Phylogenetic revision of *Petrakia* and *Seifertia* (Melanommataceae, Pleosporales): new and rediscovered species from Europe and North America

Ludwig Beenken¹, Andrin Gross¹, Valentin Queloz¹

¹Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland.

Correspondence: L. Beenken, ludwig.beenken@wsl.ch

Abstract: The phylogenetic revision of the genera *Petrakia* and *Seifertia* using LSU, ITS, *RPB2* and *TEF1* sequences and the re-evaluation of their morphological characteristics lead to several reclassifications: The genus *Pseudodidymella* as well as the genera *Mycodidymella* and *Xenostigmina* are synonymized with the genus *Petrakia*. Based on ITS sequence comparisons, it was previously suspected that the leaf spot pathogen *Pseudodidymella fagi*, which occurs on the Japanese beech *Fagus crenata* in Japan, is conspecific to the pathogen attacking the European beech *Fagus sylvatica* in Switzerland and Germany since 2008. Herein, we show that Japanese and European collections represent separate species and describe the European one as *Petrakia liobae* new to science. Apart from that, we make the new combinations *Petrakia fagi* and *Petrakia minima*. The names *Petrakia aesculi* and *Petrakia aceris* are validated. A sixty-year-old collection from Wisconsin USA, designated as *Petrakia echinata* on leaves of silver maple (*Acer saccharinum*), proved to be another species new to science and is described here as *Petrakia greenei*. Consequently, there is currently no evidence of the European *P. echinata* to occur in North America. In contrast, *P. echinata* was found to infect the North American big leaf maple (*Acer macrophyllum*) in Europe.

Antromycopsis alpina, described in 1914, was rediscovered in the Swiss Alps from dry fruits of *Rhododendron ferrugineum*. It is combined in *Seifertia* as *S. alpina*, based on molecular

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phylogenetic and morphological analyses. This anamorphic fungus appears to be native to Europe and does not cause a bud disease on *Rhododendron* in contrast to the closely related *S. azaleae*. *Seifertia shangrilaensis* is the third species of this genus that is closely related to *Petrakia*. Both genera belong to the family Melanommataceae.

Key words: foliar pathogens, neomycetes, taxonomy, DNA-barcoding, *Antromycopsis*, *Mycodidymella*, *Pseudodidymella*, *Xenostigmina*

Taxonomic novelties: New species: *Petrakia greenei* Beenken, Andr. Gross & Queloz, *Petrakia liobae* Beenken, Andr. Gross & Queloz; **New combinations:** *Petrakia fagi* (C.Z. Wei, Y. Harada & Katum.) Beenken, Andr. Gross & Queloz, *Petrakia minima* (A. Hashim. & Kaz. Tanaka) Beenken, Andr. Gross & Queloz, *Seifertia alpina* (Höhn.) Beenken, Andr. Gross & Queloz.

Introduction

Ever since humans began moving crop, forest and ornamental plants from one area to another, they have been accidentally spreading associated plant microorganisms (Santini et al. 2018). As a consequence, the number of alien fungi, also called neomycetes, is constantly increasing (e.g., in Europe: Beenken and Senn-Irlet 2016, Desprez-Loustau 2009, Sieber 2014). Some of these new fungi are serious fungal plant pathogens (Santini et al. 2013). Thus, once a new pathogen is detected, it is of major importance to perform a proper risk assessment. In addition, information about the origin of the pathogen is crucial. However, it is often tedious to determine whether a newly detected species indeed represents a recently introduced species or was simply overlooked in the past. Introduced species may look very similar to native species and can be confused with them. A good example of this is *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya and *H. albidus* (Gillet) W. Phillips. The first was

introduced from Asia to Europe in the 90s where it now causes severe ash dieback disease, whereas the second is harmless and native to Europe (Queloz et al. 2011, Baral et al. 2014). This example makes us aware of the importance of the correct identification and taxonomic classification of newly appearing fungi.

An unknown fungal leaf blotch disease with conspicuous symptoms was discovered on European beech, *Fagus sylvatica*, in Switzerland in 2008. Bright white fluffy fungal propagules appeared from summer to autumn on the surface of dark brown necrotic leaf spots. Gross et al. (2017) assigned the causing fungus to *Pseudodidymella fagi* C.Z. Wei, Y. Harada & Katum. using morphological characters and sequences of the internal transcribed spacer (ITS), the standard DNA barcoding region of fungi (Schoch et al. 2012). However, despite the striking morphological similarity of Japanese and European materials and identical ITS sequences, some doubt about conspecificity remained. *Pseudodidymella fagi* was originally described as being host specific on *Fagus crenata* Blume in Japan (Wei et al, 1997), and *P. minima* A. Hashim. & Kaz. Tanaka was recently described as being specific on *Fagus japonica* Maxim. in Japan (Hashimoto et al. 2017). Moreover, several examples exist where the ITS barcoding region is not sufficient to unequivocally separate closely related species (e.g., Beenken et al. 2012 and literature cited therein, Schoch et al. 2012). Similarly, the question arises whether the record of *Petrakia echinata* in North America indeed belongs to the same species as in Europe.

Another uncommon fungus was found on the rusty-leaved alpenrose, *Rhododendron ferrugineum*, in the Swiss alps in 2014. It was morphologically assigned to the genus *Seifertia* (Beenken and Senn-Irlet 2016). Up to now, only *Seifertia azaleae* has been known in Europe (Farr and Rossman 2019). This species was introduced from North America, and causes a bud blight disease of *Rhododendron* cultivars. The fear was that this pathogen had jumped over to the native *Rhododendron* species. Gross et al. (2017) provided evidence that the species discovered on *R. ferrugineum* is not conspecific with *S. azalea*, but did not clarify its

taxonomic position any further. Another possible *Seifertia* species was *S. shangrilaensis* which was recently described in China by Li et al. (2016b).

The focal species within *Pseudodidymella* and *Seifertia* are closely related to the genus *Petrakia* (Gross et al. 2017). In a revision of both genera using a multi-gene phylogeny approach in combination with morphological analyses, we aimed to correctly identify and classify the species according to the principles of phylogenetic classification.

Material and Methods

Sampling

For the present study, the samples listed in Gross et al. (2017) were re-analysed. New samples of infected *Fagus* and *Acer* leaves were collected in Austria, France, Germany and Switzerland in 2017, 2018 and 2019. *Seifertia* spp. occurring on *Rhododendron* spp. were collected in Switzerland. Dried specimens were deposited in the fungal collection of the ETH Zurich (ZT Myc). Additionally, two North American collections labelled as *P. echinata* from the University of Wisconsin (WIS) and type material of *P. echinata* from W and WIS were investigated (Herbarium acronyms according to Index Herbariorum 2019).

Isolation of fungi

Single mycopappus-like propagules of *Petrakia* spp. were taken from necroses on *Fagus* and *Acer* leaves and transferred to 1.5% malt extract agar (MEA) plates (15g Plant Propagation Agar (Conda), 12g Bacto Malt Extract (BD Biosciences), 100 mg streptomycin (Sigma), 1 l ddH₂O). Single ascospore isolates from ascomata of *Petrakia* spp. and single conidium isolates of *Seifertia* spp. were prepared on petri dishes with the same growth medium. All isolates were incubated at 20°C up to a mycelium size of ca. 2 cm in diameter. Approximately

1 cm² of aerial mycelium was harvested and subsequently lyophilized. A representative subset of isolates has been deposited in the culture collection of the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, the Netherlands (Table 1).

DNA extraction

DNA was extracted from lyophilized and ground mycelium with the KingFisher/Flex Purification System (ThermoFisher Scientific) according to the manufacturer's protocol and using the chemicals for automated DNA extraction from fungal samples with Kingfisher 96/Flex supplied by LGC Genomics GmbH (Berlin). For DNA-extraction from the sixty-year-old herbarium specimens, small leaf pieces (ca. 0.25 cm²) with fungal infection were excised and finely ground with a Retsch mixer mill. From the tissue powder, DNA was extracted using the DNeasy PlantPro Kit (QIAGEN[®]) following the manufacturer's protocol for plant tissue. Additionally, already available DNA-samples from Gross et al. (2017) were used.

PCR and DNA Sequencing

To amplify SSU, LSU, ITS, *TEF1* and *RPB2*, standard PCRs were performed using the following primer pairs (annealing temperatures in brackets). SSU: NS1/NS4 (48°C) (White et al. 1990); ITS: ITS1/ITS4 (50°C) (White et al. 1990); LSU: LR0R/LR6 (52°C) (Rehner and Samuels 1994, Vilgalys and Hester 1990); *TEF1*: EF1-983F/ EF1-2218R (55°C) (Rehner and Buckley 2005); *RPB2*: fRPB2-5F/fRPB2-7cR (58°C) (Liu et al. 1999). Additionally, new primer pairs specific to Melanommataceae were designed to amplify more effectively *TEF1* and *RPB2* from samples that did not work well with the primers listed above. *TEF1*: EF1-MelaF (5'-GCT GAT TGC GCC ATT CTC ATC AT-3')/EF1-MelaR (5'-TAC CAT GTC ACG GAC AGC GA-3') (54°C); *RPB2*: RPB2-MelaF (5'-AAC TTG TTC CGT ATC CTC TTC CT-3')/ RPB2-MelaR (5'-ATA CTA GCG CAR ATA CCG AGK ATC-3') (58°C). The primer combination RPB2-MelaF/fRPB2-7cR (54°C) was used to amplify the *RPB2*-sequence

of *Seifertia* spp. To amplify the single copy genes from the DNA of the old herbarium material, nested PCRs were performed as follows. For *TEF1*, the product of a PCR using EF1-983F/ EF1-2218R (55°C) was diluted 1:10 and amplified again in a nested PCR using the internal primer EF1-MelaF/ EF1-MelaR (54°C). In the same way, two nested PCRs were performed for *RPB2* from a PCR product of primer pair RPB2-MelaF/ RPB2-MelaR (58°C) using the primer pairs RPB2-MelaF/ RPB2-PetrR (5'-CCG TTT CGC CGT AGT TCT TG-3') (58°C) and RPB2-PetrF (5'-TAG TGT TGG CAG CGA AAG CA-3')/ RPB2-MelaR (58°C) to amplify two overlapping sequences. The newly designed inner primers RPB2-PetrF and RPB2-PetrR are highly specific to the *RPB2* sequences of *Petrakia* spp.

Cycle sequencing reactions using the BigDye Terminator kit v3.1 (Applied Biosystems, Foster City, CA, USA) were carried out with the same forward and reverse primers as used in the PCRs. Cleaned products were run on an ABI PRISM 3100-Avant Genetic Analyzer capillary sequencer (Applied Biosystems) as described in Beenken et al. (2012). Sequences were trimmed and edited with Sequencher 4.10 software (Gene Codes, Ann Arbor, MI, USA). Resulting sequences were compared with accessions deposited in GenBank by applying the Basic Local Alignment Search Tool (BLAST) using the nucleotide search option (blastn) (Altschul et al. 1990). All sequences generated were deposited at GenBank (Table 1).

Phylogenetic analyses

A combined alignment of ITS-LSU sequences and of *RPB2-TEF1* sequences were created. Finally, all genes were concatenated to a single ITS-LSU-*RPB2-TEF1*-alignment. Lacking sequences were supplemented with unknown bases (N). All alignments were performed using MAFFT v.7.017 (Katoh et al. 2002; Katoh and Standley 2013). Ambiguous regions within the resulting alignments were excluded from analyses with Gblocks v.0.91b (Castresana 2000). The datasets contained the newly generated sequences and corresponding sequences of Melanommataceae (Table 1) following Gross et al. 2017, Hashimoto et al. 2017 and Jaklitsch

and Voglmayr (2017). Species of Pleomassariaceae were added as an outgroup following Jaklitsch and Voglmayr (2017). The alignments were submitted to TreeBASE (study number 24199).

The datasets were analysed using the maximum likelihood (ML) method implemented in RAxML v.8.2.8 (Stamatakis 2014). Analyses were performed assuming a general time-reversible (GTR) model of nucleotide substitution, and by estimating a discrete gamma distribution (GTRGAMMA option in RAxML) with partitions according to the respective submatrices (ITS1, 5.8, ITS2, LSU, *RPB2* and *TEF1* including the codon positions in the *RPB2* and *TEF1* sequences), which allowed multiple nucleotide substitution models. One thousand runs with distinct starting trees were completed using the rapid bootstrap (BS) algorithm of RAxML. The resulting phylogenetic ML trees were midpoint rooted and visualized using the Dendroscope program (Huson et al. 2007). Additionally, Bayesian analyses were performed with MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2005) on the ITS-LSU, *RPB2-TEF1* and ITS-LSU-*RPB2-TEF1* datasets with *Pleomassaria siparia* as an outgroup. Independent GTR models using the gamma distribution approximated by four categories were implemented for all data partitions, with four chains and ten million generations, sampling every 100th tree. Post-burn-in trees were collected and the summarizations calculated only when the standard deviation of split frequencies reached levels below 0.01. Posterior probability (PP) values equal to or greater than 0.95 were considered significant.

