species are not observed (Fig. 4: clade 1). A few parasitic specimens are also observed in *A. bullata* (on cf. *Cladonia* sp.), and in *A. alpina* from the Neotropics (on *B. placophyllus*, *Cladonia* spp.) and Norway (on *Dibaeis baeomyces*). Juvenile parasitism is not observed in studied specimens of the other taxa (Figs. 3, 4).

Areolate thalli are observed for all accessions accommodated in the alpina s.l. and citrinella s.l. clades, except for *Arthrorhaphis citrinella* s.str. (Figs. 3 & 4: clade 2). Sorediate stages are rare in the investigated specimens of *A. alpina* s.l. and "*A. septentrionalis*", while the thallus areolae in most investigated specimens of *A. vulgaris* give rise to granular soredia to various extent. Nearly entirely sorediate specimens of *A. vulgaris* are frequently observed in this study that can be difficult to separate from *A. citrinella* s.str. The areolate thalli in all investigated specimens of *A. farinosa* are entirely covered in finely granular to farinose soredia, while the thalli of *A. citrinella* s.str. consist entirely of coralloid aggregations of coarsely granular soredia (Fig. 4). Distinct thallus areolae or a well-developed medulla are not observed in the latter species.

Ca-oxalate crystals are restricted to the alpina s.l. clade and present in almost all specimens (Fig. 3). The few exceptions include two accessions of "*A. septentrionalis*" from Norway and Greenland, and a single accession of *A. alpina* from South Africa (Fig. 3). Low amounts of Ca-oxalate are, however, observed in several specimens from the Neotropics and Africa. A variously developed medulla is present in nearly all accessions of the alpina s.l. clade (Fig. 3). It is mostly white, rarely pale yellow or replaced by a central cavity (Fig. 3). In the citrinella s.l. clade, a pale yellow medulla is observed in *A. bullata*, in single specimens of *A. vulgaris* and in the Neotropical *Arthrorhaphis* sp. 1 (Fig. 4). A central cavity is observed in the sequenced specimen of *A. catolechioides* (Fig. 4).

The ascospores observed for accessions recovered in the alpina s.l. clade belong to the alpina, vacillans, and the intermediary jungens types (Fig. 5). Vacillans-type ascospores (Fig. 5C) are restricted to the vacillans clade (clade 4), while jungens-type ascospores (Fig. 5D) occur in the various jungens clades (clades 5, 8, 9, and 10) and in a single specimen placed on the deep polytomy of clade 2. Alpina-type ascospores (Fig. 5B) are spread across the *A. alpina* s.l. polytomy (Fig. 3). Ascospores of the citrinella type (Fig. 5A) are observed for all taxa in the citrinella s.l. clade (Fig. 4).

■ DISCUSSION

This study provides the first integrative systematic study of *Arthrorhaphis*, combining molecular phylogenetics with

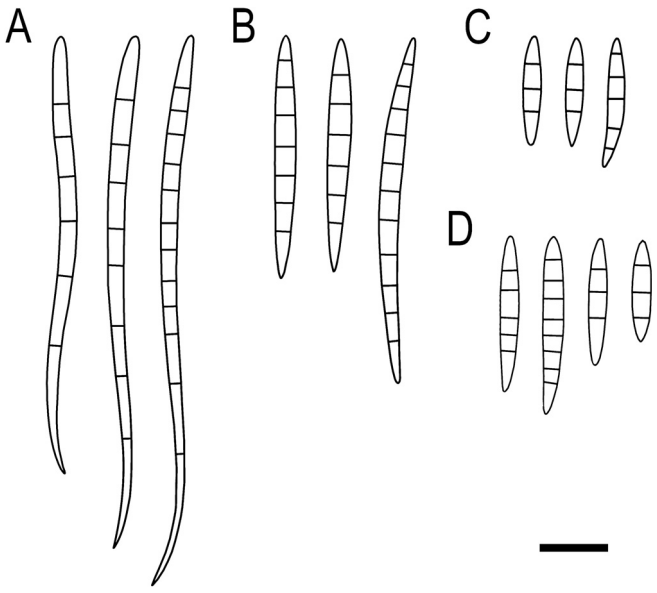

Fig. 5. Ascospore types distinguished in lichenised *Arthrorhaphis* (schematic redrawing based on illustrations in Obermayer, 1994, 1995; compare the cited literature for further details). **A**, Citrinella type; **B**, Alpina type; **C**, Vacillans type; **D**, Jungens type. — Ascospores of the citrinella type are arranged parallel, 1-seriate, while those of the alpina, vacillans, and jungens types are stacked in the asci. Ascospores of the variable jungens type are intermediary between the alpina and vacillans types, and either resembling the vacillans type but longer, or similar in size but 4–5(–7)-septate. — Scale: A–D, 10 µm.

studies of morphology and chemistry of both freshly collected and fungarium specimens. We have included all taxa in the genus except for the recently described *A. phyllobaeis*. Our BI and ML phylogenetic analyses of multilocus data provide a useful framework for assessing taxon limits, sister relationships, and character state evolution, which in addition to morphology and chemistry also include life form and anatomy. Finally, we have tested our revised species hypotheses in *Arthrorhaphis* using three different species delimitation approaches. Our results strongly improve the understanding of *Arthrorhaphis* and provide a firm basis for multiple taxonomic conclusions. Taxonomic updates include both recombinations and two new species, as well as an artificial key following our updated taxonomy of *Arthrorhaphis*.

Monophyly and phylogenetic placement of *Arthrorhaphis*. — Our results corroborate monophyly for the morphologically defined genus *Arthrorhaphis*, accommodating strictly lichenicolous as well as lichenised taxa. More than 30 genera in lineages as diverse as the Arthoniomycetes, Dothideomycetes, Eurotiomycetes, and Lecanoromycetes are reported in literature as to include both lichenised and lichenicolous species within the same genus (Diederich & al., 2018). However, to our knowledge this is the first phylogenetic study unequivocally demonstrating this for a well-circumscribed genus and a comprehensive taxon sampling.

The placement of *Arthrorhaphis* in the Ostropomycetidae (Fig. 1: clade 3) is in accordance with most molecular phylogenetic studies (Wedin & al., 2005b; Miadlikowska & al., 2006; Lumbsch & al., 2007; Pino-Bodas & al., 2017). In the current *Outline of Ascomycota: 2017* (Wijayawardene & al., 2018), however, Arthrorhaphidaceae is included as Lecanoromycetes incertae sedis. This conclusion may have been drawn by the molecular phylogenetic placement of *Arthrorhaphis* in the Lecideales (Lecanoromycetidae) by Miadlikowska & al. (2014). Such a placement is rejected by our results (Fig. 1) and further conflicts with relevant morphological characters of the ascomata. These include non-amyloid asci with only a weakly thickened tholus, sparsely branched paraphyses that are strongly conglutinated only in the epihymenium, and non-amyloid hymenial gels. These characters agree better with the Ostropales than with the Lecideales (Baloch & al., 2010), as further discussed by Poelt (1969, 1974), Poelt & Hafellner (1976), and summarised by Obermayer (1994). Our results further reject a relationship of the Arthrorhaphidaceae with Patellariales, which has been suggested by Eriksson & Hawksworth (1990). Patellariales has not been treated in our phylogeny but has been shown recently as belonging in the unrelated Dothideomycetes (Schoch & al., 2009; Boehm & al., 2015). Ontogenetic studies, not performed on *Arthrorhaphis* so far, could potentially provide further evidence for the phylogenetic position in the Ostropomycetidae, for example by demonstrating an ascoma ontogeny similar to the hemiangiocarpus development described for the Ostropales (Henssen, 1976, 1995; Henssen & Lücking, 2002).

Our molecular phylogenetic results (Fig. 1: clade 1) further corroborate a close phylogenetic relationship of the Arthrorhaphidaceae with the Protothelenellaceae (Lumbsch & al., 2007) and *Anzina carneonivea* (Wedin & al., 2005b). *Epigloea soleiformis* (Epigloeaceae) was recently shown to be related to these taxa (Pino-Bodas & al., 2017), but the type of the genus, *E. bactrospora*, has so far not been analysed. The position of clade 1 as phylogenetic sister to the Ostropales (Fig. 1: clade 2) agrees with the phylogeny of Resl & al. (2015). Taxa in the *Anzina-Arthrorhaphis-Protothelenella* clade in the Ostropomycetidae are morphologically diverse, including apothecioid and perithecioid ascomata with different exciple structures, hamathecial organisation, amyloidity of the ascomatal gels and asci. The taxa in clade 1 also show diverse life-strategies: lichenised in *Anzina carneonivea* (Scheidegger, 1985); parasitic on algae or occasionally on lichens in *Epigloea soleiformis* (Döbbeler, 1984; Pino-Bodas & al., 2017); growing on algal mats, lichenised or lichen parasitic in *Protothelenella* (Pino-Bodas & al., 2017); and lichen parasitic or lichenised in *Arthrorhaphis* (Obermayer, 1994). In addition, *A. citrinella* has been found associated with a diversity of algal types in addition to the photobiont of its *Baeomyces* host (Obermayer, 1994) and may be capable of symbiotic interactions with various free-living soil algae. Lichenisation appears to be rather unstable in clade 1 and other lineages of the Ostropomycetidae. Switches between lichenised and non-lichenised states are known from genera such as *Cryptodiscus* and *Stictis* (Stictidaceae; Baloch & al., 2010). In some species, for example, *Ostropa barbata*, *Schizoxylon albescens*, and *Stictis populorum*, both lichenised and non-lichenised individuals can be found (Wedin & al., 2005a, 2006; Baloch & al., 2010).

It is currently debated whether the non-lichenised taxa in the Ostropomycetidae have evolved from lichenised ancestors in several secondary de-lichenisation events (Resl & al., 2015) or represent the ancestral state from which the lichenised lineages have emerged (Baloch & al., 2010). Our results are not conclusive in this respect, as most of the non-lichenised or facultatively lichenised taxa are either placed as sister to the Ostropales, as in the case of the *Anzina-Arthrorhaphis-Protothelenella* clade (Fig. 1: clade 1), or sister to the majority of the Ostropales, as in the case of the Stictidaceae (Fig. 1: clade 2).

Morphology and phytochemistry. — This study widely conforms to the morphology-based species concept of Obermayer (1994, 1996, 2001). Both *Arthrorhaphis alpina* and *A. citrinella* are found to be heterogeneous at the world level and include several distinct phylogenetic clades. Fertile specimens in the alpina s.l. clade (Fig. 3) have ascospores stacked in the asci that belong either to the alpina, vacillans, or the intermediary jungens type (Fig. 5B–D), while ascospores in the citrinella s.l. clade (Fig. 4) are of the citrinella type (Fig. 5A) and parallel 1-seriate in the asci. The single notable exception are the ascospores observed in only two fertile collections of "*A. septentrionalis*" (Fig. 3: clade 1), which occur parallel 1-seriate in the apical half of the asci and are reminiscent of the citrinella type. However, the ascospores in these specimens appear immature and are difficult to interpret on the sparse material available for study.

Ca-oxalate crystals, used as cardinal character to distinguish sterile specimens of *Arthrorhaphis alpina* s.l. from *A. citrinella* (Obermayer, 1994), could be verified for nearly all specimens in the alpina s.l. clade and for none in the citrinella s.l. clade (Figs. 3, 4). Ca-oxalate crystals could not be verified for two specimens of "*A. septentrionalis*" (Fig. 3: clade 1) and one of *A. alpina* from South Africa (Fig. 3: clade 3). It may well be that the production of Ca-oxalate in these specimens was too low for detection. In general, the production of Ca-oxalate crystals and the development of a white medulla are highly variable characters that appear not randomly distributed in *A. alpina* s.l. Large amounts of Ca-oxalate crystals and a white medulla are most common in specimens from the Holarctic, while only low amounts of them are typically found in specimens from the Neotropics, tropical and temperate Africa, and the southern Indian Ocean. Such specimens may have a loosely structured medulla or a central cavity inside the areolae. It cannot be shown from our data to what extent this variation is caused by ecological factors or reflect the observed genetic heterogeneity of *A. alpina*. It should be noted, however, that we investigated only few specimens from tropical mountains and the Southern Hemisphere. The study of additional material is necessary for a sound evaluation of this variation. In agreement with Obermayer (1994), low amounts of Ca-oxalate crystals were observed also in the few specimens of *A. alpina* that were near completely dissolved into soredia.