Morphology

Morphological data of *P. liobae* were taken from Gross et al. (2017). Images of *Mycopappus*-states of *P. liobae* and of synnemata of *S. alpina* were made using the 3D image-stacking feature of a Leica DVM6 Digital microscope. Additionally, asexual states of *S. alpina*, *P.*

echinata and *P. greenei* were mounted in 2.5% KOH and photographed in transmitted light at 200, 400, and 640-times magnifications using a Zeiss Axio Scope A1 microscope with the Zen 2.3 digital equipment (Carl Zeiss Microscopy GMBH, 2011). Twenty hyphal cells and 25 conidia of *S. alpina* were measured under 1000-times magnification. The comparison of morphology of *P. greenei* and *P. echinata* was based on the measurements of each 50 macroconidia and 10 mycopappus-like propagules of the respective type material. A map with European collection locations of *P. liobae* (coordinates given in Table 2) within the distribution area of beech was generated in QGIS 2.18 using a free vector map from www.naturalearthdata.com and the distribution map of *Fagus* from Caudullo et al. (2017, 2018).

Results:

Blast search and sequence comparison

The Blast search showed that the SSU sequences (Table 1) of several species of Melanommataceae and of the species of interest here are identical or nearly identical, and are therefore not informative enough. Consequently, the SSU was excluded from further phylogenetic analyses. The final combined alignment dataset of 55 samples contained 682 phylogenetically informative sites of a total of 3455 sites. The *RPB2-TEF1* data subset (*RPB2* 331/1018, *TEF1* 234/942) with 565 of 1960 informative sites was distinctly more informative- than the ITS-LSU data subset with 117 of 1495 informative sites (ITS 73/486, LSU 44/1009).

The analyses of the ITS sequences showed that European and Japanese “*Ps. fagi*” have identical sequences and cannot be separated from each other (comp. Gross et al. 2017 and Czachura et al. 2018). *Petrakia echinata* and *P. greenei* also do not differ in their ITS-sequences. *Seifertia alpina* and *S. azaleae* are well separated by their ITS sequences (98%

identity). LSU-analysis could not resolve all genera and species of Melanommataceae. The sequences of the European “*Ps. fagi*” and the Japanese *Ps. fagi* differ consistently only in one base pair (comp. Czachura et al. 2018). The LSU sequences of the Japanese *Ps. fagi*, *P. echinata* and *P. greeniei* are identical, the same applies to *Ps. minima* and *X. zilleri*. The three *Seifertia* spp. have identical LSU sequences as well. The *RPB2* and *TEF1* sequences separate the European “*Ps. fagi*” from the two Japanese *Ps. fagi* and *Ps. minima* (97% and 98% identity, respectively). *P. echinata* and *P. greeniei* differ in four base pairs of their *TEF1*-sequences (99.6% identity) and two or one base pairs of their *RPB2*-sequences (99.8 or 99.9% identity). *Seifertia alpina* differs from *S. azaleae* (98.6% identity) and *S. shangrilaensis* (99% identity) in the *TEF1* sequence. The *RPB2* sequence of *S. alpina* and *S. azaleae* show 97.1% identity.

Phylogeny

Maximum likelihood and Bayesian phylogenetic analyses revealed congruent tree topologies. The resulting trees of the combined alignment of ITS and LSU sequences partly differed from the tree topology of the analysis based on *RPB2* and *TEF1* sequences (Fig. 1). The ITS-LSU-*RPB2-TEF1* analysis (Fig. 2) resulted in a tree topology similar to the *RPB2-TEF1* tree.

ITS-LSU phylogeny (Fig. 1A): the European “*Pseudodidymella fagi*” and the Japanese *Ps. fagi* appear close together but *Ps. minima* does not belong to their subclade. *Petrakia echinata* and *P. greeniei* are not distinguishable and form a subclade with *X. zilleri* while *M. aesculi* appears close to them. The *Seifertia* species appear between these species and *P. deviata*, which is supported by a RAxML bootstrap value (BS) of 78 and 0.99 Bayesian posterior probability (PP). *Petrakia deviata* forms the sister group to this clade containing the genera *Petrakia*, *Pseudodidymella*, *Mycodidymella*, *Xenostigmata* and *Seifertia*. *Petrakia irregularis* appears to be related (99 BS / 1.00 PP) to *Splanchnonema pupula* (Pleomassariaceae).

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236 *RPB2-TEF1* phylogeny (Fig. 1B): The European “*Ps. fagi*” is well-separated from the two

237 Japanese species *Ps. fagi* and *Ps. minima*, which appear to be sister species with high support

238 (100 BS / 1.00 PP). The *Pseudodidymella* species belong to a well-supported (100 BS / 1.00

239 PP) subclade that also includes *P. echinata*, *P. greenei*, *X. zilleri* and *M. aesculi*, whereas *P.*

240 *deviata* falls in the basal position of this subclade (99 BS / 1.00 PP). *Seifertia alpina*, *S.*

241 *azalea* and *S. shangriaiensis* are well-separated species that form a well-supported (100 BS /

242 1.00 PP) sister clade to the *Petrakia* clade.

243 Combined ITS-LSU-*RPB2-TEF1* analysis (Fig. 2): The combination of the two multi-copy n-

244 rDNAs with the two single copy genes resulted in a tree topology that is nearly consistent

245 with the *RPB2-TEF1* analysis. A well-supported (99 BS / 1.00 PP) *Petrakia* clade is split into

246 a subclade including only *P. deviata* and a subclade (100 BS / 1.00 PP) including European

247 and Japanese “*Ps. fagi*”, *Ps. minima*, *P. echinata*, *P. greenei*, *X. zilleri* and *M. aesculi*. Within

248 this clade, the Japanese *Ps. fagi* and *Ps. minima* form a well-supported subclade well

249 separated from the European species occurring on *Fagus*. The new species *P. greenei* appears

250 on a short branch within *P. echinata*. Both species and *X. zilleri* form a subclade (92 BS / 0.99

251 PP), *M. aesculi* is in sister position to them (71 BS / 0.81 PP). *Seifertia* and *Petrakia* belong to

252 the Melanommataceae and appear to be sister genera (100 BS / 1.00 PP). *Petrakia irregularis*

253 is related to the Pleomassariaceae.

254 Taken together, our multi-gene phylogeny shows that (i) To avoid a polyphyletic genus

255 *Petrakia*, the genera *Mycodidymella*, *Pseudodidymella* and *Xenostigmina* should be included

256 in it; (ii) *Pseudodidymella fagi* from Europe represents a separate species described here as

257 *Petrakia liobae* sp. nov.; (iii) the European and the North American samples of *P. echinata*

258 are not conspecific, *P. greenei* is therefore introduced as new species; (iv) the *Seifertia*

259 species collected on *R. ferrugineum* in the European Alps represents the separate species, *S.*

260 *alpina*.

261

262 **Taxonomy:**

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264 *Petrakia* Syd. & P. Syd., Annls mycol. 11(5): 406 (1913), emend. Jaklitsch & Voglmayr,

265 Sydowia 69: 90 (2017)

266 = *Blastostroma* C.Z. Wei, Y. Harada & Katum., Mycologia 90(2): 337 (1998)

267 = *Echinosporium* Woron., Vest. tflis. bot. Sada 28: 25 (1913)

268 = *Mycodidymella* C.Z. Wei, Y. Harada & Katum., Mycologia 90(2): 336 (1998)

269 = *Pseudodidymella* C.Z. Wei, Y. Harada & Katum., Mycologia 89(3): 494 (1997)

270 = *Pycnopleiospora* C.Z. Wei, Y. Harada & Katum., Mycologia 89(3): 496 (1997)

271 = *Xenostigmina* Crous, Mycol. Mem. 21: 154 (1998)

272

273 *Typus generis: Petrakia echinata* (Peglion) Syd. & P. Syd.

274

275 *Notes:* Sydow and Sydow (1913) erected the genus *Petrakia* for the anamorphic fungus

276 *Epicoccum echinatum* occurring on *Acer pseudoplatanus* in honor of the Austrian mycologist

277 Franz Petrak (1886–1973). Butin et al. (2013) discovered the teleomorph of *P. echinata* and

278 described its complete life cycle. Jaklitsch and Voglmayr (2017) emended the genus with a

279 new description including features of the sexual and asexual morphs. They transferred the

280 genera *Mycodidymella* and *Xenostigmina* to *Petrakia* based on molecular and morphological

281 data. However, Hashimoto et al. (2017) did not accept the taxonomy of Jaklitsch and

282 Voglmayr (2017) in their taxonomic revision of the mycopappus-like genera in

283 Dothideomycetes. Contrariwise, our phylogenetic analyses again confirm the reclassifications

284 of Jaklitsch and Voglmayr (2017) and additionally suggest to include the genus

285 *Pseudodidymella* within the genus *Petrakia*. The concept of Hashimoto et al. (2017) with

286 several genera with one or two species is not to be maintained based on our results. The genus

Petrakia in the old sense, only including *P. echinata* and *P. deviata*, appeared to be polyphyletic in all of our analyses (Figs. 1, 2).

In addition, the morphological data do not conflict but support the new arrangement of the genus *Petrakia*. The recorded spermogonia of *Mycodidymella*, *Petrakia* as well as *Pseudodidymella* are *Phoma*-like (Butin et al. 2013, Hashimoto et al. 2017). All species of these genera have mycopappus-like synanamorphs (Fig. 2) of more or less the same morphology. This type of anamorph is unique to the family of Melanommataceae and its order Pleosporales. The mycopappus-like propagules are scattered on necrotic leaf patches and emerge from the stromatic base on the upper leaf surface on a short stalk. The sub-globose to lentiform body of the propagule is parenchymatous, composed of more or less isodiametric roundish cells surrounded by radiating hyphal appendages (Butin et al. 2013, Gross et al. 2017, Hashimoto et al. 2017, Redhead and White 1984, Wei et al. 1997, 1998). The mycopappus-like propagules differ between the species in the length of their appendages. The propagules of species occurring on *Acer* have up to 400 µm long flexuous hyphal appendages and that on *Aesculus* has similar but shorter (up to 190 µm) appendages (Table 3). In contrast, species on *Fagus* have propagules surrounded by short (up to 150 µm) straight appendages (Table 4). The propagules break off easily at their short stems (Fig. 5D) and can be spread by wind with the help of the long hovering appendages.

The propagules of the genus *Mycopappus* Redhead & G.P. White with the species *Mycopappus alni* (Dearn. & Barthol.) Redhead & G.P. White and *M. quercus* Y. Suto & M. Kawai are not distinctly stalked and have long, conically fasciculate hyphal appendages (Redhead and White 1984, Suto and Kawai 2000, Suto and Suyama 2005, Gross et al. 2017). The genus *Mycopappus* s. str. belongs to the Sclerotiniaceae (Helotiales) (Park et al. 2013, Suto and Suyama 2005). Thus, it can be hypothesized that mycopappus-like anamorphs have evolved convergently as diaspores in the families Sclerotiniaceae and Melanommataceae, respectively, in the orders Helotiales and Pleosporales.

The species of *Mycodidymella*, *Petrakia*, *Pseudodidymella* and *Xenostigmina* were distinguished mainly by the presence and form of macroconidia (see also the identification key below). While macroconidia are lacking in the species that occur on *Fagus* spp. (Fagaceae), they are present in species that occur on *Acer* and *Aesculus* (both Sapindaceae). These macroconidia all emerge from small, stromatic, parenchymatous sporodochia, and differ only in the arrangement of septa, pigmentation and number of hyphal appendages (Fig. 3, Table 3) (Butin et al. 2013, Crous et al. 2009, Gross et al. 2017, Hashimoto et al. 2017, Li et al. 2016a, Petrak 1966, Wei et al. 1997, 1998). The ontogeny of the macroconidia (reconstructed in Fig. 3) demonstrates that there are no fundamental differences between the different types (Jaklitsch and Voglmayr 2017). Their differences are based only on different sequence of transverse and longitudinal septa, different intensity of pigmentation and different number of appendages. For example, young *Blastostroma* (= *Mycodidymella*) macroconidia (figs. 12–15 in Wei et al. 1998) as well as mature *Xenostigmina* macroconidia (fig. 15g in Crous et al. 2009; figs. 2–4 in Funk 1986) strongly resemble early stages of macroconidia of *P. greenii* (Fig. 4G) and *P. deviata* (fig. 2h in Gross et al. 2017). In conclusion, these differences in macroconidia morphology or the lack of macroconidia cannot justify the split into several small genera. Finally, all *Petrakia* species share similar ecological niches and life cycles. They are all necrotrophic leaf pathogens in their asexual phase causing leaf blotch diseases on *Acer*, *Aesculus* or *Fagus*, and are leaf litter saprotrophs during their sexual phase. Based on the considerations above, it was necessary to unify *Mycodidymella*, *Petrakia*, *Pseudodidymella* and *Xenostigmina* into one monophyletic, morphologically and ecologically well-defined genus *Petrakia*, which is the oldest valid name following Jaklitsch and Voglmayr (2017). The anamorph names *Blastostroma* and *Pycnopleiospora* are also synonyms of *Petrakia* following the international Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). This new concept of the genus includes eight *Petrakia* species. As Jaklitsch and Voglmayr (2017) have already shown, *Petrakia* belong to the

Melanommataceae as defined by Tian et al. (2015). The family Pseudodidymellaceae A. Hashim. & Kaz. Tanaka (Hashimoto et al. 2017) corresponds fully with the genus *Petrakia* as defined here. Thus, it has become monotypic and therefore superfluous. The same applies to the too-narrow family concept of Melanommataceae in Hashimoto et al. (2017), which is therein restricted only to the genus *Melanomma*.