Specimens producing soredia are present in both the alpina s.l. and the citrinella s.l. clades but are much more common in the latter. This is consistent with the results of Obermayer (1994, 1996). Only 3 of the 66 specimens in the alpina s.l. clade are sorediate. None of these were entirely dissolved into soredia, although a few such specimens were seen in the additional material examined. On the other hand, as much as 62 out of 80 specimens in the citrinella s.l. clade produce soredia to various extents. As discussed in more detail in the Taxonomy section, all specimens of *Arthrorhaphis citrinella* s.str. and *A. farinosa* are sorediate. In specimens of *A. vulgaris* (Fig. 4: clade 6) and the two accessions referred to as *Arthrorhaphis* sp. 1 from the Neotropics (Fig. 4: clade 1), the areolate thalli are variously producing granular soredia. Specimens completely devoid of soredia are rare and often show at least weak signs of beginning disruption of the surface of the areolae. In agreement with Obermayer (1994, 1996, 2001), we have not observed sorediate specimens for *A. vacillans* (Fig. 3: clade 4) and *A. catolechioides* (Fig. 4: clade 1). The same accounts for the herein described *A. bullata*. The different thallus morphologies observed in the species recognised within *A. citrinella* s.l. are described in more detail in the Taxonomy section below. Subtle differences in thallus morphology have also been observed in *A. alpina* s.l. This variation, which appears to be linked at least partly to regional populations or genetically distinct lineages, should be investigated further.

In agreement with previous studies (Obermayer, 1994, 1996, 2001; Ihlen, 1998; Hansen & Obermayer, 1999), lichen secondary chemistry is uniform in the lichenised *Arthrorhaphis* species and differences among the phylogenetic clades have not been observed. Rhizocarpic acid and epanorin have been found in all specimens studied by thin-layer chromatography. The additional pigment A1, reported for *Arthrorhaphis* by Obermayer (1994), could not be detected. Norstictic and stictic acid, observed in parasitic specimens of *A. vulgaris*, are likely derived from the host lichens *Baeomyces rufus* and *B. placophyllus*, respectively (Obermayer, 1994).

The parasitic vs the lichenised species. — Based on our limited taxon sampling, the exclusively parasitic species in *Arthrorhaphis* (Fig. 6A–E) apparently represent genetically well-delimited taxa that are placed basal to the lichenised species in the BI and ML analyses (Fig. 2). *Arthrorhaphis grisea* is the inferred phylogenetic sister to the lichenised *Arthrorhaphis* (Fig. 2), which share *Baeomyces* (*B. rufus*, more rarely *B. placophyllus*) as the lichen host. This supports the morphology-based conclusion by Obermayer (1994), that *A. grisea* is a strictly lichenicolous taxon independent from *A. citrinella* rather than merely an early parasitic stage of the latter taxon in which the lichenised thallus has not yet been developed.

The lichenised species in *Arthrorhaphis* prove morphologically and genetically diverse and encompass several previously unrecognised species as well as additional geographically structured clades (Figs. 3, 4). Increased diversification caused by a biological shift has recently been reported for the Teloschistaceae (Gaya & al., 2015) and for *Placopsis* (Schneider & al., 2016). The hypothesis that the observed diversification of the lichenised taxa in *Arthrorhaphis* is likewise driven by a shift from the lichenicolous to the lichenised habit cannot conclusively be shown on our data and needs further study.

The *Arthrorhaphis alpina* s.l. clade. — This clade is poorly resolved (Fig. 3) given our taxon sampling and selection of gene loci. Except for five accessions from circumarctic regions that are separated in a well-supported clade 1, all remaining specimens of *Arthrorhaphis alpina* are recovered in a large polytomy (clade 2) that additionally accommodates *A. alpina* var. *jungens* and *A. vacillans*. Our molecular results show *A. alpina* s.l. as a genetically heterogeneous species at the world level, which conforms to the morphological variation observed in this study and reported in literature (Obermayer, 1994, 1996). Geographical differentiation is evident in our data, indicating geographically disjunct populations or recent independent speciation events in *A. alpina* s.l. in Africa with the south Indian Ocean (clade 3: alpina 1), eastern Asia (clade 6: alpina 2), and the Neotropics (clade 7: alpina 3). A single specimen from China is included in the alpina 3 clade, which otherwise includes accessions from Africa and the south Indian Ocean. This is suggestive of long-distance dispersal like in *A. farinosa*, which is known from Japan and Sweden. However, few *Arthrorhaphis* specimens were available from across Siberia and central Asia, and populations connecting the isolated distribution areas of *A. alpina* (clade 3) and *A. farinosa* may be discovered.

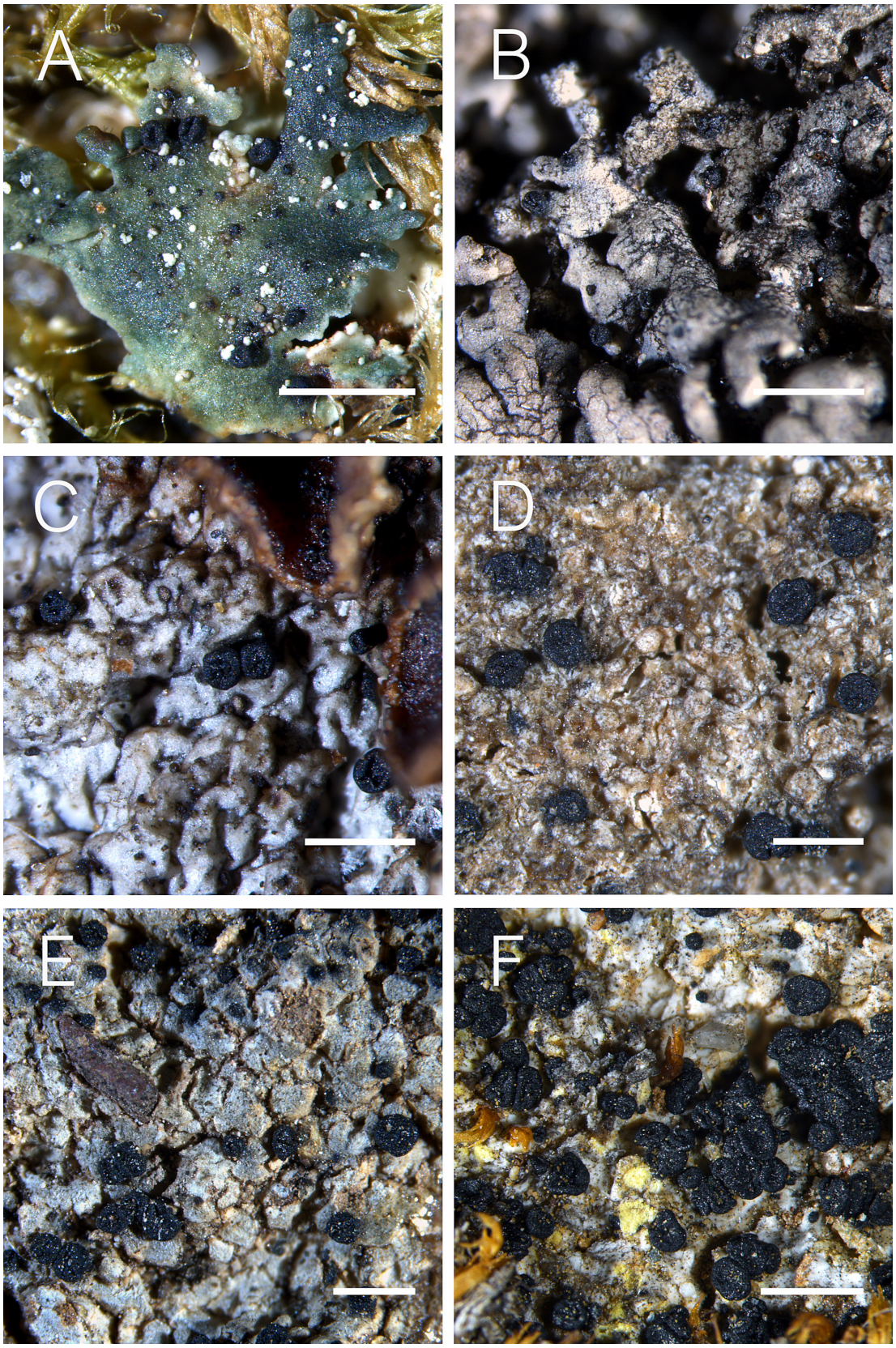

Fig. 6. **A**, *Arthrorhaphis aeruginosa* (*Tønsberg 19019*, BG, holotype); **B**, *A. arctoparmeliae* (*Kocourková & Kocourek JK5484* dpl., C); **C**, *A. olivaceae* (*Santesson 11677*, BG, isotype); **D**, *A. muddii* (*Woods s.n.*, E, holotype); **E**, *A. grisea* (*Th.M. Fries s.n.*, UPS, holotype); **F**, *A. vulgaris* (*Norrlin s.n.*, H). — Scale: A–C, 0.5 mm; D–F, 1 mm. Photos: A. Frisch.

Arthrorhaphis alpina var. *jungens* was described for specimens of *A. alpina* s.l. in central Asia that have ascospores intermediary in size and septation between *A. alpina* and *A. vacillans* (Obermayer, 1995). The ascospores of this variety were described as highly variable even within individuals, either resembling the vacillans type (16–20(–22) µm, 3-septate), equally sized but with 4–7 septa, or >23 µm but 3-septate (Obermayer, 1995, 1996). The notion of a heterogeneous *A. alpina* var. *jungens* derived from literature gains support from our phylogenetic results. Six accessions of *A. alpina* var. *jungens* from central Asia and Venezuela are recovered in three supported clades (8, 9, 10: jungens 2, 3, 4, respectively), nested within *A. alpina* s.l. Additional accessions group in a fourth clade with low support (clade 5: jungens 1). We did not detect any differences in ascospore size, shape and septation between the four clades. The concept of *A. alpina* var. *jungens* obviously includes several discrete populations within *A. alpina* s.l.

The nine included accessions of *Arthrorhaphis vacillans* are recovered as monophyletic (clade 4), but the species splits into two geographically disjunct lineages. One lineage is confined in our analysis to the Himalayan region of south-central China (western Sichuan and eastern Tibet). Lineage two accommodates specimens from the European Alps and northeastern Siberia. As already discussed for *A. farinosa*, specimens from Scandinavia or from across northern Siberia, which could link the latter two distribution areas, have not been available for this study. Except for slightly longer ascospores in the collections from China (15–23 µm vs 11–19 µm), morphological differences were not observed. With respect to the small sampling size, these differences cannot be regarded as significant. Three of the four specimens from China were identified as either *A. alpina* or *A. alpina* var. *jungens* based on the herbarium specimens, further highlighting the difficulties in species delimitation and identification within *A. alpina* s.l.

The preliminary name "*Arthrorhaphis septentrionalis*" is introduced here for five specimens from circumarctic regions in Alaska, Greenland, Europe, and eastern Siberia that form a well-supported group (Fig. 3: clade 1), phylogenetic sister to the remaining accessions of *A. alpina* s.l. (Fig. 3: clade 2). Two fertile specimens of "*A. septentrionalis*" have been investigated (TRH218, TRH272). These are distinguished within the alpina s.l. clade by ascospores that are invariably 28–52 × c. 3 µm, 5–8-septate (n = 11), parallel 1-seriate in the asci and reminiscent of the citrinella type (Fig. 5A). The ascospores fill the upper third to half of the asci only and appear immature. Calcium oxalate crystals are sparse or could not be detected at all. In the absence of ascospores or molecular data, "*A. septentrionalis*" cannot be distinguished with certainty from *A. alpina* or, when Ca-oxalate cannot be detected, *A. vulgaris*. Additional material is needed for proper characterisation of this taxon, for which reason we have made no formal taxonomic decision herein.

The *Arthrorhaphis citrinella* s.l. clade. — This clade is resolved into five well-supported phylogenetic lineages (Fig. 4). *Arthrorhaphis citrinella* var. *catolechioides* in clade 1 is herein raised to species level (see Taxonomic conclusions) due to its phylogenetic separation from the other species in *A. citrinella* s.l. and its characteristic thallus, comprised of smooth, bullate to umbrella-shaped areoles that may become hollow or folded in ridges. Particularly in muscicolous specimens, the areolae rest on black hyphal strands (Obermayer, 2001). Its sister taxon in clade 1, *Arthrorhaphis* sp. 1 from the Neotropics, differs by the strongly convex areolate to finely bullate thallus with verruculose to sub-granular surface (Mexico; voucher *Nash III 35705*, ASU-506761) or by an entirely sorediate to coarsely granular thallus (Peru; voucher *Santesson, Tehler & Thor P93:92*, SL22030). Our material of *Arthrorhaphis* sp. 1 is scanty and may represent more than one species. The specimen from Mexico is fertile and its apothecia and spores fall within the range observed for *A. citrinella* s.l. This specimen also agrees rather well with the protologue of *A. summorum* (Bouly de Lesdain, 1933). However, type material for that name (UPS-L-097009!: Mexico, Tres Marias, 14.vii.1931, *Arsène Brouard s.n.*) belongs to *A. alpina*.

The other four clades (Fig. 4: clades 3–6), accommodating all accessions of *Arthrorhaphis citrinella* s.l. from temperate to arctic-alpine regions in the Holarctic, constitute a well-supported clade 2. The phylogenetic relationships within clade 2 are not resolved, but each phylogenetic clade is characterised by a distinct thallus morphology, ecology, and distribution. The four species herein distinguished in *A. citrinella* s.l. (i.e., *A. bullata*, *A. citrinella* s.str., *A. farinosa*, and *A. vulgaris*) are described and discussed in detail in Taxonomic conclusions below.

Species hypotheses testing. — The six species delimitation analyses indicate between 14 and 21 *Arthrorhaphis* species excluding the outgroup, *Anzina carneonivea*. Most of the low 14 bGMYC, bPtP, and bP&P delimitations are congruent with our taxonomic conclusions based on ML and BI (Figs. 2–4), morphology, and chemistry. The strongest discrepancy is observed for bPtP, which infers the two specimens each of the morphologically distinct, strictly parasitic *A. olivaceae* and *A. muddii* as separate species (Table 3). At the same time, bPtP includes the morphologically and phylogenetically well-distinguished *A. vacillans* in *A. alpina*, and infers TRH272 from Greenland as species separate from "*A. septentrionalis*". Unbalanced taxon sampling, as in the current study, is known as a possible source for biased species delimitations in bPtP, resulting in over-splitting of less-sampled species in the presence of oversampled species in a dataset (Zhang & al., 2013).

The bGMYC method delimits three species in *Arthrorhaphis farinosa* for the nrITS. None of these species is supported by morphology, geography, or any of the other species delimitation analyses. "*Arthrorhaphis septentrionalis*" is included in *A. alpina* s.l. for the conserved mrSSU, while *A. vacillans* is pertained as independent species (Figs. 2, 4). Unlike bPtP, bGMYC delimits between three and five species in *A. alpina* s.l. for the mrSSU, nrITS, and *RPB1*. However, the delimitations for the three gene loci are neither congruent with each other nor with the phylogenetic clades in Fig. 3. The bGMYC approach makes use of specified ultrametric gene trees,

interpreted as species trees, for species delimitation (Fujisawa & Barraclough, 2013). Discrepancies in the phylogenetic signal of the mrSSU, nrITS, and *RPB1* loci may explain the different delimitations observed.

Results from the phylogenetic analyses indicate the presence of intraspecific geographical populations within *Arthrorhaphis alpina* s.l. (Fig. 3). Due to the limited availability of herbarium collections from the tropics and central Asia, our sampling of these populations is highly unbalanced. The bGMYC method assumes complete lineage sorting and similar evolutionary and demographic attributes, including similar and constant effective population sizes and limited geographic structure within species (Fujisawa & Barraclough, 2013). Like other delimitation methods relying on multispecies coalescence, bGMYC is prone to interpreting such lineages, reflecting intraspecific genetic structure, as different species (Sukumaran & Knowles, 2017). Examples like *A. alpina* s.l. have been reported in literature, where morphology-based species that are validated phylogenetically are split into morphologically cryptic species by species delimitation methods (Magain & al., 2018; Bustamante & al., 2019). Coalescence within local populations is rapid relative to coalescence among populations, and strong geographic variation may bias the Yule-coalescence transition threshold if sampling of populations is incomplete (Lohse, 2009; Ahrens & al., 2016).

Species delimitation using bP&P has been shown to perform well when appropriate priors are chosen, with low rates of false positives and false negatives under most evolutionary scenarios (Yang & Rannala, 2010, 2014; Zhang & al., 2011). However, appropriate priors are difficult to estimate for lichen-forming fungi, since mutation rates and population sizes are largely unknown (Magain & al., 2017). In our study of *Arthrorhaphis*, the species delimitations supported by bP&P agreed best with the phylogenetic analyses, morphologically defined species, and the other species delimitation methods when lower priors ($\theta = 0.0001$, $\tau = 0.00015$; $\theta = 0.001$, $\tau = 0.0015$) were chosen than reported for other groups of lichen-forming fungi (Košuthová & al., 2020; Magain & al., 2017). In their study on the genus *Rostania* (Peltigerales) for example, Košuthová & al. (2020) found that the priors $\theta = 0.01$, $\tau = 0.01$ and $\theta = 0.1$, $\tau = 0.1$ were working best on their set of data, while Magain & al. (2017) used $\theta = 0.0025$ to $\theta = 0.02$ for various subclades of *Peltigera* sect. *Peltigera*.

The six individual bP&P analyses performed (suppl. Tables S1–S3) support all currently accepted *Arthrorhaphis* species except for *A. catolechioides* and *A.* sp. 1, which are not delimited as separate species when the larger prior set ($\theta = 0.001$ and $\tau = 0.0015$) was chosen. All six analyses further delimit the populations from Africa and the south Indian Ocean (alpina 1) and Central and South America (alpina 3) as distinct species separate from *A. alpina* s.l. The further phylogenetic lineages in *A. alpina* s.l. tested by bP&P (suppl. Tables S2, S3) are only supported when using the smaller priors $\theta = 0.0001$, $\tau = 0.00015$. The latter is consistent with empirical and theoretical data showing that lower prior values consistently favour splitting of species, while higher values favour lumping (McKay & al., 2013). Uncertainties in chosing appropriate priors in bP&P analyses add to the inherent problem that bP&P, like other species delimitation analyses relying on the multispecies coalescent, cannot statistically distinguish between genetic structure associated with population isolation versus species boundaries (Sukumaran & Knowles, 2017). Misidentification of population structure as putative species (Carstens & al., 2013) becomes relevant particularly in large and diverse datasets as here for *Arthrorhaphis* that are expected to consist of lineages that have undergone speciation as well as others that reflect spatial structuring of populations (Sukumaran & Knowles, 2017). Additional sources including morphological, ecological and chemical data should therefore be used to correctly distinguish between structure delimited by bP&P at either species or population level (Solís-Lemus & al., 2015; Sukumaran & Knowles, 2017).

■ TAXONOMIC CONCLUSIONS

Arthrorhaphis bullata Frisch & Y.Ohmura, **sp. nov.** – Holotype: JAPAN. Nagano Pref., Chino-city, Kita Yatsugatake Mts, Kokemomo-no-niwa, 36°03′29″N, 138°20′19″E, on mosses on rock, 2100 m, 5 Sep 2014, *Ohmura 10976* (TNS barcode TNS-L-126509!).

Diagnosis. – *Arthrorhaphis bullata* is characterised within *A. citrinella* s.l. by esorediate, distinctly convex to bullate-areolate thalli in combination with ascospores (53.0–)72.0–94.0(–102.0) × (3.5–)3.8–4.5(–5.0) µm in size.

MycoBank 842543

See Fig. 7F for an image of the species.

Description. – Thallus lichenised, forming small irregular colonies over saxicolous bryophytes or plant remains, or a juvenile parasite on unidentified squamulose lichen, up to 2 cm in diam., greenish yellow, areolate; areolae discrete to mostly confluent, irregularly rounded to elliptical to lobate, convex to distinctly bullate, 0.3–1.5 mm, matt to slightly shiny, smooth to verrucose, entire; medulla up to 0.7 mm thick, pale yellow; Ca-oxalate crystals absent. Apothecia lateral or in between the areolae, 0.5–1.1 mm, single or clustered to 2–13, adnate to shortly and broadly stipitate, black, matt, the thick margin first protruding, later level with the flat to distinctly convex, smooth to ± coarsely rugose disc. Epihymenium olive green, HNO_3 green, 12–18 µm. Hymenium unpigmented to pale olive green, densely inspersed, 110–140 µm. Subhymenium up to 250 µm, dirty to brownish olive green. Exciple 70–80 µm wide, dark dirty to brownish olive green, darker towards the outer edge. Paraphyses sparsely branched and anastomosed, 1–1.5 µm wide. Asci 100–130 × 14–17 µm. Ascospores acicular, parallel in the asci, (53.0–)72.0–94.0(–102.0) × (3.5–)3.8–4.5(–5.0) µm (n = 64; l: mean = 83.0, SD = 11.04; w: mean = 4.2, SD = 0.33), (8–)11–14(–16)-septate. Pycnidia not seen.

Chemistry. – Rhizocarpic acid (major), epanorin (minor).

Distribution and ecology. – *Arthrorhaphis bullata* is known from the mountains of central Honshu and Hokkaido in Japan, and from Primorsky Territory in eastern Russia.

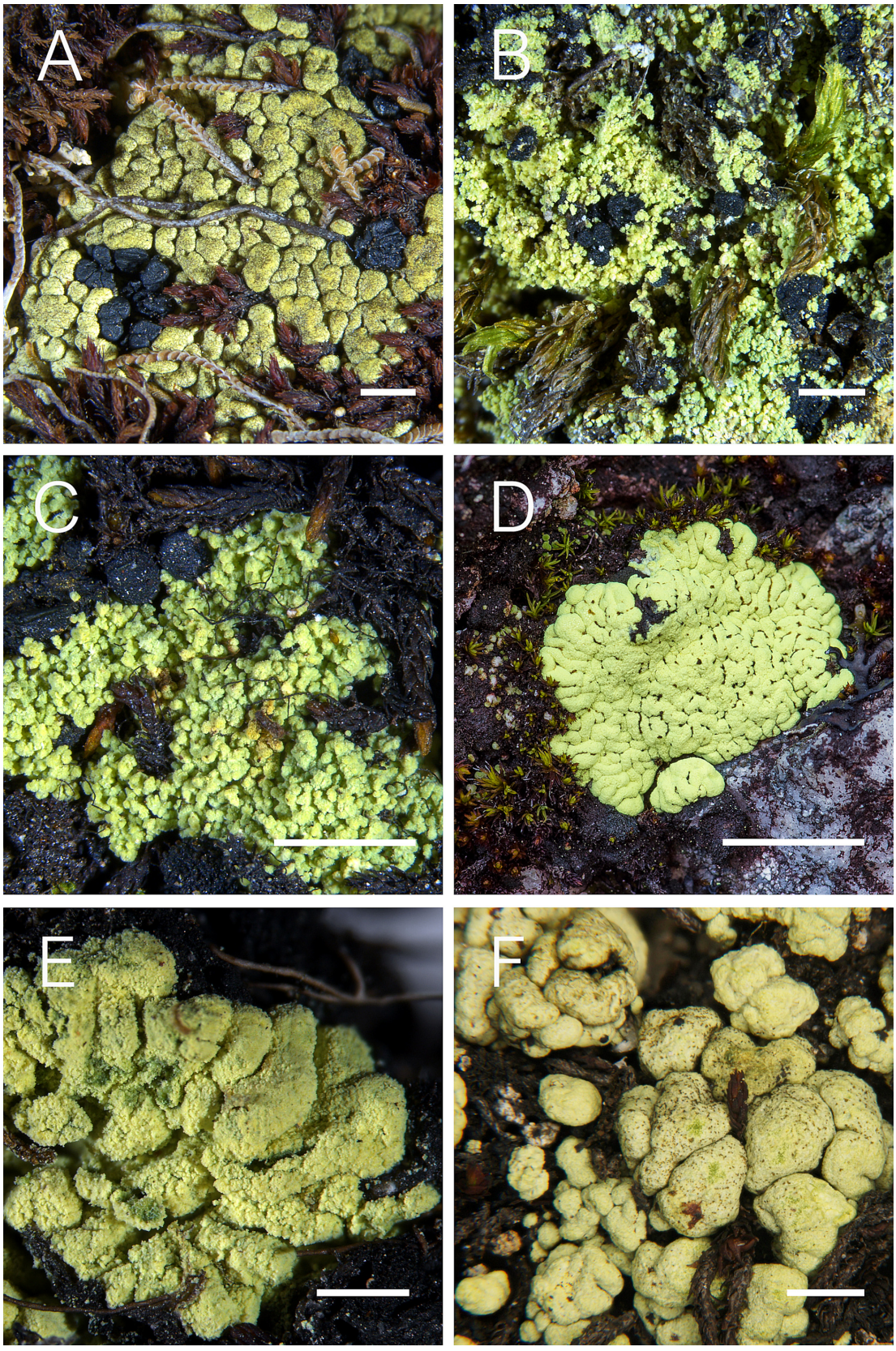

Fig. 7. A, *Arthrorhaphis catolechioides* (*Moberg & Owe-Larsson NZ2:5*, UPS); **B**, *A. citrinella* (*Odelvik 10598*, S); **C**, *A. citrinella* (*Frisch 15/No100*, TRH); **D**, *A. farinosa* (*Ohmura 9312*, TNS); **E**, *A. farinosa* (*Thor 33718*, UPS); **F**, *A. bullata* (*Ohmura 10730*, TNS). — Scale: A, B, E & F, 1 mm; C, 0.5 mm; D, 5 mm. Photos: A. Frisch.

The elevation ranges from 915 to 3000 m. *Arthrorhaphis bullata* typically grows among saxicolous acrocarpous mosses, mostly *Andreaea* spp. and Grimmiaceae, over a thin soil layer or occasionally directly on soil or rock. The species often occurs in the same localities as *A. alpina* and *A. farinosa*, and mixed collections have been seen. Juvenile parasitism on an unidentified squamulose lichen, probably the basal squamules of *Cladonia* sp., have been observed in two specimens from Honshu.