***Petrakia* species on *Acer*:**

There are four species occurring on maple leaves that are well characterised by their more or less muriform, brown macroconidia; mycopappus-like propagules with flexuous hyphal appendage up to 400 µm long (Table 3).

Petrakia aceris (Dearn. & Barthol.) Jaklitsch & Voglmayr, Sydowia 69: 90 (2017)

Basionym: *Cercospora aceris* Dearn. & Barthol., Mycologia 9(6): 362. 1917.

≡ *Mycopappus aceris* (Dearn. & Barthol.) Redhead & G.P. White, Canad. J. Bot. 63(8): 1430. 1985.

≡ *Xenostigmina aceris* (Dearn. & Barthol.) A. Hashim. & Kaz. Tanaka, Studies in Mycology 87: 198 (2017)

= *Stigmina zillieri* A. Funk, Canad. J. Bot. 65(3): 482. 1987.

≡ *Xenostigmina zillieri* (A. Funk) Crous, Mycol. Mem. 21: 155. 1998.

= *Mycosphaerella mycopappi* A. Funk & Dorworth, Canad. J. Bot. 66(2): 295. 1988.

≡ *Didymella mycopappi* (A. Funk & Dorworth) Crous, Mycol. Mem. 21: 152. 1998.

Descriptions and illustrations: Crous et al. (2009), Funk (1986).

Host and distribution: on leaves of *Acer macrophyllum* Pursh in North America.

365 *Note: Petrakia aceris* appeared in all phylogenies (Figs. 1, 2) next to *P. echinata* and *P.*
366 *greenii*.

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369 ***Petrakia deviata*** Petr., in Watzl, Beih. Botan. Centralbl., Abt. B 57: 437 (1937)

370

371 *Descriptions and illustrations:* Gross et al. (2017).

372 *Host and distribution:* on leaves of *Acer campestre* L. and *A. platanoides* L. in Georgia and
373 Switzerland.

374 *Georeferencing and typification:* Watzl (1937) collected two specimens in the Greater
375 Caucasus at the river “Baramba” in the “Chodschal” mountains in 1928. Using the short
376 expedition report of Watzl et al. (1929), we were able to locate his collection sites at the river
377 Mramba (current spelling of “Baramba”), an affluent of the river Kodori, close to the village
378 Kvemo Azhara (43.10388, 41.71438, 560 m alt.) in the Kodori mountains, in Abkhazia,
379 Georgia. Because Petrak did not select a holotype (Watzl 1937), we designated the voucher
380 W-1978-0012109, from which Gross et al. (2017) isolated DNA and sequenced the ITS
381 region as a lectotype.

382

383 LECTOTYPE designated here: GEORGIA, Abkhazia, Greater Caucasus, Kodori mountains,
384 at the river Mramba, 600 m alt. 07.09.1928, leg. O. Watzl (W-1978-0012109).

385 PARATYPE: GEORGIA, Abkhazia, Greater Caucasus, Kodori mountains, at the river
386 Mramba, 650 m alt. 27.08.1928, leg. O. Watzl (W-1978-0011955).

387

388 *Notes: Petrakia deviata* has an exclusive sister position with respect to the remaining *Petrakia*
389 species in the combined phylogenetic analysis (Fig. 2). It is morphologically very similar to *P.*

390 *echinata*, *P. greenei* and *P. aceris* which also occur on *Acer* spp. Thus, it belongs without
 391 doubt to the genus *Petrakia*. Ascomata are unknown to date.
 392
 393
 394 ***Petrakia echinata*** (Peglion) Syd. & P. Syd., Annls mycol. 11(5): 407 (1913)
 395 *Basionym*: *Epicoccum echinatum* Peglion, Malpighia 8: 459 (1895)
 396 $\equiv$ *Echinosporium echinatum* (Peglion) Woron., Vest. tflis. bot. Sada 35: 39 (1915)
 397 $=$ *Echinosporium aceris* Woron., Vest. tflis. bot. Sada 28: 25 (1913)
 398 Fig. 4H
 399 *Descriptions and illustrations*: Butin et al. (2013), Gross et al. (2017), Kirisits (2007), Li et al.
 400 (2016a).
 401 *Host and distribution*: mainly on leaves of *Acer pseudoplatanus* L. in Eurasia. Single reports
 402 on leaves of *A. campestre* L., *A. monspessulanum* L., *A. $\times$ coriaceum* Bosc ex Tausch (all
 403 three from Switzerland), *A. macrophyllum* Pursh from Germany, *A. opalus* Mill. from Czech
 404 Republic (Petrak 1966, van der AA 1968 as *A. italicum*).
 405
 406 NEOTYPE designated here: CZECH REPUBLIC, Hranice (Mährisch Weisskirchen),
 407 Podhorn, 08. Oct. 1913, macroconidia on leaves of *Acer pseudoplatanus*, F. Petrak, Flora
 408 Bohemiae et Moraviae exsiccate, II Serie 1. Abteilung: Pilze, Lfg. 18, Nr. 900; HOLOTYPE:
 409 W 1970-0025323; ISOTYPE investigated: WIS-f-00757559; Z-Myc 8039; ZT-Myc 60356
 410 (Petrak's exsiccate including further isotypes is present in many herbaria).
 411 *Specimens examined*: CZECH REPUBLIC, Hranice (Mährisch Weisskirchen), Podhorn, Oct.
 412 1934, macroconidia on leaves of *Acer pseudoplatanus*, F. Petrak, Mycotheca generalis 1352
 413 (Z-Myc 8037); —, Oct. 1913, macroconidia on leaves of *Acer pseudoplatanus*, F. Petrak,
 414 Flora moravica /ZT-Myc 60355); Eisgrub in Mähren, Oct. 1913, macroconidia on leaves of
 415 *Acer italicum*, leg. H. Zimmermann, F. Petrak, Flora Bohemiae et Moraviae exsiccate, II Serie

1. Abteilung: Pilze, Lfg. 18, Nr. 900/b (Z-Myc 8038). GERMANY, Bavaria, Freising,
 arboretum Weltwald Freising, 48.41798, 11.66662, alt. 480 m, macroconidia and
 mycopappus-like anamorphs on living leaves of *Acer macrophyllum*, 18. Sep. 2016, O.
 Holdenrieder/160918.1 (ZT-Myc 59961); —, ascomata and macroconidia on hibernated fallen
 leaves of *A. macrophyllum*, 30. Apr. 2019, L. Beenken (ZT-Myc 59962); —, mycopappus-
 like anamorph on living leaves of *A. macrophyllum*, 05. Aug. 2019, L. Beenken (ZT-Myc
 59963). SWITZERLAND, canton of Vaud, Swiss National Arboretum of Aubonne, 46.51948,
 6.35878, alt. 570 m, macroconidia and mycopappus-like anamorphs on living leaves of *A.*
pseudoplatanus, 10. Sep. 2017, L. Beenken (ZT Myc 59957); —, 46.51948, 6.35878, alt. 570
 m, macroconidia and mycopappus-like anamorphs on living leaves of *A. campestre*, 10. Sep.
 2017, L. Beenken (ZT Myc 59958); —, 46.51918, 6. 35951, alt. 570 m, macroconidia and
 mycopappus-like anamorphs on living leaves of *A. monspessulanum*, 10. Sep. 2017, L.
 Beenken (ZT Myc 59959); —, 46.51918, 6. 35951, alt. 570 m, Macroconidia and
 mycopappus-like anamorphs on living leaves of *A. × coriaceum*, 10. Sep. 2017, L. Beenken
 (ZT Myc 59960).

Notes: Peglion (1895) described *Epicoccum echinatum* occurring on leaves of *A.*
pseudoplatanus in Avellino, Italy. Sydow and Sydow (1913) transferred it in their new genus
Petrakia based on material collected by Petrak. Unfortunately, Peglion's original material
 could not be found (comp. Van der AA 1968). Therefore, we propose Petrak's collection as
 the neotype of *Petrakia echinata* to ensure taxonomic stability.

Acer campestre, *A. monspessulanum* and *A. × coriaceum*, a natural hybrid between *A.*
monspessulanum and *A. opalus*, as well as *A. macrophyllum* are new hosts of *P. echinata*
 (Farr and Rossman 2019). All specimens displayed typical mycopappus-like anamorphs and
 macroconidia of *P. echinata*. The infected trees of *A. campestre*, *A. monspessulanum* and *A. ×*
coriaceum grew close to an also infected *A. pseudoplatanus* tree in a Swiss arboretum.

442 *Acer macrophyllum* is native to the west coast of North America and is the natural host of *P.*
443 *aceris*. Planted trees of this species were found heavily infected by *P. echinata* in an
444 arboretum in southern Germany in 2016 and 2019. *Petrakia echinata* occurs also very
445 frequently on *A. pseudoplatanus* trees in this forest that could be the source of the host shift to
446 *A. macrophyllum*. However, the findings of both anamorphic stages in 2016, ascomata in
447 spring 2019 and again *Mycopappus* stages in summer 2019 show that *P. echinata* can perform
448 its complete life cycle on *A. macrophyllum* as described in Butin et al. (2013). *Petrakia*
449 *echinata* is unknown in North America up to now. The only records (Farr and Rossman
450 2019) on *A. saccharinum* collected in a natural forest in Wisconsin by Greene (1960) turned
451 out as belonging to a different new species (see next paragraph).

452

453

454 ***Petrakia greenei* Beenken, Andr. Gross & Queloz sp. nov.**

455 MycoBank 832673 Fig. 4 A–G

456 *Etymology*: Named in honour of Henry Campbell Greene (1904–1967), collector of the only
457 known material of the species. He was “an authority on parasitic fungi and for more than a
458 quarter of a century Curator of the Cryptogamic Herbarium at the University of Wisconsin”
459 (Backus and Evans 1968).

460

461 *Sexual morph*: unknown. *Synanamorphs*: macroconidia and mycopappus-like propagules in
462 groups together on dark brown, more or less circular necroses (0.5–3.5 cm in diameter) on the
463 adaxial surface of living leaves.

464 Mycopappus-like propagules shortly stalked, sub-globose to ellipsoid, body ca. 100–250 µm
465 in diameter, multicellular, parenchymatous, consisting of more or less isodiametric, globose
466 cells 7–10 (20) µm in diameter, colourless to pale brown, with up to 50, filamentous,
467 colourless hyphal appendages, ca. 100–300 µm long and 3–5 µm wide.

468 *Macroconidia* formed on epiphyllous sporodochia, embedded in the leaf tissues with a cone-
469 shaped stroma, ca. 100–250 μm in diameter, mature sporodochia blackish brown;
470 macroconidia dark brown, muriform by transverse, longitudinal and oblique septa, ellipsoid to
471 elongated spindle-shaped, 26.0–48.5 (av. = 33.4) μm long, 14.5–26.0 (av. = 20.0) μm wide,
472 length/width ratio 1.24–2.60 (av. = 1.69), cells angular, nearly cubic with (2)4–7(10) μm edge
473 length, cell walls dark-brown, smooth, primary septa darker coloured and thicker (up to
474 0.3 μm) than next formed septa; macroconidia bearing one apical and 0–4 (5) side projections,
475 projections straight with conical to roundish tips, 5–35 μm long and 3.5–4.5 μm wide,
476 colourless to light brown, mainly without septa; pedicels up to 20 μm long and 4–6 μm wide.

477
478 *Host and distribution:* on leaves of *Acer saccharinum* L., only known from the type locality
479 in Wisconsin, USA (Greene 1960).