Etymology. – The name of the new species refers to the bullate, esorediate areoles that characterise the species within *Arthrorhaphis citrinella* s.l.

Notes. – *Arthrorhaphis bullata* is easily distinguished from *A. citrinella* and *A. farinosa* by the esorediate, distinctly convex to bullate-areolate thallus. Esorediate specimens of *A. vulgaris* occurring in Europe and North America may be difficult to separate in the sterile state, but the ascospores are consistently smaller, (34.0–)51.0–72.0(–89.0) × (2.0–)2.2–3.2(–3.5) µm vs (53.0–)72.0–94.0(–102.0) × (3.5–)3.8–4.5(–5.0) µm in *A. bullata*. The Australasian *A. catolechioides* differs by areolae with a smoother and shinier surface that are either hollow and folded in ridges or rest in umbrella-like fashion on black hyphal strands (Obermayer, 2001). In the absence of sequence data or well-developed ascospores, *A. bullata* can be distinguished from *A. alpina* in eastern Asia with certainty only by the absence of Ca-oxalate crystals in the medulla.

Selected specimens examined (a total of 17 specimens seen). – JAPAN. Honshu. Yamanashi Pref., Kofu-city, Mt Fuji, 35°23′11″N, 138°42′20″E, 12 Oct 2012, *Ohmura 9439* (TNS); ibid., Minami-Alps-city, Sensui Pass, 35°44′44″N, 138°14′02″E, 3 Sep 2012, *Frisch 12/Jp391* (TNS). Nagano Pref., Chino-city, Kita Yatsugatake Mts, 36°03′29″N, 138°20′19″E, 5 Sep 2014, *Ohmura 10976* (TNS); ibid., Minamisaku Distr., Kita Yatsugatake Mts, 36°02′49″N, 138°21′14″E, 15 Jun 2011, *Ohmura 8230* (TNS); ibid., Shimoina Distr., Akaishi Mts, Mt Hijiri, 29 Aug 2001, *Inoue 29671* (TNS). Fukushima Pref., Minamiaizu Distr., Mt Hiuchi, 7 Oct 2001, *Inoue 30223* (TNS). Yamagata Pref., Yuza-machi, Mt Chokai, 20–21 Aug 1984, *Inoue 16916* (TNS). Akita Pref., Sukawako–Mt Magusa–Mt Kurikoma, 22 Aug 1983, *Inoue 16735* (TNS); ibid., Moriyoshi-machi, Mt Moriyoshi, 23 Sep 1982, *Inoue 22975* (TNS). Hokkaido. Kato Distr., Kitaurimaku, Senjokuzure, 5 Jul 2014, *Kashiwadani 51466* (TNS). RUSSIA. Primorsky Territory, Partizansky Distr., c. 19 km ESE of Monakino, 43°20′43″N, 133°39′26″E, 12 Sep 2014, *Ohmura 11643* (TNS).

Arthrorhaphis catolechioides (Obermayer) Frisch, Y.Ohmura, Holien & Bendiksby, **comb. & stat. nov.** ≡ *Arthrorhaphis citrinella* var. *catolechioides* Obermayer in McCarthy, Fl. Austral. 58A: 226. 2001 – Holotype: AUSTRALIA. Tasmania, Tarn Shelf, Mt Field, 18 Dec 1971, *Bratt 71/1696* (HO n.v.).

MycoBank 842544

See Fig. 7A for an image of the species.

Notes. – For a description of this taxon, see Obermayer (2001). Our sequenced specimen agrees well with the protologue (Obermayer, 2001). The isolated position in the *Arthrorhaphis citrinella* s.l. clade (Fig. 4) warrants recognition at the species level. *Arthrorhaphis catolechioides* is currently only known from Australasia.

Specimens examined. – NEW ZEALAND. Canterbury, Arthurs Pass National Park, Temple Basin above the pass near the ski area, 6 Feb 1964, *Wetmore 12454* (MIN 872107); Wellington, Tongariro National Park, Taranaki Falls, 7 Apr 1992, *Moberg & Owe-Larsson NZ2:5* (UPS-L-106737).

Arthrorhaphis citrinella (Ach.) Poelt ≡ *Lichen citrinellus* Ach. in Kongl. Vetensk. Acad. Nya Handl. 1795: 135. 1795 – Lectotype (designated by Obermayer in Nova Hedwigia 58: 301. 1994): Suecia (H-ACH No. 262 A [barcode H9501180]!).

MycoBank 344680

See Fig. 7B,C for images of the species.

Description. – Thallus lichenised, forming small irregular colonies over saxicolous bryophytes, up to 2.5 cm in diam., often dispersed and poorly delimited, (greenish) yellow, usually entirely formed of loose, rarely compacted coralloid aggregations of coarse granular soredia, 0.05–0.15(–0.2) mm; medulla absent; Ca-oxalate crystals absent. Apothecia laterally or centrally attached to the granular thallus, more rarely separated, single or clustered to 2–8, 0.4–1.0 mm, adnate to shortly and broadly stipitate, black, matt, the thick margin first protruding, later level with the flat to distinctly convex, more or less coarsely rugose disc. Epihymenium dirty to brownish olive green, HNO_3 green, 15–25 µm. Hymenium unpigmented to pale olivish green, densely inspersed, 90–140 µm. Subhymenium 50–90 µm, dirty to brownish olive green. Exciple 55–80 µm wide, dark dirty to brownish olive green, darker towards the outer edge. Paraphyses sparsely branched and anastomosed, 1–1.5 µm wide. Asci 100–130 × 10–13 µm. Ascospores acicular, parallel in the asci, (45.0–)58.0–88.0(–102.0) × (2.0–)2.5–3.5(–4.0) µm (n = 63; l: mean = 73.1, SD = 14.72; w: mean = 2.9, SD = 0.51), (6–)7–11(–15)-septate. Pycnidia absent.

Chemistry. – Rhizocarpic acid (major), epanorin (minor).

Distribution and ecology. – *Arthrorhaphis citrinella* is common and widespread in Scandinavia. It has been further confirmed for Austria (on morphology), Iceland, and Scotland, and might be more widely distributed in the Northern Hemisphere. The elevation ranges from sea-level to 1800 m. *Arthrorhaphis citrinella* typically overgrows acrocarpous mosses (*Andreaea*, *Bryum*, *Grimmia*, *Schistidium*, *Tortula*, etc.) on exposed to shaded steep rock walls and boulders, on acidic to more basic rock types. The species has often been found associated with *Lepraria* spp., *Racodium rupestre*, and filamentous cyanobacteria (*Scytonema*). Parasitic juvenile stages on other lichens have not been observed.

Notes. – In its current narrow circumscription, *Arthrorhaphis citrinella* is characterised by rather small, poorly delimited thalli formed of loose to compacted aggregations of coarsely

granular soredia, and by the absence of parasitic stages on *Baeomyces* spp. (rarely on other lichens). Discrete areolae, which in strongly sorediate specimens of *A. vulgaris* are usually at least indicated, and a well-delimited medulla are lacking. All specimens in this study for which ecological information was available were collected from steep rock walls and siliceous boulders, overgrowing saxicolous bryophytes rather than soil. For a distinction from *A. farinosa*, see under that species.

Selected specimens examined (a total of 36 specimens seen). – AUSTRIA. Steiermark, Schladminger Tauern, Gasselhöhehütte zum Mittersee, 47°21′25″N, 13°35°45″E, 26 Aug 2001, *Obermayer 9090* (GZU). FINLAND. Uusimaa, Varttila, Kivelänkallio, Grid 27°E 6707 330, 1 Sep 1991, *Pykälä 8793* (H); Etelä-Karjala, Parikkala, Melkoniemi S, Leunanmäki, Grid 27°E 6825 624, 7 Aug 1986, *Vitikainen 11794* (H). Etelä-Savo, Sulkava, Sairalanmäki, Grid 27°E 68471 5637, 5 Aug 1986, *Vitikainen 11657* (H). GREAT BRITAIN. Scotland, VC 90, Angus, Glen Clova, Ben Reid, Jun 1954, *Duncan s.n*. (E00721892); ibid., VC 105, West Ross, Beinn Fhada, Allt a Choire Chaoil, Grid: NH 0033 2127, 28 Jul 2010, *Harrold PH10346* (E00468586). ICELAND. Austurland, S-Múlasýsla, Stöðvarfjörður, Hvalsnes, 64°49′N, 13°53′W, 10 Jul 1997, *Svane 97 SS 9745 D* (C). NORWAY. Telemark, Vinje, E of Båtstodi, UTM_{WGS84}: 32V MM 2289 2223, 1 Apr 2010, *Timdal 11259* (O-L-161820). Rogaland, Rennesøy, Helland, UTM_{WGS84}: 32V LL 096 562, 28 Mar 2011, *Johnsen s.n*. (BG-L-92402). Hordaland, Granvin, E of Havås, UTM_{WGS84}: 32V LN 72 13, 5 Oct 1994, *Ihlen 465* (BG-L-32814). Sogn og Fjordane, Aurland, Flåm, UTM_{WGS84}: 32V LN 979 486, 8 Sep 1993, *Tønsberg 19156* (BG-L-24848). Nord-Trøndelag, Steinkjer, Mokk farm, 63°58′19.50″N, 12°07′36.96″E, 4 Aug 2015, *Frisch 15/No100* (TRH-L-652426). SWEDEN. Bohuslän, Lysekil, Skaftö, Islandsberg, 29 Aug 1992, *Hafellner 30507* (GZU). Dalarna, Särna parish, Fulufjället N.P., Skärhamrarna, 61°37′14.04″N, 12°47′37.20″E, 3 Jul 2016, *Thor 33549* (UPS). Södermanland, Österhaninge parish, Tyresta National Park, Lycksjön, UTM_{WGS84}: RN 6564333 1638101, 11 Jan 2009, *Thor 23013* (UPS-L-192446).

Arthrorhaphis farinosa Frisch & Y.Ohmura, **sp. nov.** – Holotype: SWEDEN. Dalarna, Idre parish, Mt Knittarna, the diabase rock face Skäret, 61°45′38.94″N, 12°34′03.06″E, old mixed forest dominated by *Picea abies* and *Pinus sylvestris*, on boulder below the rock face, 739 m, 4 Jul 2016, *Thor 33718* (UPS!).

Diagnosis. – *Arthrorhaphis farinosa* is characterised within *A. citrinella* s.l. by the typically well-delimited, distinctly areolate thalli with finely granular to farinose surface of the areolae.

MycoBank 842545

See Fig. 7D,E for images of the type and additional material.

Description. – Thallus lichenised, forming small, typically well-delimited colonies over saxicolous bryophytes and cyanobacteria, up to 1.8 cm in diam., (greenish) yellow, areolate; areolae discrete to mostly confluent, irregularly rounded to elliptical, moderately convex to bulging, 0.5–2 mm, the surface usually completely disintegrated into finely granular to farinose soredia of 0.02–0.08 mm; medulla absent; Ca-oxalate crystals absent. Apothecia (1 specimen) between the areolae, 0.5–0.8 mm, shortly and broadly stipitate, black, matt, the thick margin level with the flat, coarsely rugose disc. Epihymenium dirty to brownish olive green, HNO_3 green, 15–25 µm. Hymenium unpigmented to pale olive green, densely inspersed, 110–120 µm. Subhymenium 40–60 µm, dirty to brownish olive green. Exciple 40–50 µm wide, dark dirty to brownish olive green, darker towards the outer edge. Paraphyses sparsely branched and anastomosed, 1–1.5 µm wide. Asci 105–120 × 10–13 µm. Ascospores acicular, parallel in the asci, 70–85 × 3.5–4.0 µm, 6–9-septate. Pycnidia absent.

Chemistry. – Rhizocarpic acid (major), epanorin (minor).

Distribution and ecology. – This species is known from the mountains of central Honshu, Hokkaido, Primorsky Territory in eastern Russia, and a restricted area of north-western Dalarna (Sweden). The elevation ranges from 590 to 740 m in Sweden, 1610 m in Russia, and 1450 to 2360 m in Japan. *Arthrorhaphis farinosa* grows on acrocarpous mosses – mostly *Andreaea* spp. and Grimmiaceae – and colonies of cyanobacteria (*Stigonema*) on exposed to shaded base- and mineral-rich rocks including diabase in boulder fields and open forests, including spruce and pine dominated forests in Sweden. The species is often associated with *Lepraria* spp. Parasitic stages on other lichens have not been observed.

Etymology. – The name of the new species refers to the finely granular to farinose thallus surface.

Notes. – *Arthrorhaphis farinosa* is a distinctive species within *A. citrinella* s.l. It is characterised by small, usually well-delimited colonies growing over saxicolous bryophytes or tufts of cyanobacteria. The thalli are formed of typically confluent, convex to bulging areolae with a soft velvety to almost mealy appearance caused by the thallus surface being dissolved into finely granular to almost farinose soredia. A well-delimited medulla and Ca-oxalate crystals have not been observed. Specimens of *A. citrinella* s.str. growing in the same locality and elsewhere are readily distinguished by often poorly delimited thalli formed of coarser granular soredia (0.05–0.15(–0.2) mm) in loose to compacted coralloid aggregations. Discrete areolae or well-delimited thalli are absent. Almost all investigated specimens of *A. farinosa* are sterile, but two apothecia were found on the holotype from Sweden. The ascospores were mostly young and only few well-developed ones have been observed. Ascomatal characters agree with the other species of *A. citrinella* s.l. and no clear differences could be observed.

Contrary to the other species in *Arthrorhaphis citrinella* s.l., *A. farinosa* has been collected on base-rich substrates including diabase and unspecified calcareous rock.

Selected specimens examined (a total of 15 specimens seen). – JAPAN. Honshu. Yamanashi Pref., Minami-Alps-city, from Kitazawa Pass to Sensui Pass, 35°44′40″N, 138°

13′38″E, 28 Jun 2012, *Ohmura 8975* (TNS). Iwate Pref., Mt Yakeishi, 26 Aug 1983, *Inoue 16652* (TNS). Akita Pref., Higashinaruse-mura, Mt Yakeishi, 11 Aug 1982, *Inoue 22978* (TNS). Hokkaido. Kato Distr., Kitaurimaku, Senjokuzure, 5 Jul 2014, *Kashiwadani 51465* (TNS). RUSSIA. Primorsky Territory, Partizansky Distr., c. 19 km ESE of Monakino, 43°20′43″N, 133°39′26″E, 12 Sep 2014, *Ohmura 11644* (TNS). SWEDEN. Dalarna, Särna parish. Fulufjället National Park, Skärhamrarna, 61°37′14.34″N, 12°47′32.64″E, 3 Jul 2016, *Thor 33526* (UPS); ibid., 61°37′12.78″N, 12°47′43.32″E, 3 Jul 2016, *Thor 33551* (UPS). Idre parish, Mt Blocktjärnåsen, Gethammaren, 61°43′41.22″N, 12°37′14.58″E, 3 Jul 2016, *Thor 33606* (UPS).

Arthrorhaphis vulgaris (Schaer.) Frisch, Y.Ohmura, Holien & Bendiksby, **comb. & stat. nov.** ≡ *Lecidea flavovirescens* var. *vulgaris* Schaer., Lich. Helv. Spic.: 162. 1833 – **Lectotype (designated here [MBT 10005504]):** SWITZERLAND. [Bern], ad sylvarum oras, *Schaerer*, *Lich. Helvet. exs. no. 204* (G!; isolectotypes: GZU n.v., M n.v., UPS!).

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= *Bacidia flavovirescens* var. *detrita* Vain. in Acta Soc. Fauna Fl. Fenn. 53(1): 223. 1922 – Lectotype (designated by Obermayer in Nova Hedwigia 58: 302. 1994): FINLANDIA. Tavastia borealis, Pihlajavesi, ad terram, 1871, *Vainio s.n*. (TUR-V No. 20972!).

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See Fig. 6F for an image of the species.

Description. – Thallus lichenised, forming small irregular colonies on acidic soils, terricolous bryophytes or plant remains, or a juvenile parasite on *Baeomyces* spp., up to 6 cm in diam., (greenish) yellow, areolate; areolae discrete to mostly confluent, irregularly rounded to elliptical to lobate, moderately to strongly convex to distinctly bullate, 0.2–1.7 mm, matt to slightly shiny, smooth to strongly verrucose, entire to cracked to ± disintegrated into fine to coarsely granular soredia of 0.03–0.15 mm; medulla up to 0.5 mm thick, yellow, often absent; Ca-oxalate crystals absent. Apothecia lateral to or in between the areolae or separate from the lichenised thallus, 0.3–1.5 mm, single or clustered to 2–15, adnate to shortly and broadly stipitate, black, matt, the thick margin first protruding, later level with the flat to distinctly convex, ± coarsely rugose disc. Epihymenium dirty to brownish olive green, HNO_3 green, 12–25 µm. Hymenium unpigmented to pale olivish green, densely inspersed, 80–130 µm. Subhymenium 40–75 µm, dirty to brownish olive green. Exciple 40–80 µm wide, dark dirty to brownish olive green, darker towards the outer edge. Paraphyses sparsely branched and anastomosed, 1–1.5 µm wide. Asci 80–115 × 10–12 µm. Ascospores acicular, parallel in the asci, (34.0–)51.0–72.0(–89.0) × (2.0–)2.2–3.2(–3.5) µm (*n* = 201; *l*: mean = 61.6, SD = 10.60; *w*: mean = 2.7, SD = 0.47), (5–)7–11(–16)-septate. Pycnidia absent.

Chemistry. – Rhizocarpic acid (major), epanorin (minor); ± stictic acid and ± norstictic acid (from the host).

Distribution and ecology. – *Arthrorhaphis vulgaris* appears to be the most common and widely distributed taxon in *A. citrinella* s.l. Specimens have been seen from across the Northern Hemisphere, including northern North America, Greenland, Iceland, Europe, and northern Siberia. The species has been found in temperate-montane to arctic-alpine regions and usually grows on bare acidic soils, among terricolous bryophytes, and over plant remains in open habitats with sparse or open vegetation such as pastures, rocky places, arctic-alpine heathlands and tundra, or road-banks. The elevation ranges from sea-level to 3000 m. Except for *A. bullata* and *A. alpina* s.l., it is the only lichenised species in the genus where juvenile parasitism on *Baeomyces* spp. (or other terricolous lichens) has been observed among the studied specimens.

Notes. – Contrary to *Arthrorhaphis citrinella* s.str., typical specimens of *A. vulgaris* have a thallus formed of compact areolae, even so the areolate thallus organisation may be obscured in strongly sorediate individuals. Such individuals may be difficult to place if poorly developed, but only few such specimens have been seen. The two species are virtually indistinguishable in characters of their ascomata, but our data indicate a small but noticeable difference in ascospore size for *A. vulgaris*, (34.0–)51.0–72.0(–89.0) × (2.0–)2.2–3.2(–3.5) µm vs (45.0–)58.0–88.0(–102.0) × (2.0–)2.5–3.5(–4.0) µm in *A. citrinella*. The variation in ascospore size, however, is pronounced within both taxa. *Arthrorhaphis citrinella*, furthermore, seems to be restricted to steep to vertical rock faces, overgrowing saxicolous bryophytes, while *A. vulgaris* is a primarily terricolous species that, however, is frequently found on rock walls and outcrops in soil filled fissures and on ledges covered by a thin soil layer.

The few specimens of "*Arthrorhaphis septentrionalis*" seen for this study do not allow for a reliable separation of this taxon from *A. vulgaris* without molecular data, particularly when Ca-oxalate crystals cannot be demonstrated in the medulla. Fertile material of "*A. septentrionalis*" differs by the much shorter ascospores located in the apical portion of the asci, but the relevance of this character is not clear and needs evaluation on a larger set of specimens.

For a separation from *Arthrorhaphis farinosa* and *A. bullata*, see under those species.

Selected specimens examined (a total of 68 specimens seen). – AUSTRIA. Kärnten, Saualpe W von Wolfsberg, 46°54′10″N, 14°39′50″N, 7 Sep 2013, *Hafellner 82296* (GZU). Salzburg, Schladminger Tauern, SSW-facing slopes of Preber, 47°12′15″N, 13°53′00″E, 17 Aug 2005, *Obermayer 10945* (GZU). Vorarlberg, Silvretta-Gruppe, Kl. Lobspitze 46°54′45″N, 10°05′30″E, 26 Aug 2008, *Hafellner 81282* (GZU). CANADA. Alberta, Jasper National Park, Bald Hills at NW end of Maligne Lake, 52°44′N, 117°40′, 2 Aug 1995, *Rosentreter 9435* (GZU). British Columbia, Wells Gray Provincial Park, Battle Mountain, 51°55′28″N, 119°53′23″W, 22 Jul 2008, *Ahti & al. 68741* (H). Newfoundland, Butterpot Provincial Park, Big Otter Pond, 47°23′56.40″N, 53°02′34.80″W, 9 Sep 2007, *Lendemer 10201* (Lichens of Eastern North America Exsiccati 275; ASU, BG, GZU, H, M, S).

GERMANY. Bavaria, Allgäuer Alpen, Sigiswanger Horn, 7 Sep 2004, *Dornes K_OA 0855* (M-0166793). Hesse. Main-Kinzig-Kreis, Sinntal, Stoppelsberg, 500–550 m, 10 Apr 1990, *Frisch 90/77* (hb. Frisch). GREENLAND. Northeast Greenland National Park, Constable Bugt, 83°34′ N, 32°01′W, 7 Aug 2007, *Hansen s.n.* (Lichenes Groenlandici Exsiccati 1031; S). Kujalleq, Narsaq community, Tugtugtooq, Sildefjord, 1 Aug 2005, *Alstrup s.n.* (C). ICELAND. Austurland, Stöðvarfjörður, Hvalsnes, Aug 1997, *Nordin 4905* (UPS). FINLAND. Uusimaa, Kirkkonummi, Porkkala, Grid 27°E 665 35, 11 Oct 1991, *Ahti 50869a & Scutari* (H). ITALY. Udine, Karnische Alpen, Mt Crostis N von Comeglians, 2240 m, 17 Aug 1994, *Hafellner 78774* (GZU). KOSOVO. Bogićevica, west of Deçan, 20°06′16″N, 42°34′28″E, 21 Aug 2012, *Mayrhofer 19361 & Zekaj* (GZU). NORWAY. Buskerud, Hol, UTM_{ED50}: MN 610 204, 19 Jul 1996, *Tønsberg 23922* (BG). Telemark, Drangedal, Henneseid Ø, UTM_{WGS84}: 32V NL 1249 4655, 23 Aug 2010, *Klepsland JK10-L248* (O). Hordaland, Odda, Sveinsgjerd, UTM_{WGS84}: 32V LM 64 54, 16 Jul 1993, *Ihlen 233* (BG). Møre og Romsdal, Tresfjord, Lindsetheiane W of Nonsfjellet, 62°27′44.40″ N, 07°07′07.38″E, 3 Jul 2015, *Frisch 15/No47* (TRH-L-652385). Nord-Trøndelag, Grong, Mt Geitfjellet, UTM_{WGS84}: 33W, UM 68 46, 26 Jul 1993, *Ihlen 379* (BG-L-15726). Troms, Storfjord, S of Lávkajárvi, c. 500 m N of Skurcojohka, UTM_{WGS84}: DB 794-798 785-790, 8 Aug 2003, *Lindblom 1243* (BG). Finnmark, Porsanger, Luovosvarre, 10 km SE of Skoganvarre, 16 Aug 1967, *Vitikainen 3295* (H). RUSSIA. Murmansk, Podpakta Bay, 29 Jun 2010, *Konoreva s.n.* (H). Komi, Vorkuta, Paga river, 66°22′00.12″N, 62°52′00.12″E, 26 Jun 2007, *Hermansson 15589c* (UPS). Krasnoyarsk, Taimyr Peninsula, c. 8 km W of urochishche Belyi Yar, 70°05′ N, 87°43′E, 7 Aug 1999, *L. Zanokha s.n.* (M). SLOVAKIA. In monte Beniška supra transitum Čertovica 27 Aug 1985, *Farkas & Vězda s.n.* (BG). SLOVENIA. Pohorje, Gipfelplateau des Črni vrh SW Ribniča na Pohorju, 18 Jun 1991, *Mayrhofer & al. 10047* (GZU). SWEDEN. Gästrikland, Torsåker parish, 3100 m SO om Torsåkers kyrka, 60°29′32.90″N, 16° 30′53.00″E, 23 May 2009, *Hellström 9262* (S). Jämtland, Kall parish, Bjelkes copper mines, 63°27′55.80″N, 13°05′48.87″E, 30 Aug 2014, *Nordin 7674* (UPS). Lycksele Lappmark, Sorsele parish, Vuornavagge, 66°02′N, 16°11′E, 4 Jul 2003, *Ihlen 1298* (UPS). SWITZERLAND. Bern, Berner Alps, Grimselpass, 46°33′35″N, 08°19′40″E, 24 Aug 2006, *Hafellner 69409* (GZU). Graubünden, Urner Alps, Gotthard group, Oberalppass, 46°39′20″N, 08°40′15″E, 23 Aug 2006, *Hafellner 75549* (GZU). Valaise, Bagnes, Pte du Parc, 583.990, 094.084, 14 Aug 2008, *Vust 951* (G). UNITED STATES OF AMERICA. Alaska, Kenai Peninsula Borough, along Lost Lake Trail, 60° 14′20″N, 149°25′40″W, 28 Aug 2010, *Hafellner 79990* (GZU). Maine. Washington Co., Steuben, Dyer Neck, Eagle Hill, Humboldt Field Research Institute, 44°27′29″N, 67°55′ 29–54″W, 7 Jul 2008, *Harris 54722* (NY).