480
481 HOLOTYPE: USA, Wisconsin, Vernon, Wildcat Mt. State Park near Ontario, 09. Sep. 1959,
482 H.C. Greene (WIS-f-0027755). ISOTYPES (not seen, researched in MyCoPortal 2019): BPI
483 454846, ARIZ-M-AN03761, ILLS s. N., RMS0015971, WSP48230.

484
485 *Additional specimen examined:* USA, Wisconsin, Vernon, Wildcat Mt. State Park near
486 Ontario, 13. Sep. 1960, H.C. Greene (WIS-f-0027756)

487
488 *Note:* *Petrakia greenei* from North America is very closely related to the European *P.*
489 *echinata* and differs only in a few base pairs of their *RPB2* and *TEF1* sequences from it. Its
490 macroconidia look similar to those of *P. echinata* but can be well distinguished by their
491 shapes and number of primarily formed transverse septa (Table 3). These differences seem to
492 be the result of differences in their ontogenies (Fig. 3). In *P. greenei*, the young macroconidia
493 initially form several (2-5) transverse septa and elongate in this process, longitudinal septa are

formed later in the ontogeny, resulting in spindle-shaped macroconidia (Fig. 4G). In contrast, the conidia of *P. echinata* immediately start forming longitudinal septa after the first transverse septum (Fig. 4G). Thus, transverse and longitudinal septa are formed approximately in similar quantity resulting in a similar growth in all directions and finally subglobose macroconidia. Both species also likely differ in their distribution and host choice. However, it still needs appropriate infection experiments to validate their host preferences as soon as living material of *P. greenei* is available. It is astonishing that there are only two sixty-year-old records of *P. greenei*, both from one and the same locality in Wisconsin. Especially since its host the silver maple is widespread in the eastern North America and often planted as ornamental tree. Thus, more field studies are needed to determine its exact distribution and host spectrum in order to assess its phytosanitary relevance. In summary, despite the comparably small molecular differences we are convinced that the description of the new species *P. greenei* is justified especially due to the evident morphological differences (Table 3).

Petrakia* species on *Aesculus

Only one species is known on horse chestnut. It differs from all other species by colourless slightly curved macroconidia, having only transverse septa, and by mycopappus-like propagules with appendages up to 190 µm long (Table 3).

Petrakia aesculi (C.Z. Wei, Y. Harada & Katum.) Jaklitsch & Voglmayr, Sydowia 69: 91 (2017)

Basionym: *Mycodidymella aesculi* C.Z. Wei, Y. Harada & Katum., Mycologia 90(2): 336. 1998.

520 = *Mycopappus aesculi* C.Z. Wei, Y. Harada & Katum., Mycologia 90(2): 336. 1998.

521 = *Blastostroma aesculi* C.Z. Wei, Y. Harada & Katum., Mycologia 90(2): 338. 1998.

522

523 *Descriptions and illustrations:* Wei et al. (1998), Hashimoto et al. (2017).

524 *Host and distribution:* on leaves of *Aesculus turbinata* Blume in Japan.

525

526 *Note:* *Petrakia aesculi* appeared in all phylogenies (Figs. 1, 2) as closely related to *P. aceris*,

527 *P. greenii* and *P. echinata*.

528

529

530 ***Petrakia* species on *Fagus***

531 Three morphologically very similar species can be distinguished mainly by their hosts and

532 distribution. They have no macroconidia, and their mycopappus-like propagules differ in the

533 length of their straight appendages (all shorter than 150 µm) and size of ascospores (Table 4).

534

535

536 ***Petrakia fagi* (C.Z. Wei, Y. Harada & Katum.) Beenken, Andr. Gross & Queloz, **comb. nov.****

537 MycoBank MB 829464

538 *Basionym:* *Pseudodidymella fagi* C.Z. Wei, Y. Harada & Katum., Mycologia 89(3): 495

539 (1997)

540 = *Pycnopleiospora fagi* C.Z. Wei, Y. Harada & Katum., Mycologia 89(3): 496 (1997)

541

542 *Descriptions and illustrations:* Wei et al. (1997), Hashimoto et al. (2017).

543 *Host and distribution:* on leaves of *Fagus crenata* Blume in Japan.

544

545

546 ***Petrakia liobae* Beenken, Andr. Gross & Queloz sp. nov.**

547 MycoBank MB 829463. Figs. 2, 5

548 = *Pseudodidymella fagi* C.Z. Wei, Y. Harada & Katum. ss. Gross et al. (2017), Chech &

549 Wiener (2017), Czachura et al. (2018) and Ogris et al. (2019).

550

551 *Etymology*: Named in honour of Dr. Lioba Paul. She discovered the new species during a

552 walk together with Dr. Ottmar Holdenrieder, 1997–2016 Professor of Forest Pathology and

553 Dendrology at the ETH Zurich, in a beech forest near Zurich in 2008.

554

555 *Sexual morph*: ascomata dark brown to black, sub-globose to lenticular, subcuticular to semi-

556 immersed in the host tissue, 137.5–222.5 (av. = 180) μm in diameter, 87.5–162.5 (av. =

557 112.9) μm in height with a sunken centrum in dry state, while distinctly cone-shaped when

558 wet; ostiolum round to irregularly shaped, 15–50 (av. = 30.3) μm in diameter;

559 pseudoparaphyses septate, colourless; asci bitunicate, 51–60 (av. = 54.6) μm long and 8.5–11

560 (av. = 9.7) μm wide; ascospores equally two-celled, slightly constricted at septa, with

561 distinctly pointed, rounded ends, 16–23 (av. = 19.5) μm long and 5–6 (av. = 5.4) μm wide,

562 walls colourless, smooth. Mature ascomata in groups on leaf litter of beech in spring (April –

563 May) at the time of beech leaf flush. Spermogonia not observed.

564 *Anamorph*: mycopappus-like propagules, shortly stalked, sub-globose to lentiform,

565 multicellular, parenchymatous, consisting of more or less isodiametric cells, 185–292 (av. =

566 241) μm in diameter, with up to 80 filamentous hyphal appendages; appendages six-septate,

567 94–150 (av. = 118) μm long and 5.5–7.5 (av. = 6.25) μm wide, originating from colourless or

568 slightly pigmented, globular monilioid hyphae, 8–15 (av. = 12) μm in diameter. In groups on

569 dark brown, irregularly shaped necroses on living beech leaves in summer to late autumn

570 (July – October).

571

572 *Type specimens:*

573 HOLOTYPE: anamorph, mycopappus-like propagules: SWITZERLAND, Canton Zurich,
574 Zürichberg, on living leaves of *Fagus sylvatica*, 47.38953°N, 8.55951°E, 650 m alt. 16. Sept
575 2016 leg. Ottmar Hodenrieder / 110916.6 (ZT Myc 57657); ex-type living culture: CBS
576 142337.

577

578 PARATYPE: sexual morph, ascomata: SWITZERLAND, Canton Zurich, Birmensdorf, on
579 leaf litter of *Fagus sylvatica*, 47.36857°N, 8.41749°E, 515 m alt. 06. May 2016 leg. Andrin
580 Gross / AG-160506.1 (ZT Myc 57669); living culture: CBS 142338.

581

582 *Specimens* examined and used for the distribution map (Fig. 5F) are given in Table 2.

583 *Further descriptions and illustrations:* Gross et al. (2017), Cech and Wiener (2017), Czachura
584 et al. (2018) and Ogris et al. (2019). Culture characteristics on malt extract agar (MEA) and
585 potato dextrose agar (PDA) are described in Czachura et al. (2018).

586

587 *Hosts, distribution and habitats:* Currently, *P. liobae* is only known in Europe (Fig. 5F):

588 Austria, western France (Pyrenees), Germany, Slovakia, Slovenia and Switzerland (as *P. fagi*
589 in Cech and Wiener 2017, Czachura et al. 2018, Gross et al. 2017 and Ogris et al. 2019),

590 occurring on *Fagus sylvatica* L. and was found on *F. orientalis* Lipsky in the Munich

591 Botanical Garden. The *Mycopappus*-state was mainly found on the shade-leaves of young,

592 understory beech trees or low-hanging beech branches in the innermost parts of beech forests.

593 In dry years, it was only observed in rather humid forests, such as in canyons, on river sides

594 or close to bogs. Thus, we conclude that the *Mycopappus*-state needs high air humidity for

595 growth, dispersal and infection.

596

Notes: Using only the ITS region, the universal DNA barcode marker for fungi (Schoch et al. 2012), the European fungal collections from *Fagus sylvatica* and *F. orientalis* were not distinguishable from the Japanese *P. fagi* on *F. crenata*. Therefore, Gross et al. (2017) identified them as *P. fagi* and assumed that the species was introduced into Europe from Japan. The use of sequences of the single copy genes *RPB2* and *TEF1* for the phylogenetic analyses (Fig. 1B, 2) completely changes the results and conclusions of Gross et al. (2017), in that the European taxon is well-separated from the two Japanese species *P. fagi* and *P. minima*. *Petrakia liobae* is morphologically very similar to the other two species occurring on *Fagus* spp. (Table 4). The sexual morph of *P. liobae* differs from *P. fagi* in only slightly smaller ascomata and wider ascospores. Its mycopappus-like propagules differ from those of *P. fagi* and *P. minima* in somewhat longer hyphal appendages with more septa. Ogris et al. (2019) confirmed the susceptibility of *F. orientalis* against *P. liobae* (as *P. fagi*) and tested its pathogenicity on *Quercus petraea* (Matt.) Liebl. and *Castanea sativa* Mill. by infection experiments. *Petrakia liobae* can cause necrotic lesions on *Quercus* and *Castanea* leaves but no Myccopappus-like propagules were developed in vitro (Ogris et al. 2019). Thus, only *Fagus* spp. appear to be correct hosts.

Petrakia minima (A. Hashim. & Kaz. Tanaka) Beenken, Andr. Gross & Queloz, **comb. nov.**

MycoBank MB 829465

Basionym: *Pseudodidymella minima* A. Hashim. & Kaz. Tanaka, in Hashimoto, Matsumura, Hirayama, Fujimoto & Tanaka, Stud. Mycol. 87: 198 (2017)

Description and illustrations: Hashimoto et al. (2017).

Host and distribution: on leaves of *Fagus japonica* Maxim. in Japan. Sexual state unknown.

623

624 **Identification key for the eight species of *Petrakia* based on their anamorphs:**

625 **1*** With macroconidia and mycopappus-like anamorphs with appendages of up to 400 µm

626 long, on *Acer* or *Aesculus* (Sapindaceae)....**2**

627 **1** Only with mycopappus-like anamorphs with appendages shorter than 150 µm,

628 macroconidia lacking, on *Fagus* (Fagaceae) ...**6**

629 **2** Macroconidia curved, 50–75 x 5 µm, only with transverse septa, colourless, on *Aesculus*

630 *turbinata* in Japan...***P. aesculi***

631 **2*** Macroconidia clavate to globular, more than 9 µm wide, with transverse and longitudinal

632 septa, pigmented, on *Acer*....**3**

633 **3** Macroconidia clavate, 35–45 x 10–12 µm, only with single longitudinal septa, pale brown,

634 without long appendages, on *Acer macrophyllum* in North America...***P. aceris***

635 **3*** Macroconidia wider, with many transverse and longitudinal septa, distinctly muriform,

636 with long appendages...**4**

637 **4** Macroconidia with only one appendage at the tip, spindle-shaped, 20–45 x 10–20 µm,

638 middle brown, on *Acer platanoides* and *A. campestre* ...***P. deviata***

639 **4*** Macroconidia with many hyphal appendages, dark brown ...**5**

640 **5*** Macroconidia more or less isodiametric, irregularly globose, 20–35 µm in diameter, on

641 *Acer* spp. in Eurasia...***P. echinata***

642 **5** Macroconidia distinctly elongated, irregularly spindle-shaped, 25–48 x 14–26 µm, on *Acer*

643 *saccharinum* in North America ...***P. greenei***

644 **6** Mycopappus appendages < 50 µm, on *Fagus japonica*....***P. minima***

645 **6*** Mycopappus appendages > 60 µm.....**7**

646 **7** Mycopappus appendages up to 130 µm long, on *Fagus crenata* in Japan...***P. fagi***

647 **7*** Mycopappus appendages up to 150 µm long, on *Fagus sylvatica* and *F. orientalis* in

648 Europe....***P. liobae***

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Species excluded from *Petrakia*:

The following three species described in the genus *Petrakia* differ mainly from *Petrakia* s. str. in that they lack mycopappus-like anamorphs and grow on a different type of substrate. Their macroconidia only have a superficial similarity to those of *Petrakia* spp. (Van der Aa 1968, Bedlan 2017, Wong et al. 2002) but differ in their structure. Sexual states are unknown. They are not plant leaf pathogens but saprotrophic on decaying plant material. Genetic sequences of *P. juniperi* and *P. paracochinensis* are not available to date.

Petrakia irregularis Aa, Acta bot. neerl. 17: 221 (1968)
Notes: *Petrakia irregularis* was isolated from dead branches of *Acer pseudoplatanus* in the Netherlands and described from culture (Van der Aa 1968). In phylogenetic analyses, *P. irregularis* did not appear in the *Petrakia* or Melanommataceae clades but is closely related to species of the Pleomassariaceae (Fig. 1A, 2).

Petrakia juniperi Bedlan, J. Kulturpfl. 69(5): 174 (2017)
Host and distribution: on dead juniper wood in Austria (Bedlan 2017)

Petrakia paracochinensis M.K.M. Wong, Goh & K.D. Hyde, in Wong, Goh, McKenzie & Hyde, Cryptog. Mycol. 23(3): 198 (2002)
Host and distribution: on decaying culms of grasses in China (Wong et al. 2002)
Notes: The macroconidia of *P. paracochinensis* highly resemble those of *Ernakulamia cochinensis* (Subram.) Subram. (Tetraplosphaeriaceae, Pleosporales), which occur on rotten leaves of palms (Delgado et al. 2017, Wong et al. 2002). Both species are saprotrophic on decaying tissue of Monocots in the tropics.

675
676
677 ***Seifertia*** Partr. & Morgan-Jones, Mycotaxon 83: 348 (2002)
678 *Typus generis: Seifertia azaleae* (Peck) Partr. & Morgan-Jones
679
680 *Notes:* The genus *Seifertia* was established by Partridge and Morgan-Jones (2002) and
681 confirmed molecularly by Seifert et al. (2007) with only one species, *S. azaleae*. Li et al.
682 (2016b) described *S. shangrilaensis* as the second species of *Seifertia* and we add *S. alpina* as
683 the third species of the genus. The three species have identical LSU sequences but are easily
684 distinguishable by their *TEFI* sequences and their morphology (Table 5). The genus *Seifertia*
685 belongs to the Melanommataceae and forms the sister genus of *Petrakia* in the final
686 phylogeny (Fig. 2) (comp. Jaklitsch and Voglmayr 2017). There are no morphological
687 features that verify this very close relationship between both genera. Their anamorphs are
688 completely different and the ascomata of *Seifertia* are unknown. The genus *Seifertia* seems to
689 be specialized on the genus *Rhododendron* (Ericaceae), where a transition from saprotrophy
690 to necrotrophic parasitism can be observed. Additional hyphomycetes with similar synnemata
691 belong to other fungal groups (Seifert et al. 2007, Stalpers et al. 1991).
692
693
694 ***Seifertia alpina*** (Höhn.) Beenken, Andr. Gross & Queloz, **comb. nov.** MycoBank MB
695 829466. Fig. 6
696 *Basionym: Antromycopsis alpina* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1
697 123: 141 (1914)
698
699 *Host and distribution:* on dry fruit capsules and pedicels of *Rhododendron ferrugineum* L. of
700 the previous year in the Austrian (Höhn 1914) and Swiss Alps.

701

702 LECTOTYPE of *Antromycopsis alpina* Höhn. designated here: AUSTRIA, Lower Austria,

703 Raxalpe, on *Rhododendron ferrugineum*, 23. May 1905, leg. F. Buchholz, Herbarium v.

704 Höhnelt no. 2967 (FH 01093953). This type specimen contains one slide with dried-out

705 preparation of two intact synnemata (Figs. 6 H, I). ISOLECTOTYPE: —, Fungi coll. F.

706 Buchholz no. 1772 (FH 000888809). This specimen contains dried parts of *R. ferrugineum*

707 bearing only one synnema (Fig. 6 G).

708

709 EPITYPE of *Antromycopsis alpina* Höhn. designated here: SWITZERLAND, Canton of

710 Grisons, Sils i. E., Val Fex, Avers, 46.40341, 9.76943, 1990 m alt., on *R. ferrugineum*, 02.

711 Jul. 2017, leg. B. Senn-Irlet (ZT Myc 59953).

712

713 *Specimens additionally examined*: SWITZERLAND, Canton of Bern, Guttannen, 46.59035,

714 8.32263, 1610 m alt., on *R. ferrugineum*, 14. May. 2014, leg. J. Gilgen (ZT Myc 57692); —,

715 Canton of Valais, Natters, Riederalp, Oberaletsch, 46.39301, 8.00549, 1780, 1610 m alt., on

716 *R. ferrugineum*, 09. Jul. 2016, leg. L. Beenken (ZT Myc 58033).

717

718 *Notes*: Höhnelt (1914) described the species *Antromycopsis alpina* as follows (translated from

719 German): “Synnemata scattered or in a small bundle, black with whitish heads. Stalk black,

720 200–800 µm long, 50–60 µm wide, composed of 4–5 µm wide, parallel-arranged hyphae. At

721 the tip, hyphae spreading brush-like and turning into chains consisting of conidia that form a

722 roundish, 200 to 300 µm-wide head. Chains of conidia quite long. Conidia oblong, pointed on

723 both ends, colourless to smoke-grey-brown, 4–12 x 3–4 µm (mainly 6–7 µm long). Occurring

724 on fruit umbels and especially on pedicels of *Rhododendron ferrugineum* in the Raxalpe area

725 in Lower Austria, May 1905 leg. Fedor Buchholz.” Stalpers et al. (1991) examined the type

726 collection of *A. alpina* and considered it to be synonymous with *Pycnostysanus azaleae* (= *S.*

azaleae). The recent collections investigated here from the Swiss Alps fit very well with the type material (Fig. 6) and Höhnelt's (1914) original description. They show only marginal discrepancies in the size of conidia and stalk length (Table 5). They occur on the same substrate in the same habitat as in Höhnelt's collection. Without a doubt, the Swiss collections belong to *A. alpina*, which is here reclassified as *Seifertia alpina*. Because of the sparse type material and its poor condition, we designated an epitype from our collections. Both the morphological (Table 5) and phylogenetic analyses (Fig. 1, 2) show that *S. alpina* represents a distinct species, which is closely related to *S. azaleae* and *S. shangrilaensis*. As far as we know, this is the first rediscovery of this species after its initial discovery more than a hundred years ago. One reason for this may be that such tiny alpine species are easily overlooked and are consequently under-sampled (comp. Fluri et al. 2017). Furthermore, *S. alpina* appears to be very rare in spite of its very common substrate. Since its first discovery in 1905 and its re-discovery in the Bernese Alps by J. Gilgen 2014, the species has only been collected twice more, even though the first author and Beatrice Senn-Irlet (personal communication) have intensively searched for it in the Swiss and Bavarian Alps.

Seifertia azaleae (Peck) Partr. & Morgan-Jones, Mycotaxon 83: 350 (2002)
Basionym: Periconia azaleae Peck, Bull. Buffalo Soc. nat. Sci. 1(2): 69 (1873) [1874]
 ≡ *Briosia azaleae* (Peck) Dearn., Mycologia 33(4): 365 (1941)
 ≡ *Cephalotrichum azaleae* (Peck) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 453 (1898)
 ≡ *Pycnostysanus azaleae* (Peck) E.W. Mason, Mycol. Pap. 5: 130 (1941)
 ≡ *Sporocybe azaleae* (Peck) Sacc., Syll. fung. (Abellini) 4: 608 (1886)

Host and distribution: on *Rhododendron* spp., introduced worldwide (Farr and Rossman 2019), presumable origin is North America.

753

754 *Specimens examined:* SWITZERLAND, Geneva, Parc des Eaux-Vives, 46.20845, 6.16776,
755 375 m alt. on *Rhododendron* sp., 11. Oct. 2015, leg. L. Beenken (ZT Myc 57693); —,
756 Canton of Zurich, Birmensdorf, Eidgen. Forschungsanstalt WSL, 47.360139, 8.454917, 560
757 m alt. on *Rhododendron* sp., 21. Sep. 2017, leg. L. Beenken (ZT Myc 59954).

758

759 *Notes:* Peck (1873) described *Periconia azaleae* (= *S. azalea*) as occurring on “twigs, capsules
760 and old galls of *Azalea nudiflora* [= *Rhododendron periclymenoides* (Michx.) Shinners] in
761 New Scotland”, New York. Schmitz (1920) and Davis (1939) are the first to reported the bud
762 blight disease of native and cultivated *Rhododendron* spp. caused by *S. azaleae* in North
763 America. The disease arrived in Great Britain in the 1920s (Howell and Wood 1962) and
764 approximately fifty years later in continental Europe (Viennot-Bourgin 1981). Kaneko et al.
765 (1988) detected the bud blight on the native *Rhododendron japonicum* (A. Gray) Suringar in
766 Japan in the 1980s. In contrast to North America and Asia, *S. azaleae* was only found on
767 exotic *Rhododendron* cultivars and never on native species in Europe (Farr and Rossman
768 2019, Beenken and Senn-Irlet 2016). Endrestøl (2017) give a current review on *S. azaleae* and
769 its association with the *Rhododendron* leafhopper *Graphocephala fennahi* Young.

770

771

772 ***Seifertia shangrilaensis*** Jin F. Li, Phook. & K.D. Hyde, in Li, Phookamsak, Mapook,
773 Boonmee, Bhat, Hyde & Lumyong, Phytotaxa 273 (1): 36 (2016)

774

775 *Host and distribution:* on living and dead rachides of *Rhododendron decorum* Franch. in
776 Yunnan Province, China.

777

Note: Li et al. (2016b) could not finally determine whether *S. shangrilaensis* is only “epiphytic” or parasitic on *R. decorum*.

Discussion:

Phylogeny

The molecular analyses presented here demonstrated that single-gene phylogenies can lead to misinterpretation. The molecular phylogenetic analyses of the combined ITS and partial LSU-regions compared to the combined phylogeny of the single copy genes *RPB2* and *TEF1* resulted in trees with different topologies (Fig. 1). This can partly be explained by the fact that the ITS-LSU dataset contains much less phylogenetic information than the protein coding genes. The lacks of significant support for most backbone nodes in the ITS-LSU phylogeny (Fig. 1A), resulting in a less reliable tree topology, is supportive for this hypothesis. Incongruences between the phylogenetic signal in datasets of single copy genes and of the ITS-region have already been reported from other fungal groups (e.g., Den Bakker et al. 2004, Nuytinck et al. 2007). It is also known that ITS cannot always resolve closely related species (Beenken et al. 2012, Schoch et al. 2012). Nevertheless, it is remarkable that *P. liobae* and *P. fagi* did not even appear as sister species in the *RPB2-TEF1* phylogeny despite their identical ITS sequences. The ITS-LSU phylogeny (Fig. 1A) mirrors the relationship between the host plants of *P. fagi*, *P. liobae* and *P. minima*. *Fagus crenata*, *F. sylvatica* and *F. orientalis* are closely related whereas *F. japonica* belongs to another lineage of the genus *Fagus* (Renner et al. 2017). In contrast, the *RPB2-TEF1* (Fig. 1B), as well as the combined analysis (Fig. 2), produced a biogeographic signal. The two species from Japan, *P. fagi* and *P. minima*, appeared as sister species and were well-separated from the European *P. liobae*. This conflict between the datasets can likely be explained by ancient hybridization events or incomplete lineage sorting (Schardl and Craven 2003, Stukenbrock 2016) during the evolution of

Petrakia on *Fagus* species. One could speculate that *P. fagi* originated through the hybridization of the other two species because of its different position in the ITS versus *RPB2* and *TEF1* phylogenies. Further investigations are necessary to validate this hypothesis. Likewise, the morphologically well separated *P. echinata* and *P. greenii* are not separated with ITS and LSU but with *RPB2* and *TEF1*. In the ITS-LSU analysis (Fig. 1A), *Seifertia* spp. appeared within the *Petrakia*-clade (comp. Gross et al. 2017). In contrast, *Seifertia* was placed outside of the genus *Petrakia* in the analysis based on *RPB2* and *TEF1* (Fig. 1B) and the combined dataset (Fig. 2) where it forms a sister genus. This conflict may also have been caused by the insufficient phylogenetic information of ITS and LSU sequences. In conclusion, the phylogenies based on the combined dataset was more consistent with the morphological and ecological data in *Petrakia* and *Seifertia* and we therefore assume that they are more in agreement with the phylogenetic truth in Melanommataceae than the analyses based on ITS and LSU alone.