Artificial key to the genus *Arthrorhaphis*. — The morphologically poorly characterised "*Arthrorhaphis septentrionalis*" (Fig. 8F) and *Arthrorhaphis* sp. 1 are not included in the key. Characters for the parasitic species have been compiled from Obermayer (1994), Santesson & Tønsberg (1994), Kocourková & Van den Boom (2005), and Etayo (2017).

1. Lichenised thallus absent; species strictly lichenicolous 2
1. Lichenised thallus present; lichenicolous stages present or absent 7
2. On the thallus of foliose or squamulose lichens 3
2. On the thallus of crustose lichens 6
3. Causing aeruginose discolouration of the host thallus; on squamules and podetia of *Cladonia* spp. ..... ***A. aeruginosa*** (Fig. 6A)
3. Aeruginose discolouration of the host thallus absent; on other lichens 4
4. Asci predominantly 4-spored; hymenium 110–150 µm; on *Phyllobaeis imbricata* ..... ***A. phyllobaeis***
4. Asci predominantly 6- or 8-spored; hymenium ≥150 µm; on other lichens 5
5. Asci predominantly 6-spored; hymenium 200–250 µm; on *Arctoparmelia incurva* ... ***A. arctoparmeliae*** (Fig. 6B)
5. Asci 8-spored; hymenium 150–180 µm; on *Melanohalea olivacea* ..... ***A. olivaceae*** (Fig. 6C)
6. Hymenium (except epihymenium) ± clear; ascospores 3.5–4.5(–5) µm wide, 10–15-septate; on *Dibaeis baeomyces* ..... ***A. muddii*** (Fig. 6D)
6. Hymenium strongly inspersed; ascospores 2.5–3.5 (–4.5) µm wide, 7–9(13)-septate; on *Baeomyces rufus* ..... ***A. grisea*** (Fig. 6E)
7. Ascospores of the alpina, jungens or vacillans type; Ca-oxalate crystals in the medulla usually present 8
7. Ascospores of the citrinella type; Ca-oxalate crystals absent in the medulla or beneath the soredia (*A. citrinella* s.l.) 10
8. Ascospores (vacillans type); soredia absent ..... ***A. vacillans***
8. Ascospores of the alpina or jungens type; soredia present or absent 9
9. Ascospores alpina type ..... ***A. alpina* var. *alpina* s.l.** (Fig. 8A,C,E)
9. Ascospores jungens type ..... ***A. alpina* var. *jungens* s.l.** (Fig. 8B,D)
10. Soredia or granules absent; thallus distinctly bullate-areolate; parasitic stages absent 11
10. Soredia or granules present (occasionally indistinct); thallus areolae present or absent; parasitic stages present or absent 12
11. Thallus surface ± smooth and shiny; areolae folded in ridges and with central cavity or resting in umbrella-like fashion on black hyphal strands; Australasia ..... ***A. catolechioides*** (Fig. 7A)
11. Thallus surface ± verrucose, matt to slightly shiny; areolae convex to distinctly bullate, not folded in ridges; pale yellow medulla present; East Asia ... ***A. bullata*** (Fig. 7F)
12. Thallus forming small compact colonies on saxicolous bryophytes and cyanobacteria; thallus surface entirely disintegrated into finely granular to farinose soredia;

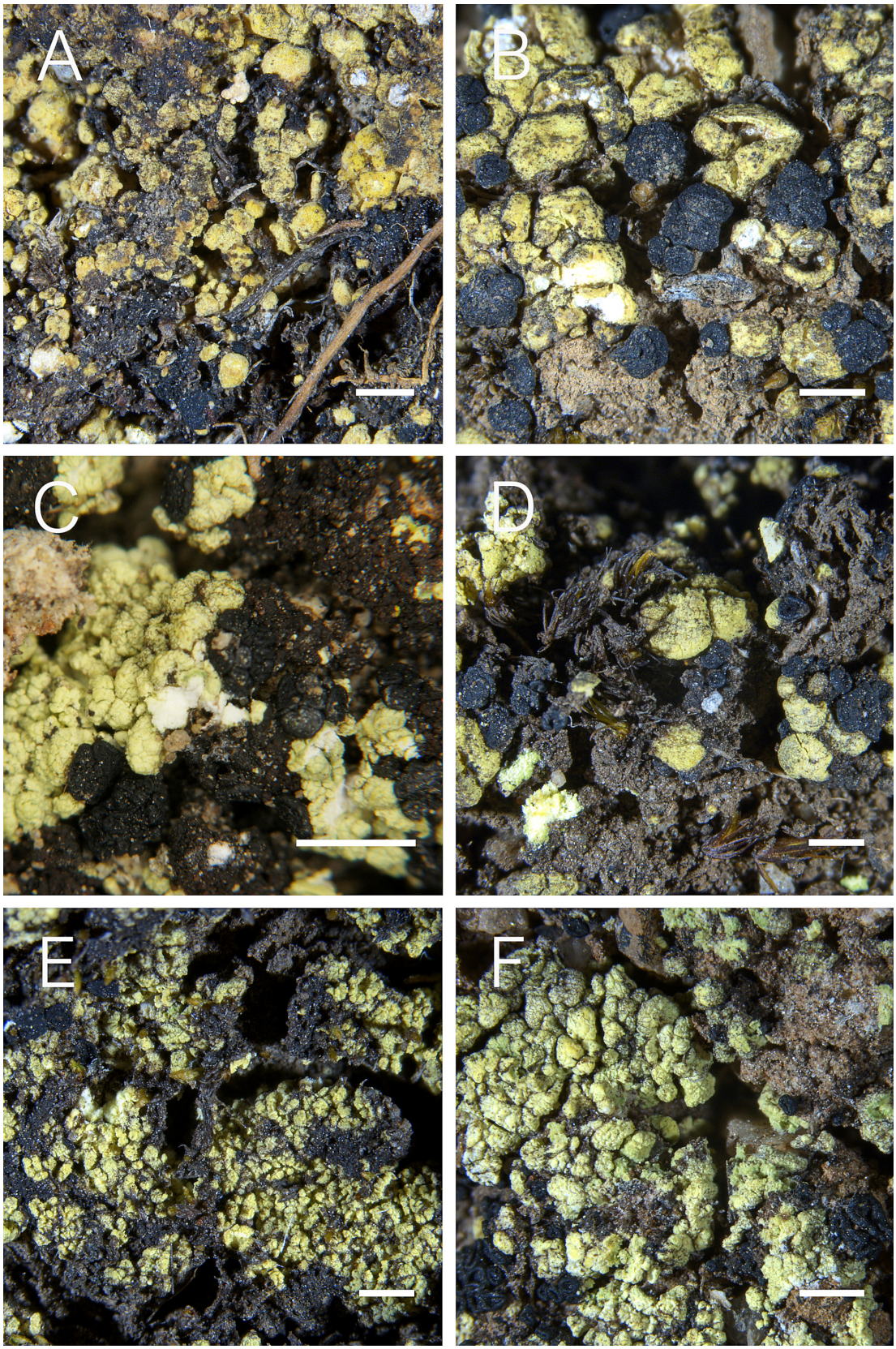

Fig. 8. A, *Arthrorhaphis alpina* (Schaer., Lichenes Helvetici Exsiccati 532, G, lectotype); **B**, *A. alpina* var. *jungens* (Lichenotheca Graecensis 23, E, isotype); **C**, *A. alpina* (*Ohmura 10119*, TNS); **D**, *A. alpina* var. *jungens* (Kalb, Lichenes Neotropici 577, M); **E**, *A. alpina* (*Brusse 4515*, UPS); **F**, "*A. septentrionalis*" (*Hansen 026*, C). — Scale: A–F, 1 mm. Photos: A. Frisch.

parasitic stages absent; East Asia and Scandinavia ....***A. farinosa*** (Fig. 7D,E)

12. Thallus otherwise; parasitic stages present or absent 13
13. Thallus entirely of small loose to compact aggregations of granular soredia on saxicolous bryophytes; parasitic stages absent; Europe and Iceland..... .....***A. citrinella*** (Fig. 7B,C)

13. Thallus of discrete to confluent areolae on soil, terricolous bryophytes and plant remains, or parasitic on *Baeomyces* spp. (rarely on other terricolous lichens); areolae breaking into soredia, rarely completely disintegrated or esorediate; widespread in the Northern Hemisphere..... ..... ***A. vulgaris*** (Fig. 6F)

■ CONCLUSIONS

The present study contributes significantly to our current understanding of the genus *Arthrorhaphis*. The molecular phylogenetic results support *Arthrorhaphis* as a monophyletic genus that belongs in the Ostropomycetidae. The genus accommodates both lichenicolous and lichenised taxa. The hypothesis that the diversification of the lichenised species was triggered by the transition to a lichenised life strategy needs further testing.

Our data show that the marked morphological heterogeneity observed in the lichenised *Arthrorhaphis* species is paralleled by a strong genetic diversification within previously accepted taxa. At least five morphologically and genetically distinct species have been recognised within *Arthrorhaphis citrinella* s.l., while *A. alpina* s.l. could not be fully resolved. A strong geographic signal is evident in *A. alpina* s.l., with distinct geographically defined populations recovered for the Arctic, tropical Africa (incl. the western Indian Ocean), and the Neotropics.

Our multispecies coalescence species delimitation analyses, based on single-locus (bGMYC) and multilocus (bPtP, bP&P) datasets, are largely congruent with our species hypotheses based on the combined phylogenetic and morphological data. They cannot, however, unequivocally clarify the molecular structure observed in *Arthrorhaphis alpina* s.l. as either representing additional species or spatial geographic variation at population level. Both an extended taxon sampling as well as additional molecular markers are probably needed for solving the complex phylogenetic structure of *A. alpina* s.l., mainly in central Asia, Africa, and the Neotropics. Nevertheless, with the well-founded taxonomic updates provided herein, which include both recombinations and new species, we are considerably closer to a natural classification of the genus. Our artificial key that follows our updated taxonomy of *Arthrorhaphis* will hopefully be helpful to the users.

■ AUTHOR CONTRIBUTIONS

MB, AF, and HH designed the study. AF further developed the design of the study and had a principal role in the following tasks: molecular and morphological data production, molecular analyses, species descriptions, and manuscript writing. HH and YO contributed substantially to the morphological data acquisition and material for sequencing. YO further contributed to the molecular data production and species descriptions. MB contributed to the molecular analyses, interpretation of data, and dissemination of results. All co-authors contributed to the manuscript and revised it critically. All authors have read and approved the final version of the manuscript and agreed to be accountable for all aspects of the work. AF, https://orcid.org/0000-0003-3521-9312; YO, https://orcid.org/0000-0003-2557-2761; HH, https://orcid.org/0000-0003-3913-4746; MB, https://orcid.org/0000-0002-7534-6466.

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Appendix 1. List of specimens included in the phylogenetic analyses, their voucher information and corresponding GenBank accession numbers.

Information is presented in the following order and format: ***Taxon***; Sequence-ID, *Voucher* (Institution), Country, mrSSU, nLSU, ITS, *RPB1* (* indicates sequences obtained in this study; – indicates missing sequences).