Morphology

The revision of the genus *Petrakia* has also shown how difficult the correct weighting of morphological characters for taxonomic classification can be. The separation of the genera *Pseudodidymella*, *Mycodidymella*, *Petrakia* and *Xenostigmina* has been based on the presence or absence of macroconidia and their morphology, respectively. This splitting contradicts the molecular phylogenetic analysis and would result in a paraphyletic genus *Petrakia* (Fig. 2). The study of the ontogeny of macroconidia shows that their early stages have common characteristics and that the differences between them can be explained as variations of the same plan (Fig. 3). In general, the absence or loss of a feature like macroconidia alone cannot justify a separate genus. In contrast, the mycopappus-like propagules turned out to be a good character that unites the genus *Petrakia* in accordance with the molecular data (Fig. 2). It

seems that the genus *Petrakia* developed originally on Sapindaceae, especially on the genus *Acer*. During or after the host jump to the genus *Fagus*, it has lost the ability to form macroconidia but retained the generic character of mycopappus-like propagules.

Origin

Seifertia alpina is obviously a species that is native to the European Alps but was overlooked during the last century likely due to its rarity and inconspicuousness. In contrast, the symptoms of *P. liobae* are very conspicuous (Fig. 5A–E), and occur on one of the most ecologically and economically important timber trees in Europe. Its symptoms could be confused with those of *Apiognomonina errabunda* (Roberge ex Desm.) Höhn. (Butin 2011), but this is only possible if the clearly visible, white fluffy mycopappus-like propagules (Fig. 5A–E) are lacking. Nowadays, the species appears to be very common in humid beech forests, especially in Switzerland and southern Germany (Fig. 5F). Most of the time, we have managed to find it when searching for it in suitable habitats. We therefore consider it unlikely that *P. liobae* was simply overlooked by European forest pathologists and mycologists over the last few centuries. The review of both recent and old forest pathological and mycological literature gives no indication that a beech disease with the symptoms of *P. liobae* was present in Europe before 2008. Consequently, we assume that *P. liobae* was recently introduced to Central Europe from an unknown origin. This is further suggested by the fact that surveys for this pathogen in beech forests in Poland have been unsuccessful up to now, whereas it has been found recently in neighbouring Slovakia (Cazachura et al. 2018, M. Piątek, personal communication). According to current data, it is probable that *P. liobae* is currently spreading north- and eastwards.

Our molecular phylogenetic analyses reveal that *P. liobae* is distinct from the Japanese species, yet related to them, especially to *P. fagi*. Therefore, the origin may be assumed to be eastern Asia, where the diversity hotspot of the genus *Fagus* is located (Denk and Grimm

2009). However, we cannot exclude the possible origin of *P. liobae* to be somewhere in Europe at a location that has not been exhaustively investigated to the same degree as Central Europe. It is noteworthy in this context that *P. liobae* has also been found in the French Pyrenees, which is considered to be one of the glacial refugia of *F. sylvatica* (Magri et al. 2006). The refuge areas of *F. sylvatica* in southern Europe (Magri et al. 2006) could also represent possible refugia for beech pathogens, and their recent range expansion could be driven by common factors such as climate change or anthropogenic movements. A further possible origin is the neighbouring Middle East, which is within the distribution area of *F. orientalis* (Magri et al. 2006) (Fig. 5F). *Petrakia deviata* has a highly disjunctive distribution area with its first discovery in the Central Caucasus (Watzl 1937) and recent findings in Switzerland (Gross et al. 2017). Up to now, the known distributions of these two *Petrakia* species are only fragmentary. More collection sites (presence and absence data) are necessary to answer the question of their origin and current distribution. Population genetic or genomic studies would also provide insights, as, for example, Gross et al. (2014) and McMullan et al. (2018) have conducted to clarify the origin of *Hymenoscyopus fraxineus* in Europe. Our study also clarifies that *P. echinata* was not introduced from Europe to North America but a sister species of it, *P. greenei*, occurs there. However, *P. echinata* has the ability to infest *A. macrophyllum*. This case of a European pest that infects a North American tree in Europe is a good example for the concept of “sentinel” or “ex-patria” plantings as described in Eschen et al. (2019): Woody plants are planted outside of their native range to test whether there is any pathogen/pest in the new environment that can infest them. Thus, ex-patria planting can help to identify potential pathogens/pests before they will be imported. In conclusion, the European *P. echinata* could become an invasive maple-tree disease in North America if introduced there.

Conclusion

This balanced overview of all available morphological and molecular data let us conclude that the genera *Mycodidymella*, *Pseudodidymella* and *Xenostigmina* are synonymous to *Petrakia*. Thus, *Petrakia* becomes a morphologically, ecologically and genetically well-characterized monophyletic genus in the Melannomataceae. *Seifertia* is a sister genus of *Petrakia* with three species originating in Asia, Europe and North America. It has also been shown that the n-rDNAs alone, in particular also the barcoding ITS region, are often not sufficient to correctly separate species. We argue that the exact determination and taxonomic classification of species are important to detect new pathogens, to assess their pest risk and to raise efficient quarantine measures in order to prevent possible invasions in the future.

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911 European beech”.

912

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1107 **Table 1.** Specimens used in the phylogenetic study, including GenBank accession numbers of
1108 ITS, LSU, SSU, *RPB2* and *TEF1* sequences.

1109

1110 **Table 2.** *Petrakia liobae* specimen collection data.

1111

1112 **Table 3.** *Petrakia* spp. on Sapindaceae.

1113

1114 **Table 4.** *Petrakia* spp. on *Fagus* spp.

1115

1116 **Table 5.** *Seifertia* spp. on *Rhododendron* spp.

1117

1118 **Fig. 1.** Two phylogenetic trees in comparison: **A.** Tree based on combined ITS-LSU
1119 sequences; **B.** Tree based on combined *RPB2-TEF1* sequences. Both presented maximum-
1120 likelihood trees were calculated using RAxML v.8.2.8. RAxML bootstrap support > 50 % /
1121 Bayesian posterior probabilities > 0.95 are given at nodes. At terminal nodes, species names
1122 are given according to the previous classification of Hashimoto et al. (2017) followed by
1123 voucher number, country of origin and host species. Species occurring on *Fagus* spp. are
1124 highlighted in green, on the Sapindaceae, *Acer* and *Aesculus*, in yellow and *Seifertia* spp. on
1125 *Rhododendron* in pink. Scale bars represent the number of substitutions per site.

1126

1127 **Fig. 2.** Phylogenetic positions of *Petrakia* and *Seifertia* species in the Melanommataceae
1128 based on maximum-likelihood analysis with RAxML v.8.2.8 recovered from combined ITS-
1129 LSU-*RPB2-TEF1* sequences. RAxML bootstrap support > 50 % / Bayesian posterior
1130 probabilities > 0.95 are given at nodes. The insert shows a mycopappus-like propagule of
1131 *Petrakia liobae* (stained cotton blue, bar = 10 µm) indicating the clade of all species with a

mycopappus-like anamorph. At terminal nodes, species names are given according to the previous classification of Hashimoto et al. (2017) followed by voucher number, country of origin and host species. *Petrakia* species occurring on *Fagus* spp. highlighted in green, on the Sapindaceae, *Acer* and *Aesculus*, in yellow and *Seifertia* spp. on *Rhododendron* in pink. Scale bars represent the number of substitutions per site.

Fig. 3. Ontogeny of *Petrakia* macrospores. The different types result mainly from the different septation modes. (Reconstructed from the literature cited in text and own observations, schematic drawings not to scale).

Fig. 4. A–G *Petrakia greenii*. **A.** Infected leaf of *Acer saccharinum* showing circular necroses on its upper side. **B.** Necrosis with mycopappus-like propagules. **C.** Necrosis with sporodochia bearing macroconidia. **D.** Mycopappus-like propagule. **E.** Hyphal appendage arise from mycopappus-like propagule. **F.** Macroconidia. **G.** Elongated early stages of macroconidia showing only transverse septa. **H.** *Petrakia echinata*, isodiametric early stages of macroconidia showing transverse and longitudinal septa. A–G from type material (WIS-f-0027755), H. from (WIS-f-00757559, Isotype). Scale bars: A = 1 cm; B, C = 200 µm; D = 50 µm; E = 10 µm; F–H = 20 µm.

Fig. 5. *Petrakia liobae*. **A.** Wet leaf of *Fagus sylvatica* with black necrotic blotches bearing white mycopappus-like propagules. **B.** Necrosis on *F. sylvatica* leaf with mycopappus-like propagules. **C.** Mycopappus-like propagule (top view), **D.** Mycopappus-like propagule showing the short stalk at the bottom (side view). **E.** Leaf of *F. orientalis* with necrosis bearing mycopappus-like propagules. **F.** European map showing the collection points of *P. liobae* (red dots) within the natural distribution areas of *F. sylvatica* (light green) and *F.*

1157 *orientalis* (dark green). A is from ZT Myc 57684; B–D were made from a fresh specimen (ZT
1158 Myc 59943) using the 3D image-stacking feature of a Leica DVM6 Digital microscope; E is
1159 from ZT Myc 59949. Scale bars: B = 1 mm; C, D = 100 μ m.

1160

1161 **Fig. 6.** *Seifertia alpina*. **A–C, E, F** Epitype (ZT Myc 59953). **A.** Dry fruit capsule of
1162 *Rhododendron ferrugineum* with black synnemata of *S. alpina*. **B.** Single synnema. **C.** Head
1163 of a young synnema. **D.** Older synnema head with ripe thick-walled conidia (ZT Myc
1164 58033). **E.** Part of the synnema stalk. **F.** Part of the synnema head showing conidiogenous
1165 cells producing conidia. **G.** Isolectotype (FH 00888809): single synnema (in red circle) on *R.*
1166 *ferrugineum*. **H–I.** Lectotype (FH 01093953). **H.** Microscope slide hand-labelled by v.
1167 Höhnelt. **I.** Synnema showing the stalk with hyphae and the conidia-producing head
1168 (embedding medium of the original preparation has dried out). A, B images were made using
1169 the 3D image-stacking feature of a Leica DVM6 Digital microscope. G–I were photographed
1170 by G. E. Tocci (Harvard). Scale bars: A = 2 mm; B = 100 μ m; C, D = 50 μ m; E, F = 20 μ m;
1171 G = 500 μ m; I = 100 μ m

Species	Previous name	Voucher	Host	State	Country	CBS-No.	GenBank Accession No.				
							ITS	LSU	SSU	RPB2	TEF1
<i>Alpinaria rhododendri</i>		WU 36914 [‡]	<i>Rhododendron ferrugineum</i>	As	AT	CBS 141994	KY189973	KY189973	KY190004	KY189989	KY190009
<i>Alpinaria rhododendri</i>		HHUF 30554	<i>Rhododendron brachycarpum</i>	As	JP	CBS 142901	LC203335	LC203360	LC203314	LC203416	LC203388
<i>Aposphaeria corallinolutea</i>		MFLU 15-2752	<i>Prunus padus</i>	As	RU	—	KY554202	KY554197	KY554200	KY554207	KY554205
<i>Herpotrichia juniperi</i>		—	<i>Juniperus nana</i>	—	CH	CBS 200.31	—	DQ678080	DQ677978	DQ677975	DQ677925
<i>Melanomma japonicum</i>		HHUF 26520 ^H	—	As	JP	CBS 142905	LC203321	LC203339	LC203293	LC203395	LC203367
<i>Melanomma pulvis-pyrius</i>		HHUF 30542	<i>Acer mono var. mayrii</i>	As	JP	CBS 142906	LC203322	LC203340	LC203294	LC203396	LC203368
<i>Petrakia aceris</i>	<i>Xenostigmia zilleri</i>	CPC 14379	<i>Acer macrophyllum</i>	Mc	CA	CBS 124109	FJ839625	LC203361	LC203315	LC203417	LC203389
<i>Petrakia aceris</i>	<i>Xenostigmia zilleri</i>	CPC 4011	<i>Acer sp.</i>	Mp	CA	CBS 115685	FJ839638	LC203362	LC203316	LC203418	LC203390
<i>Petrakia aesculi</i>	<i>Mycodidymella aesculi</i>	HHUF 22892	<i>Aesculus turbinata</i>	As	JP	CBS 142914	LC194192	LC203348	LC203302	LC203404	LC203376
<i>Petrakia aesculi</i>	<i>Mycodidymella aesculi</i>	HHUF 30549	<i>Aesculus turbinata</i>	Mp	JP	CBS 142913	LC203329	LC203347	LC203301	LC203403	LC203375
<i>Petrakia aesculi</i>	<i>Mycodidymella aesculi</i>	HHUF 30550	<i>Aesculus turbinata</i>	Mp	JP	CBS 142916	LC203331	LC203350	LC203304	LC203406	LC203378
<i>Petrakia deviata</i>		ZT Myc 57658	<i>Acer platanoides</i>	Mc	CH	CBS 8083	KY231233	MK502020	—	MK502054	MK502077
<i>Petrakia deviata</i>		ZT Myc 57663	<i>Acer platanoides</i>	Mc	CH	—	KY231231	MK502022	MK502030	MK502056	MK502079
<i>Petrakia deviata</i>		ZT Myc 57659	<i>Acer platanoides</i>	Mc	CH	CBS 8082	KY231228	MK502021	MK502029	MK502055	MK502078
<i>Petrakia echinata</i>		WU 36921	<i>Acer pseudoplatanus</i>	Mc	AT	—	KY189981	KY189981	—	KY189997	KY190016
<i>Petrakia echinata</i>		WU 36922	<i>Acer pseudoplatanus</i>	Mc	AT	—	KY189980	KY189980	KY190007	KY189996	KY190015
<i>Petrakia echinata</i>		ZT Myc 24157	<i>Acer pseudoplatanus</i>	As	DE	CBS 13072	JQ655727	LC203351	LC203305	LC203407	LC203379
<i>Petrakia echinata</i>		ZT Myc 24161	<i>Acer pseudoplatanus</i>	As	CH	CBS 13070	JQ691628	LC203352	LC203306	LC203408	LC203380
<i>Petrakia echinata</i>		ZT Myc 24162	<i>Acer pseudoplatanus</i>	Mc	CH	CBS 13071	JQ691629	MK502023	MK502031	MK502057	MK502080
<i>Petrakia echinata</i>		ZT Myc 24163	<i>Acer pseudoplatanus</i>	Mp	CH	CBS 13069	JQ691630	MK502024	MK502032	MK502058	MK502081
<i>Petrakia echinata</i>		ZT Myc 59957	<i>Acer campestre</i>	Mp	CH	—	MK562058	MK567979	—	MK577790	MK577788
<i>Petrakia echinata</i>		ZT Myc 59958	<i>Acer monspessulanum</i>	Mp	CH	CBS 145961	MK562059	MK567980	—	MK577791	MK577789
<i>Petrakia echinata</i>		ZT Myc 59962	<i>Acer macrophyllum</i>	As	DE	CBS 145952	MN310550	MN310561	—	MN317129	MN317131
<i>Petrakia fagi</i>	<i>Pseudodidymella fagi</i>	HHUF 22903 ^H	<i>Fagus crenata</i>	Mp	JP	—	LC150787	LC203356	LC203310	LC203412	LC203384
<i>Petrakia fagi</i>	<i>Pseudodidymella fagi</i>	HHUF 30515	<i>Fagus crenata</i>	Mp	JP	CBS 142917	LC150785	LC203353	LC203307	LC203409	LC203381
<i>Petrakia fagi</i>	<i>Pseudodidymella fagi</i>	HHUF 30516	<i>Fagus crenata</i>	Mp	JP	CBS 142918	LC150786	LC203354	LC203308	LC203410	LC203382
<i>Petrakia fagi</i>	<i>Pseudodidymella fagi</i>	HHUF 30517	<i>Fagus crenata</i>	Mp	JP	—	LC150788	LC203355	LC203309	LC203411	LC203383
<i>Petrakia fagi</i>	<i>Pseudodidymella fagi</i>	HHUF 30553	<i>Fagus crenata</i>	Mp	JP	—	LC203332	LC203357	LC203311	LC203413	LC203385
<i>Petrakia greenei</i>		WIS-F-0027755 ^H	<i>Acer saccharinum</i>	Mc	US	—	MN310551	MN310562	—	MN317130	MN317132
<i>Petrakia irregularis</i>		CBS 306.67	<i>Acer pseudoplatanus</i>	Mc	NL	CBS 306.67	MH858977	MH870670	—	—	—
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	KRAM F-59424	<i>Fagus sylvatica</i>	Mp	SK	CBS 145227	MH393365	MH393364	—	—	—
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	WU 41173	<i>Fagus sylvatica</i>	Mp	AT	—	MK501992	MK502005	—	MK502039	MK502062
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 57656	<i>Fagus sylvatica</i>	Mp	CH	CBS 142336	KY231227	MK502006	MK502033	MK502040	MK502063
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 57657 ^H	<i>Fagus sylvatica</i>	Mp	CH	CBS 142337	KY231243	MK502007	MK502034	MK502041	MK502064
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 57667	<i>Fagus sylvatica</i>	Mp	CH	—	KY231239	MK502008	MK502035	MK502042	MK502065
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 57668	<i>Fagus sylvatica</i>	Mp	CH	—	KY231234	MK502009	—	MK502043	MK502066
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59926	<i>Fagus sylvatica</i>	Mp	CH	—	MK501993	MK502010	—	MK502044	MK502067
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59928	<i>Fagus sylvatica</i>	Mp	CH	CBS 145957	MK501994	MK502011	—	MK502045	MK502068
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59930	<i>Fagus sylvatica</i>	Mp	CH	CBS 145956	MK501995	MK502012	—	MK502046	MK502069
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59931	<i>Fagus sylvatica</i>	Mp	CH	—	MK501996	MK502013	—	MK502047	MK502070
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59933	<i>Fagus sylvatica</i>	Mp	CH	—	MK501997	MK502014	—	MK502048	MK502071
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59938	<i>Fagus sylvatica</i>	Mp	CH	—	MK501998	MK502015	—	MK502049	MK502072
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59948	<i>Fagus sylvatica</i>	Mp	DE	CBS 145954	MK501999	MK502016	—	MK502050	MK502073
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59949	<i>Fagus orientalis</i>	Mp	DE	CBS 145955	MK502000	MK502017	MK502036	MK502051	MK502074
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59951	<i>Fagus sylvatica</i>	Mp	DE	CBS 145954	MK502001	MK502018	—	MK502052	MK502075
<i>Petrakia liobae</i>	<i>Pseudodidymella fagi p.p.</i>	ZT Myc 59952	<i>Fagus sylvatica</i>	As	FR	CBS 145958	MK502002	MK502019	—	MK502053	MK502076
<i>Petrakia minima</i>	<i>Pseudodidymella minima</i>	HHUF 30551 ^H	<i>Fagus japonica</i>	Mp	JP	CBS 142921	LC203333	LC203358	LC203312	LC203414	LC203386
<i>Petrakia minima</i>	<i>Pseudodidymella minima</i>	HHUF 30552	<i>Fagus japonica</i>	Mp	JP	CBS 142922	LC203334	LC203359	LC203313	LC203415	LC203387
<i>Pleomassaria siparia</i>		CBS H-258	<i>Betula verrucosa</i>	Mp	NL	CBS 279.74	AB554089	DQ678078	DQ678027	DQ677976	DQ677923
<i>Praetumpfia obducens</i>		WU 36897 [‡]	<i>Fraxinus excelsior</i>	As	AT	CBS 141474	KY189984	KY189984	KY190008	KY190000	KY190019
<i>Seifertia alpina</i>	<i>Antromycopsis alpina</i>	ZT Myc 58033	<i>Rhododendron ferrugineum</i>	Sy	CH	CBS 145959	MK542906	MK502025	—	—	MK502082
<i>Seifertia alpina</i>	<i>Antromycopsis alpina</i>	ZT Myc 59953 [‡]	<i>Rhododendron ferrugineum</i>	Sy	CH	CBS 145960	MK502003	MK502026	MK502037	MK502059	MK502083
<i>Seifertia azalea</i>		ZT Myc 57693	<i>Rhododendron sp.</i>	Sy	CH	—	KY231242	MK502027	—	MK502060	MK502084
<i>Seifertia azalea</i>		ZT Myc 59954	<i>Rhododendron sp.</i>	Sy	CH	CBS xxx	MK502004	MK502028	MK502038	MK502061	MK502085
<i>Seifertia shangrilaensis</i>		MFLU 16-0238 ^H	<i>Rhododendron decorum</i>	Sy	CN	—	—	KU954100	KU954101	—	KU954102
<i>Splanchnonema pupula</i>		MFLU 14-0807 ^H	<i>Acer pseudoplatanus</i>	As	IT	—	KP659196	KP659197	—	—	—

Voucher: [‡] = Epitype, ^H = Holotype. State: As = Ascomata, Mc = Macroconidia, Mp = Mycopappus -state, Sy = Synemmata. Countries indicated by international abbreviations.

CBS-numbers of strains isolates in the present study are shown in bold. GenBank accession numbers of sequences generated in the present study are shown in bold.

Table 2. Petrakia liobae specimen collection data.