Arthrorhaphis aeruginosa R.Sant. & Tønsberg; Ph1, *Frisch 17/No127* (TRH), Norway, OL895459*, OL895652*, OL895799*, –; Ph2, *Frisch 17/No128* (TRH), Norway, OL895460*, OL895653*, OL895800*, –. ***Arthrorhaphis alpina*** (Schaer.) R.Sant.; TRH085, *Holien 13183* (TRH), Norway, OL895374*, OL895573*, OL895717*, OL896832*; TRH122, *Nordin 7305* (UPS), Sweden, OL895368*, OL895567*, OL895711*, OL896826*; TRH126, *Nordin 4486* (UPS), South Africa, OL895414*, OL895614*, OL895758*, OL896871*; TRH127, *Nordin 3786* (UPS), Mexico, OL895412*, OL895612*, OL895756*, OL896869*; TRH129, *Tibell 22025* (UPS), India, OL895432*, OL895633*, OL895773*, OL896882*; TRH130, *Bendiksby & al. 12448* (O), Norway, OL895369*, OL895568*, OL895712*, OL896827*; TRH131, *Klepsland JK10-L327* (O), Norway, OL895366*, –, OL895709*, OL896824*; TRH132, *Breili L3810* (O), Norway, OL895372*, OL895571*, OL895715*, OL896830*; TRH133, *Lich. Groenl. Exs. 1031* (O), Greenland, OL895433*, OL895634*, OL895774*, OL896883*; TRH134, *Timdal 10629* (O), Norway, OL895367*, OL895566*, OL895710*, OL896825*; TRH135, *Løfall & al. Bpl-L11028* (O), Norway, OL895373*, OL895572*, OL895716*, OL896831*; TRH142, *Lich. Groenl. Exs. 981* (O), Greenland, OL895423*, OL895623*, –, OL896875*; TRH143, *Brusse 4515* (O), South Africa, OL895416*, OL895616*, OL895760*, OL896873*; TRH146, *Buck 44215* (NY), Costa Rica, OL895409*, OL895609*, OL895753*, OL896866*; TRH152, *Vust s.n.* (G), Switzerland OL895426*, OL895626*, OL895768*, –; TRH175, *Harrold PH10156* (E), Scotland, –, OL895627*, –, OL896877*; TRH195, *Nash III 35812* (ASU), Mexico, OL895408*, OL895608*, OL895752*, OL896865*; TRH218, *Ahti 63787* (H), U.S.A., OL895404*, OL895602*, OL895746*, OL896859*; TRH220, *Ahti 54867* (H), Iceland, OL895371*, OL895570*, OL895714*, OL896829*; TRH221, *Poulsen 1005* (H), Kerguelen, OL895415*, OL895615*, OL895759*, OL896872*; TRH222, *Ahti 65577* (H), Russia, OL895403*, OL895601*, OL895745*, OL896858*; TRH238, *Matveeva s.n.* (M), Russia, OL895425*, OL895625*, OL895767*, OL896876*; TRH240, *Triebel & Rambold 6964* (M), South Africa, OL895417*, OL895617*, OL895761*, –; TRH241, *Harris 16085* (M), Dominican Republic, OL895411*, OL895611*, OL895755*, OL896868*; TRH245, *Santesson 29452* (UPS), Venezuela, OL895410*, OL895610*, OL895754*, OL896867*; TRH248, *Tibell 17732* (UPS), Chile, OL895434*, OL895635*, OL895775*, –; TRH249, *Brusse 4515* (O), South Africa, OL895419*, OL895619*, OL895763*, –; TRH250, *Santesson 21200* (UPS), Tanzania, OL895418*, OL895618, OL895762*, –; TRH257, *Frisch 15/No67 a* (TRH), Norway, OL895348*, OL895546*, OL895687*, OL896804*; TRH258, Frisch *15/No67 b* (TRH), Norway, OL895370*, OL895569*, OL895713*, OL896828*; TRH263, *Søchting 9726* (C), Reunion, OL895413*, OL895613*, OL895757*, OL896870*; TRH269, *Svane 97 SS 9745 D* (C), Iceland, OL895424*, OL895624*, OL895766*, –; TRH272, *Hansen 26* (C), Greenland, OL895349*, OL895547*, OL895688*, OL896805*; TRH277, *Hafellner & Wittmann 38125* (GZU), Austria, OL895429*, OL895660*, OL895770*, –; TRH289, *Sebernegg & Mayrhofer s.n.* (GZU), Austria, OL895427*, OL895628*, OL895769*, OL896878*; TRH290, *Obermayer 11408* (GZU), Austria, OL895428*, OL895629*, –, OL896879*; TRH291, *Hafellner & Miadlikowska 59127* (GZU), Austria, OL895430*, OL895631*, OL895771*, OL896880*; TRH292, *Hafellner 81242* (GZU), Austria, OL895431*, OL895632*, OL895772*, OL896881*; TRH293, *Hafellner 72328* (GZU), Austria, OL895446*, OL895643*, –, OL896891*; TRH294, *Obermayer 4107* (GZU), China, OL895435*, OL895636*, –, OL896884*; TRH296, *Obermayer 4105* (GZU), China, OL895445*, OL895642*, OL895786*, OL896890*; TRH297, *Obermayer 4111* (GZU), China, OL895447*, –, OL895787*, –; TRH331, *Timdal CHO04/01* (O), China, OL895361*, OL895561*, OL895703*, OL896819*; YO10119, *Ohmura 10119* (TNS), Russia, OL895406*, OL895604*, OL895748*, OL896861*; YO10543, *Ohmura 10543* (TNS), Japan, OL895405*, OL895603*, –, OL896860*. ***Arthrorhaphis arctoparmeliae*** Kocourk. & van den Boom; TRH158, *Kocourková JK6498* (PRM), Czech Republic, OL895461*, –, OL895803*, –. ***Arthrorhaphis bullata*** Frisch & Y.Ohmura; AF12Jp391, *Frisch 12/Jp391* (TNS), Japan, –, –, OL895704*, –; HK51466, *Kashiwadani 51466* (TNS), Japan, OL895364*, OL895564*, OL895707*, OL896822*; YO10730, *Ohmura 10730* (TNS), Japan, OL895362*, OL895562*, OL895705*, OL896820*; YO10731, *Ohmura 10731* (TNS), Japan, OL895363*, OL895563*, OL895706*, OL896821*; YO9265, *Ohmura 9265* (TNS), Japan, OL895365*, OL895565*, OL895708*, OL896823*. ***Arthrorhaphis catolechioides*** (Obermayer) Frisch, Y.Ohmura, Holien & Bendiksby; TRH244, *Moberg & Owe-Larsson NZ2:5* (UPS), New Zealand, –, OL895605*, OL895749*, OL896862*. ***Arthrorhaphis citrinella*** (Ach.) Poelt; TRH099, *Holien 3442* (TRH), Norway, OL895346*, OL895544*, OL895685*, OL896802*; TRH100, *Holien 418-80* (TRH), Norway, OL895396*, OL895594*, OL895738*, –; TRH101, *Holien 296-80* (TRH), Norway, OL895397*, OL895595*, OL895739*, –; TRH138, *Timdal 11851* (O), Norway, OL895347*, OL895545*, OL895686*, OL896803*; TRH174, *Harrold PH10346* (E), Scotland, OL895398*, OL895596*, OL895740*, OL896853*; TRH177, *Odelvik 10598* (S), Sweden, OL895343*, OL895541*, OL895682*, OL896799*; TRH210, *Johnsen s.n.* (BG), Norway, OL895400*, OL895598*, OL895742*, OL896855*; TRH224, *Pykälä 9911* (H), Finland, OL895399*, OL895597*, OL895741*, OL896854*; TRH227, *Pykälä 8793* (H), Finland, OL895401*, OL895599*, OL895743*, OL896856*; TRH256, *Frisch 15/No100* (TRH), Norway, OL895345*, OL895543*, OL895684*, OL896801*; TRH268, *Svane 97 SS 9745 D* (C), Iceland, OL895344*, OL895542*, OL895683*, OL896800*; TRH316, *Holien 14932* (TRH), Norway, OL895402*, OL895600*, OL895744*, OL896857*. ***Arthrorhaphis farinosa*** Frisch & Y.Ohmura*; AF12Jp392, *Frisch 12/Jp392* (TNS), Japan, –, –, OL895690*, –; HK51465, *Kashiwadani 51465* (TNS), Japan, OL895352*, OL895550*, OL895692*, OL896808*; TRH243, *Thor 16012* (UPS), Sweden, OL895354*, OL895552*, OL895694*, OL896810*; TRH323, *Thor 33718* (UPS), Sweden, OL895355*, OL895553*, OL895695*, OL896811*; TRH324, *Thor 33589* (UPS), Sweden, –, OL895554*, OL895696*, OL896812*; TRH326, *Thor 33557* (UPS), Sweden, OL895356*, OL895556*, OL895698*, OL896813*; TRH327, *Thor 33606* (UPS), Sweden, OL895358*, –, –, OL896816*; TRH328, *Thor 33580* (UPS), Sweden, –, OL895555*, OL895697*, –; TRH329, *Thor 33551* (UPS), Sweden, OL895357*, OL895558*, OL895700*, OL896815*; TRH330, *Thor 33506* (UPS), Sweden, –, OL895557*, OL895699*, OL896814*; YO9266, *Ohmura 9266* (TNS), Japan, OL895353*, OL895551*, OL895693*, OL896809*; YO9312, *Ohmura 9312* (TNS), Japan, OL895351*, OL895549*, OL895691, OL896807*. ***Arthrorhaphis grisea*** Th.Fr.; TRH 089, *Holien 8789* (TRH), Norway, OL895378*, OL895577*, OL895721*, OL896836*; TRH090, *Holien 10029* (TRH), Norway, OL895379*, OL895578*, OL895722*, OL896837*; TRH144, *Timdal 12808* (O), Norway, OL895376*, OL895575*, OL895719*, OL896834*; TRH145, *Klepsland JK11-L476* (O), Norway, OL895377*, OL895576*, OL895720*, OL896835*; TRH161, *Hafellner 71561* (M), Austria, OL895457*, OL895650*, OL895797*, OL896896*;

Appendix 1. Continued.