Country	Location	Latitude	Longitude	Altitude	Host	State	Date	Collector/Reference	Voucher
AT	Salzburg, Golling, Bluntautal	47.57410	13.13212	500 m	<i>F. s.</i>	Mp	30/07/2016	Th. Cech	n/a
AT	Upper Austria, Windischgarten, Haslersgatter	47.73750	14.37944	1150 m	<i>F. s.</i>	Mp	16/09/2016	H. Voglmayr	WU 41173
CH	AI, Alpstein Brülletobel	47.27990	9.46595	1110 m	<i>F. s.</i>	Mp	07/08/2016	L. Beenken	ZT Myc 57673
CH	BE, Bern, forest Dählhölzli	46.93749	7.46028	540 m	<i>F. s.</i>	Mp	09/08/2017	L. Beenken	ZT Myc 59925
CH	BE, Bern, Tiefenau, forest Thornebodewald	46.97169	7.45509	510 m	<i>F. s.</i>	Mp	09/08/2017	L. Beenken	ZT Myc 59926
CH	BE, open-air museum Ballenberg	46.74937	8.09116	700 m	<i>F. s.</i>	Mp	25/08/2016	L. Beenken	ZT Myc 57677
CH	GL, Linthal, forest Schleimen	46.92869	8.98254	1276 m	<i>F. s.</i>	Mp	11/09/2016	A. Gross	ZT Myc 57685
CH	GL, Luchsingen	46.96789	9.02801	720 m	<i>F. s.</i>	Mp	23/08/2016	L. Beenken	ZT Myc 57676
CH	JU, Delémont, forest En Tairèche	47.37434	7.29878	725 m	<i>F. s.</i>	Mp	17/07/2016	V. Queloz	ZT Myc 57660
CH	LU, Hasle, Balmoos	46.96408	8.05886	965 m	<i>F. s.</i>	Mp	21/08/2018	L. Beenken	ZT Myc 59927
CH	SG, Fischingen, forest	47.41519	8.91344	830 m	<i>F. s.</i>	Mp	24/07/2016	L. Beenken	ZT Myc 57671
CH	TI, Rovio, forest at the creek Sovaglia	45.93225	8.99879	570 m	<i>F. s.</i>	Mp	25/07/2017	L. Beenken	ZT Myc 59928
CH	TI, Rovio, forest at the creek Sovaglia	45.93225	8.99879	570 m	<i>F. s.</i>	Mp	15/10/2017	L. Beenken	ZT Myc 59929
CH	TI, Vezio	46.04310	8.88331	690 m	<i>F. s.</i>	Mp	27/09/2016	A. Gross	ZT Myc 57691
CH	VD, Aubonne, Arboretum	46.51125	6.36994	553 m	<i>F. s.</i>	Mp	13/10/2015	O. Holdenrieder	ZT Myc 57688
CH	VD, Aubonne, at the creek L'Aubonne	46.50616	6.37444	505 m	<i>F. s.</i>	Mp	10/08/2017	L. Beenken	ZT Myc 59931
CH	VD, Montherod, near Arboretum Aubonne	46.51460	6.36048	605 m	<i>F. s.</i>	Mp	10/08/2017	L. Beenken	ZT Myc 59930
CH	ZH, Andelfingen, forest at river Thur	47.59604	8.65379	355 m	<i>F. s.</i>	As	13/05/2017	L. Beenken	ZT Myc 59932
CH	ZH, Birmensdorf, forest Egg	47.36857	8.41749	515 m	<i>F. s.</i>	Mp	07/10/2015	A. Gross	ZT Myc 57667
CH	ZH, Birmensdorf, forest Egg	47.36857	8.41749	515 m	<i>F. s.</i>	As	06/05/2016	A. Gross	ZT Myc 57669 ^P
CH	ZH, Birmensdorf, forest Ramerenwald	47.36146	8.44638	550 m	<i>F. s.</i>	Mp	28/07/2017	L. Beenken	ZT Myc 59933
CH	ZH, Flaach, forest at river Thur	47.59601	8.61166	350 m	<i>F. s.</i>	As	13/05/2017	L. Beenken	ZT Myc 59934
CH	ZH, Flaach, forest at river Thur	47.59601	8.61166	350 m	<i>F. s.</i>	Mp	30/07/2017	L. Beenken	ZT Myc 59935
CH	ZH, forest Sihlwald	47.26808	8.52703	870 m	<i>F. s.</i>	Mp	31/08/2016	L. Beenken	ZT Myc 57680
CH	ZH, forest Sihlwald	47.23878	8.57168	590 m	<i>F. s.</i>	As	10/05/2017	L. Beenken	ZT Myc 59936
CH	ZH, Hettlingen, forest Gmeindholz	47.55869	8.69526	450 m	<i>F. s.</i>	As	13/05/2017	L. Beenken	ZT Myc 59937
CH	ZH, Hettlingen, forest Gmeindholz	47.55868	8.69973	455 m	<i>F. s.</i>	Mp	30/07/2017	L. Beenken	ZT Myc 59938
CH	ZH, Kollbrunn, forest Röhrlitobel	47.46401	8.81959	620 m	<i>F. s.</i>	Mp	10/07/2016	L. Beenken	ZT Myc 57670
CH	ZH, Kollbrunn, Tüfelschilen	47.46429	8.80062	550 m	<i>F. s.</i>	Mp	22/07/2017	L. Beenken	ZT Myc 59939
CH	ZH, Marthalen, forest Niederholz	47.61075	8.60568	360 m	<i>F. s.</i>	As	17/05/2017	L. Beenken	ZT Myc 59955
CH	ZH, Marthalen, forest Niederholz	47.61618	8.61171	365 m	<i>F. s.</i>	As	20/05/2017	L. Beenken	ZT Myc 59940
CH	ZH, Stadlerberg, forest	47.54150	8.44861	620 m	<i>F. s.</i>	Mp	16/07/2017	L. Beenken	ZT Myc 59941
CH	ZH, Steg, Brüttental	47.34044	8.94847	750 m	<i>F. s.</i>	Mp	14/08/2016	L. Beenken	ZT Myc 57675
CH	ZH, Wald, at the creek Schmittbach	47.28925	8.93611	760 m	<i>F. s.</i>	Mp	12/08/2018	L. Beenken	ZT Myc 59943
CH	ZH, Weiach, Haggenberg	47.54205	8.43819	620 m	<i>F. s.</i>	Mp	16/07/2017	L. Beenken	ZT Myc 59942
CH	ZH, Winterthur, forest Eschenberg	47.48288	8.72328	530 m	<i>F. s.</i>	As	16/05/2015	L. Beenken	ZT Myc 57666
CH	ZH, Winterthur, forest Eschenberg	47.47327	8.71635	515 m	<i>F. s.</i>	Mp	01/08/2016	L. Beenken	ZT Myc 57672
CH	ZH, Winterthur, forest Eschenberg	47.48742	8.73097	500 m	<i>F. s.</i>	Mp	20/07/2017	L. Beenken	ZT Myc 59944
CH	ZH, Winterthur, forest Lindberg	47.50777	8.74304	520 m	<i>F. s.</i>	Mp	23/07/2017	L. Beenken	ZT Myc 59945
CH	ZH, Zurich, forest at Zürichberg	47.38953	8.55951	647 m	<i>F. s.</i>	Mp	09/09/2008	L. Paul & O. Holdenrieder	ZT Myc 57656
CH	ZH, Zurich, forest at Zürichberg	47.38953	8.55951	647 m	<i>F. s.</i>	Mp	16/09/2011	O. Holdenrieder	ZT Myc 57657 ^H
DE	BW, Swabian Alp, Gomadingen	48.38268	9.38085	770 m	<i>F. s.</i>	Mp	28/08/2019	L. Beenken	ZT Myc 59964
DE	BW, Black Forest, Albtal	47.68695	8.13346	515 m	<i>F. s.</i>	Mp	12/08/2016	L. Beenken	ZT Myc 57674
DE	BW, Konstanz, close to the university	47.69379	9.17904	460 m	<i>F. s.</i>	Mp	04/08/2017	L. Beenken	ZT Myc 59946
DE	BY, Bernrieder Park	47.86221	11.29614	620 m	<i>F. s.</i>	Mp	10/09/2016	L. Beenken	ZT Myc 57684
DE	BY, Gauting, forest at the river Würm	48.03872	11.37138	575 m	<i>F. s.</i>	Mp	21/08/2017	L. Beenken	ZT Myc 59947
DE	BY, Leutstetten, forest Wildmoos	48.02222	11.38350	600 m	<i>F. s.</i>	Mp	21/08/2017	L. Beenken	ZT Myc 59948
DE	BY, Munich, botanical garden	48.16224	11.49968	520 m	<i>F. o.</i>	Mp	16/09/2016	L. Beenken	ZT Myc 57690
DE	BY, Munich, botanical garden	48.16224	11.49968	520 m	<i>F. o.</i>	Mp	21/08/2017	L. Beenken	ZT Myc 59949
DE	BY, Munich, forest Allacher Forst	48.20447	11.47704	500 m	<i>F. s.</i>	Mp	06/09/2016	L. Beenken	ZT Myc 57683
DE	BY, Munich, forest Allacher Forst	48.20452	11.47827	505 m	<i>F. s.</i>	Mp	26/08/2017	L. Beenken	ZT Myc 59950
DE	BY, Murnau, forest Oberried	47.67508	11.16276	670 m	<i>F. s.</i>	Mp	15/09/2016	L. Beenken	ZT Myc 57689
DE	BY, Pähl, Hartschimmel	47.93747	11.18007	695 m	<i>F. s.</i>	Mp	14/09/2016	L. Beenken	ZT Myc 57688
DE	BY, Paterzeller Eibenwald	47.86042	11.05142	610 m	<i>F. s.</i>	Mp	12/09/2016	L. Beenken	ZT Myc 57686
DE	BY, Schäftlarn, forest	47.98536	11.46671	590 m	<i>F. s.</i>	Mp	13/09/2016	L. Beenken	ZT Myc 57687
DE	TH, Martinroda, forest Veronikaberg	50.73252	10.90397	510 m	<i>F. s.</i>	Mp	24/08/2017	L. Beenken	ZT Myc 59951
FR	Pyrenees, Laruns, Lac de Bisous-Artigues	42.86340	-0.45183	1430 m	<i>F. s.</i>	As	05/06/2017	A. Gross	ZT Myc 59952
SI	Kamniška Bela	46.32020	14.60161	620 m	<i>F. s.</i>	Mp	01/08/2018	Ogris <i>et al.</i> (2019)	LJF 7014
SI	Ljubljana	46.05195	14.47859	320 m	<i>F. s.</i>	Mp	01/08/2018	Ogris <i>et al.</i> (2019)	LJF s.N.
SK	Košice Region, Spišská Nová Ves	48.90000	20.55002	530 m	<i>F. s.</i>	Mp	01/08/2017	P. Czachura	KRAM F-59424

Countries indicated by international abbreviations. Locations: Swiss Cantons and German states are abbreviated as follow: AI = Appenzell Innerrhoden, BE = Bern, BY = Bavaria, BW = Baden-Württemberg, GL = Glarus, JU = Jura, LU = Luzern, SG = St. Gallen, TH = Thuringia, TI = Ticino, VD = Vaud, ZH = Zurich. Hosts: *F. s.* = *Fagus sylvatica*, *F. o.* = *Fagus orientalis*. State: As = Ascomata, Mp = Mycopappus-like. Vouchers: ^H = Holotype, ^P = Paratype.

Table 3. Petrakia spp. on Sapindaceae

	<i>P. aceris</i> ¹	<i>P. deviata</i> ²	<i>P. echinata</i> ^{2 3}	<i>P. greenei</i>	<i>P. aesculi</i> ⁴
Host	<i>Acer macrophyllum</i>	<i>Acer campestre</i> , <i>Acer platanoides</i>	<i>Acer pseudoplatanus</i> , <i>Acer spp.</i>	<i>Acer saccharinum</i>	<i>Aesculus turbinata</i>
Distribution	North America	Eurasia	Eurasia	North America	Asia
Ascomata:	–	–	+	–	+
<i>Mycopappus</i>-state:	+	+	+	+	+
Diameter of main body	ca. 150 µm	62–200 µm	65–180 µm	100–250 µm	200–325
Cells of main body	8–15 x 5–15 µm	9–15 µm in diam.	6–12 µm in diam.	7–10(20) µm in diam.	10–15 x 7.5–13.5 µm
Number of Appendages	10–25	10–25	10–25	15–50	
Appendage length	100–300 µm	175–400 µm	100–350 µm	100–300 µm	140–190
Appendage width	4.5–6 µm	3–4.5 µm	2–4 µm	3–5 µm	5–7.5
Septa per appendage	2–4	+	+	+	5–7
Macroconidia:	+	+	+	+	+
Shape	clavate	ovate	sub globose	spindle-shaped	curved
Length	35–45µm	20–42 µm	20–40 µm	26–48.5 µm	20–100 µm
Width	10–12µm	11–19 µm	18–30 µm	14.5–26 µm	5–7.5 µm
Length/wide ratio	ca. 3–3.8	ca. 2–2.5	0.9–1.5	1.2–2.6	ca. 10–15
Septation	cross septate to muriform	distinct muriform	distinct muriform	distinct muriform	only cross septate
Number of cross septa ⁵	3–8	6–9	1–3	2–5	3–13
Colour	pale brown	brown	dark braun	dark braun	colourless
Number of Appendages	–	1 apical	3–10	1–6	0
Appendage length	–	14–18 µm	5–35 µm	5–35 µm	–
Appendage width	–	2.5–5 µm	3.5–4.5 µm	3.5–4.5 µm	–

Data copied from: ¹ Readhead and White (1985), Funk (1986), Crouse et al. 2009; ² Gross et al. 2017; ³ Butin et al. 2013, Kirisits 2007, Sydow and Sydow 2013; own observations; ⁴ Wei et al. 1998. ⁵ Primarily formed transverse septa that extend over the entire width of the conidia.

Table 4. Petrakia spp. on Fagus spp.

	<i>P. liobae</i>	<i>P. fagi</i> ¹	<i>P. minima</i> ¹
Host	<i>F. sylvatica</i> (<i>F. orientalis</i>)	<i>F. crenata</i>	<i>F. japonica</i>
Distribution	Europe	Japan	Japan
Ascomata:	+	+	–
Diameter	135–180–225 µm	200–300 µm	–
Hight	87–112.9–163 µm	175 µm	–
Asci length	51–54.6–60 µm	49–60.3–77 µm	–
Asci width	8.5–9.7–11 µm	10–11.5–14 µm	–
Ascospore length	16–19.5–23 µm	18.5–20.5–24 µm	–
Ascospore width	5–5.4–6 µm	4–4.3–5 µm	–
Spermatia	–	+	–
<i>Mycopappus</i>-state:	+	+	+
<i>Mycopappus</i> diameter	300–500 µm	290–387.2–500 µm	110–164.4–220 (240) µm
Diameter of main body	185–241–295 µm	160–227.4–315 µm	78–115–168 µm
Cells of main body	8–12–15 µm in diam.	11.5–15x7.5–11.5 µm	7.5–10 µm in diam.
Number of Appendages	>80	63–138	65–135
Appendage length	94–118–150 µm	67–97.1–133 µm	27–35.5–44 µm
Appendage width	5.5–6.25–7.5 µm	3–3.7–5	3–4.4–6
Septa per appendage	1–6	1–4	(0)1–2

¹ Data compiled from Hashimoto et al. (2017). Mesured values are given in minimum–mean–maximum.

Table 5. Seifertia spp. on Rhododendron spp.

	<i>S. alpina</i> ¹	<i>S. alpina</i> ²	<i>S. azaleae</i> ³	<i>S. shangrilaensis</i> ⁴
Hosts	<i>R. ferrugineum</i>	<i>R. ferrugineum</i>	<i>R. peryclymenoides</i> , <i>R. spp. cult.</i>	<i>R. decorum</i>
Mode of nutrition	saprotrophic	saprotrophic	necrotrophic	saprotrophic / necrotrophic
Substrate	Dry fruits, pedicels	Dry fruits, pedicels	Bud blight, twigs	Living and dead rachides
Origin	Austria	Switzerland	North America	China
Synnemata stalk	200–800 x 50–60 µm	80–340 x 50–65 µm	500-2500 x 200-500 µm	1000–2300 µm x 120–200 µm
Stalk hyphae	4–5 µm wide	3.5–5.0 µm wide	4–7µm wide	9.5–12.6 µm wide
Conidiogenous hyphae	4–5 µm wide	4.0–5.0 µm wide	4–7 µm wide	9.5–12.6 µm wide
Conidia	4–12 x 3–4 µm	5.5–13.3 x 3.8–5.5 µm	4–12 x 4–8 µm	2.5–6 × 2.5–3.5 µm

Data compiled from: ¹ Höhnelt (1914); ² own observations; ³ Endrestøl (2017), Partridge and Morgan-Jones (2002) and Viennot-Bourgin (1981); ⁴ Li et al. (2016b).

Figure1

ITS-LSU

RPB2-TEF1

Figure2

ITS-LSU-RPB2-TEF1

Figure 3

Figure 4

Figure 5

Figure 6

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