TRH169, *Hafellner 71561* (M), Austria, OL895458*, OL895651*, OL895798*, OL896897*; TRH315, *Holien 14933* (TRH), Norway, OL895456*, OL895649*, OL895796*, –. ***Arthrorhaphis alpina* var. *jungens*** Obermayer & Poelt; TRH170, *Obermayer 3020* (E), China, OL895453*, OL895646*, OL895793*, –; TRH171, *Sharma & al. L1* (E), Nepal, OL895375*, OL895574*, OL895718*, OL896833*; TRH235, *Lich. Neotropici 577* (M), Venezuela, OL895421*, OL895621*, OL895764*, –; TRH279, *Obermayer 3489* (GZU), China, OL895452*, OL895645*, OL895792*, OL896894*; TRH282, *Obermayer 3061* (GZU), China, OL895450*, –, OL895790*, OL896892*; TRH283, *Obermayer 4108* (GZU), China, OL895449*, –, OL895789*, –; TRH285, *Obermayer 2921* (GZU), China, OL895420*, OL895620*, –, OL896874*; TRH286, *Poelt N86-L1322* (GZU), Nepal, OL895444*, –, OL895785*, –; TRH287, *G. & S. Miehe 13227a* (GZU), Nepal, OL895443*, –, OL895784*, –; TRH295, *Obermayer 4112* (GZU), China, OL895451*, OL895644*, OL895791*, OL896893*; TRH299, *Poelt K91-489* (GZU), Pakistan, OL895448*, –, OL895788*, –; TRH300, *Lich. Neotropici 577* (GZU), Venezuela, OL895422*, OL895622*, OL895765*, –. ***Arthrorhaphis muddii*** Obermayer; TRH159, *Palice s.n.* (PRM), Czech Republic, OL895455*, OL895648*, OL895795*, –; TRH313, *Frisch 15/No120* (TRH), Norway, OL895454*, OL895647*, OL895794*, OL896895*. ***Arthrorhaphis olivaceae*** R.Sant. & Tønsberg; AS126, *Suija 126* (TU), Estland, –, OL895654*, OL895801*, –; TRH260, *Alstrup s.n.* (C), Greenland, –, OL895655*, OL895802*, –. ***Arthrorhaphis* sp. 1**; TRH183, *Tehler & Thor P93:92* (S), Peru, –, OL895607*, OL895751*, OL896864*; TRH200, *Nash III 35705* (ASU), Mexico, OL895407*, OL895606*, OL895750*, OL896863*. ***Arthrorhaphis vacillans*** Th.Fr. & Almq.; TRH128, *Obermayer 09691* (UPS), China, OL895442*, OL895641*, OL895782*, OL896889*; TRH162, *Walker s.n.* (M), Russia, OL895436*, OL895637*, –, OL896885*; TRH163, *Matveeva s.n.* (H), Russia, OL895437*, OL895638*, OL895776*, –; TRH232, *Matveeva s.n.* (M), Russia, OL895440*, OL895639*, OL895779*, OL896887*; TRH236, *Dupla Graecensia Lich. 210* (M), Tibet, OL895441*, OL895640*, OL895780*, OL896888*; TRH276, *Hafellner 46885* (GZU), Austria, OL895438*, –, OL895777*, –; TRH278, *Hafellner 33278* (GZU), Austria, OL895439*, –, OL895778*, OL896886*; TRH280, *Obermayer 4102* (GZU), China, –, –, OL895781*, –; TRH298, *Obermayer 8261* (GZU), China, –, –, OL895783*, –. ***Arthrorhaphis vulgaris*** (Schar.) Frisch, Y.Ohmura, Holien & Bendiksby; Ihlen1372, *Ihlen 1372* (UPS), Sweden, AY853309, AY853357, –, –; Nordin4905, *Nordin 4905* (UPS), Iceland, AY853308, AY853356, –, DQ915592; TRH086, *Holien 11481* (TRH), Norway, OL895341*, OL895539*, OL895680*, OL896797*; TRH088, *Holien 7611* (TRH), Norway, OL895340*, OL895538*, OL895679*, OL896796*; TRH097, *Holien 10028* (TRH), Norway, OL895321*, OL895519*, OL895660*, OL896777*; TRH098, *Holien 8130a* (TRH), Norway, OL895388*, OL895587*, OL895730*, OL896846*; TRH124, *Nordin 7674* (UPS), Sweden, OL895319*, –, OL895658*, OL896775*; TRH125, *Hermansson 15589 c* (UPS), Russia, OL895331*, OL895529*, OL895670*, OL896787*; TRH136, *Timdal 9134* (O), Norway, OL895335*, OL895533*, OL895674*, OL896791*; TRH137, *Bendiksby & al. 12867* (O), Norway, OL895322*, OL895520*, OL895661*, OL896778*; TRH139, *Klepsland JK10-L248* (O), Norway, OL895333*, OL895531*, OL895672*, OL896789*; TRH140, *Haugan 7753* (O), Norway, OL895381*, OL895580*, OL895724*, OL896839*; TRH141, *Haugan 1665* (O), Norway, OL895320*, OL895518*, OL895659*, OL896776*; TRH147, *Harris 54722* (NY), U.S.A., OL895330*, OL895528*, OL895669*, OL896786*; TRH148, *Lich. East. N. Amer. 275* (NY), Canada, OL895318*, OL895517*, OL895657*, OL896774*; TRH160, *Kocourková & Kocourek 2155* (PRM), Czech Republic, OL895383*, OL895582*, OL895725*, OL896841*; TRH164, *Frisch 15/No40* (TRH), Norway, OL895317*, OL895516*, OL895656*, OL896773*; TRH176, *Odelvik & Hellström 09262* (S), Sweden, OL895323*, OL895521*, OL895662*, OL896779*; TRH178, *Lich. Groenl. Exs. 1031* (S), Greenland, OL895332*, OL895530*, OL895671*, OL896788*; TRH191, *Obermayer 2216* (MIN), Austria, OL895385*, OL895584*, OL895727*, OL896843*; TRH199, *Lich. East. N. Amer. 275* (ASU), Canada, OL895380*, OL895579*, OL895723*, OL896838*; TRH203, *Björk 12042* (BC), Canada, OL895382*, OL895581*, –, OL896840*; TRH204, *Björk 12908* (BC), Canada, OL895327*, OL895525*, OL895666*, OL896783*; TRH205, *Björk 19539* (BC), Canada, OL895328*, OL895526*, OL895667*, OL896784*; TRH208, *Tønsberg 43760* (BG), U.S.A., OL895329*, OL895527*, OL895668*, OL896785*; TRH214, *Frisch 15/No47 dpl.* (TRH), Norway, OL895324*, OL895522*, OL895663*, OL896780*; TRH215, *Frisch 15/No45* (TRH), Norway, OL895325*, OL895523*, OL895664*, OL896781*; TRH223, *Ahti 68741* (H), Canada, OL895334*, OL895532*, OL895673*, OL896790*; TRH225, *Konoreva s.n.* (H), Russia, OL895326*, OL895524*, OL895665*, OL896782*; TRH226, *Konoreva s.n.* (H), Russia, OL895350*, OL895548*, OL895689*, OL896806*; TRH228, *Skytén 5722* (H), Finland, OL895387*, OL895586*, OL895729*, OL896845*; TRH233, *Dupla Graecensia Lich. 337* (M), Austria, OL895384*, OL895583*, OL895726*, OL896842*; TRH234, *Zanokha s.n.* (M), Russia, OL895386*, OL895585*, OL895728*, OL896844*; TRH237, *Matveeva s.n.* (M), Russia, –, OL895534*, OL895675*, OL896792*; TRH259, *Frisch 15/No65* (TRH), Norway, OL895339*, OL895537*, OL895678*, OL896795*; TRH264, *Alstrup s.n.* (C), Greenland, OL895337*, OL895535*, OL895676, OL896793*; TRH267, *Hansen 289* (C), Greenland, OL895338*, OL895536*, OL895677*, OL896794*; TRH273, *Frisch 15/No122* (TRH), Norway, OL895342*, OL895540*, OL895681*, OL896798*; TRH305, *G. & S. Miehe 8683 a* (GZU), Nepal, –, –, OL895747*, –; TRH306, *Hafellner & al. 79990* (GZU), Alaska, OL895389*, OL895588*, OL895731*, –; TRH307, *Hafellner 82296* (GZU), Austria, OL895390*, OL895589*, OL895732*, OL896847*; TRH308, *Hafellner 81282* (GZU), Austria, OL895391*, OL895590*, OL895733*, OL896848*; TRH309, *Hafellner 82100* (GZU), Austria, OL895392*, OL895591*, OL895734*, OL896849*; TRH310, *Mayrhofer 19361* (GZU), Kosovo, OL895393*, OL895592*, OL895735*, OL896850*; TRH311, *Hafellner 69409* (GZU), Switzerland, OL895395*, –, OL895737*, OL896852*; TRH312, *Mayrhofer 16027* (GZU), Slovenia, OL895394*, OL895593*, OL895736*, OL896851*; TRH333, *Rui & Timdal 16114* (O), Switzerland, OL895359*, OL895559*, OL895701*, OL896817*; TRH334, *Breili L4387* (O), Norway, OL895360*, OL895560*, OL895702*, OL896818*. ***Absconditella sphagnorum*** Vězda & Poelt; –, –, –, EU940247, EU940095, –, –. ***Acarospora laqueata*** (Stizenb.) Stizenb.; –, –, –, DQ991757, AY640943, –, DQ782860. ***Agyrium rufum*** (Pers.) Fr.; –, –, –, EF581823, EF581826, –, EF581822. ***Ainoa mooreana*** (Carroll) Lumbsch & I.Schmitt; –, –, –, AY212850, AY212828, –, DQ870928. ***Anzina carneonivea*** (Anzi) Scheid.; –, –, –, AY212851, AY212829, –, AF274077. ***Arctomia borbonica*** Magain & Sérus.; –, –, –, JX030033, JX030031, –, JX030035. ***Aspicilia caesiocinerea*** (Nyl. ex Malbr.) Arnold; –, –, –, DQ986892, DQ986778, –, DQ986851. ***Baeomyces placophyllus*** Ach.; –, –, –, AY300878, AF356658, –, DQ870936. ***Baeomyces rufus*** (Huds.) Rebent.; –, –, –, KJ766359, KJ766532, –, KJ766837. ***Botryotinia fuckeliana*** (de Bary) Whetzel; –, –, –, AY544732, AY544651, –, DQ471116. ***Candelaria concolor*** (Dicks.) Stein; –, –, –, DQ986806, DQ986791, –, –. ***Candelariella reflexa*** (Nyl.) Lettau; –, –, –, DQ912272, DQ912331, –, DQ912354. ***Catolechia wahlenbergii*** (Ach.) Flot.; –, –, –, KJ766370, KJ766542, –, KJ766845. ***Collema subconveniens*** Nyl.; –, –, –, KJ766379, KJ766547, –, KJ766848. ***Cryptodiscus gloeocapsa*** (Nitschke ex Arnold) Baloch, Gilenstam & Wedin; –, –, –, FJ904696, –, –, KC191651. ***Diploschistes scruposus*** (Schreb.) Norman; –, –, –, KF688501, KF688489, –, KF688515. ***Fissurina insidiosa*** C.Knight & Mitt.; –, –, –, DQ972995, DQ973045, –, KJ766924. ***Fissurina* sp. AFTOL 2101**; –, –, –, KJ766393, KJ766560, –, KJ766853. ***Glyphis cicatricosa*** Ach.; –, –, –, HQ639610, HQ639630, –, KC020296. ***Graphis scripta*** (L.) Ach.; –, –, –, AY853322, AY853370, –, DQ870947. ***Gyalecta friesii*** Flot. ex Körb.; –, –, –, KJ766400, KJ766566, –, KJ766854. ***Gyalecta jenensis*** (Batsch) Zahlbr.; –, –, –, KR017330, KR017187, –, KR017455. ***Hymenelia epulotica*** (Ach.) Lutzoni; –, –, –, KJ766404, KJ766569, –, KJ766826. ***Hymenelia lacustris*** (With.) M.Choisy; –, –, –, AY853323, AY853371, –, –. ***Hypocenomyce scalaris*** (Ach. ex Lilj.) M.Choisy; –, –, –, DQ912274, DQ782914, –, DQ782854. ***Lecidea fuscoatra*** (L.) Ach.; –, –, –, DQ912275, DQ912332, –, DQ912355. ***Lecidea plana*** Kremp.; –, –, –, KJ766423, KJ766587, –, –. ***Lecidoma demissum*** (Rutstr.) Gotth.Schneid. & Hertel; –, –, –, DQ986881, DQ986759, –, –. ***Lepra amara*** (Ach.) Hafellner; –, –, –, –, JN941357, –, JN992650. ***Leptogium azureum*** (Sw.) Mont.; –, –, –, KJ766427, KJ766594, –, KJ766868. ***Lobaria anomala*** (Brodo & Ahti) T.Spribille & McCune; –, –, –, DQ912298, DQ883794, –, DQ883737. ***Lobothallia radiosa*** (Hoffm.) Hafellner; –, –, –, KJ766430, KJ766596, –, KJ766870. ***Loxospora elatina*** (Ach.) A.Massal.; –, –, –, KR017350, KR017192, –, KR017485. ***Loxospora ochrophaea*** (Tuck.) R.C.Harris; –, –, –, DQ986900, DQ986750, –, DQ986822. ***Moelleropsis humida*** (Kullh.) Coppins & P.M.Jørg.; –, –, –, AY853329, AY853378, –, DQ870946. ***Mollisia cinerea*** (Batsch) P.Karst.; –, –, –, DQ976372, DQ470942, –, DQ471122. ***Myriospora scabrida*** (Hedl. ex H.Magn.) K.Knudsen & Arcadia; –, –, –, EU870695, LN810877, –, –. ***Ocellularia minutula*** Hale; –, –, –, KJ766445, KJ766607, –, –. ***Ochrolechia yasudae*** Vain.; –, –, –, DQ986902, DQ986776, –, DQ986848. ***Ophioparma ventosa*** (L.) Norman; –, –, –, KJ766447, KJ766610, –, KJ766828. ***Ostropa barbara*** (Fr.) Nannf.; –, –, –, AY584626, AY584642, –, –. ***Peltigera degenii*** Gyeln.; –, –, –, AY584628, AY584657, –, DQ782826. ***Pertusaria pertusa*** (L.) Tuck.; –, –, –, –, JN941360, –, JN992653. ***Phlyctis argena*** (Ach.) Flot.; –, –, –, DQ986880, DQ986771, –, –. ***Placopsis gelida*** (L.) Linds.; –, –, –, AY212859, AY212836, –, DQ870984. ***Placynthiella uliginosa*** (Schrad.) Coppins & P.James; –, –, –, DQ986877, DQ986774, –, DQ986845. ***Pleopsidium chlorophanum*** (Wahlenb.) Zopf; –, –, –, DQ991756, DQ842017, –, DQ782858. ***Porina***

Appendix 1. Continued.

aenea (Wallr.) Zahlbr.; –, –, –, HM244754, –, –, KC191665. ***Porina exocha*** (Nyl.) P.M.McCarthy; –, –, –, KF833333, KF833332, –, KF833345. ***Porpidia albocaerulescens*** (Wulfen) Hertel & Knoph; –, –, –, DQ986871, DQ986757, –, DQ986828. ***Protothelenella corrosa*** (Körb.) H.Mayrhofer & Poelt; –, –, –, AY607746, AY607734, –, DQ870988. ***Protothelenella sphinctrinoidella*** (Nyl.) H.Mayrhofer & Poelt; –, –, –, AY607747, AY607735, –, DQ870989. ***Rhizocarpon oederi*** (Weber) Körb.; –, –, –, DQ986788, DQ986804, –, –. ***Rimularia insularis*** (Nyl.) Rambold & Hertel; –, –, –, KC222182, KC222205, –, KC222188. ***Sagiolechia protuberans*** (Ach.) A.Massal.; –, –, –, HM244757, HM244775, –, –. ***Sphaeropezia* sp. EB-2012**; –, –, –, JX266156, JX266158, –, –. ***Stictis radiata*** (L.) Pers.; –, –, –, KR017334, –, –, KR017484. ***Thelotrema lepadinum*** (Ach.) Ach.; –, –, –, KR017324, KR017184, –, KR017451. ***Thrombium epigaeum*** (Pers.) Wallr.; –, –, –, AY607750, AY607740, –, –. ***Trapeliopsis flexuosa*** (Fr.) Coppins & P.James; –, –, –, KJ766505, KJ766668, –, KJ766833. ***Tremolecia atrata*** (Ach.) Hertel; –, –, –, AY853347, AY853397, –, –. ***Umbilicaria aprina*** Nyl.; –, –, –, DQ986814, DQ986799, –, DQ986840. ***Varicellaria hemisphaerica*** (Flörke) I.Schmitt & Lumbsch; –, –, –, DQ973000, –, –, DQ902341. ***Wawea fruticulosa*** Henssen & Kantvilas; –, –, –, DQ871023, DQ007347, –, DQ871005. ***Xylographa parallela*** (Ach.) Fr.; –, –, –, KJ766516, KJ766679, –, KJ766902.