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Notes on *Buelliella* (Dothideomycetes, Ascomycota): phylogenetic position of *B. lecanorae* and description of the asexual stage of *B. physciicola*

Notas sobre *Buelliella* (Dothideomycetes, Ascomycota): posición filogenética de *B. lecanorae* y descripción del estado asexual de *B. physciicola*

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Abstract

The polyphyletic genus *Buelliella* includes lichen-inhabiting species that belong either to *Asterotexiales* or *Asterinales* in Dothideomycetes. In this paper, we provide phylogenetic information for one additional *Buelliella* species—*B. lecanorae*. In addition, we present a first description of an asexual stage in *Buelliella*—for *B. physciicola*—based on the matching of molecular data and host choice.

Keywords: Anamorph-teleomorph connection; *Epithamnolia*; fungal systematics; *Lecanora*; lichenicolous fungi; *Phaeophyscia*; *Physciaceae*.

Resumen

El género polifilético *Buelliella* incluye especies que habitan en líquenes y que pertenecen a *Asterotexiales* o *Asterinales* en Dothideomycetes. En este trabajo, proporcionamos información filogenética para una especie adicional de *Buelliella*: *B. lecanorae*. Se describe por primera vez el esta-

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do asexual en *Buelliella*, para *B. physciicola*, basada en la concordancia de los datos moleculares y la elección del hospedador.

Palabras clave: Conexión anamorfo-teleomorfo; *Epithamnolia*; sistemática fúngica; *Lecanora*; hongos liquenícolas; *Phaeophyscia*; *Physciaceae*.

INTRODUCTION

Lichenicolous fungi represent a specialized group of parasitic, parasymbiotic and saprotrophic fungi that grow on the thalli or reproductive bodies of lichens (Diederich *et al.*, 2018). The genus *Buelliella* Fink ex Hafellner includes lichen-inhabiting fungi characterized by apothecioid ascomata that are initially closed, but opening irregularly in the centre when mature. They have bitunicate, 8-spored asci that are I– and K/I– and have a distinct ocular chamber. The ascospores are 1-septate, smooth, brown and slightly constricted near the septum (Hafellner, 1979; Ertz & Diederich, 2015). The genus includes 14 species (Index Fungorum: https://www.indexfungorum.org) accepted by Hafellner (1979) or described at a later date. Sequence data are available for three of them—*Buelliella physciicola* Poelt & Hafellner, *B. poetschii* Hafellner (Ertz & Diederich, 2015), and the type species *B. minimula* (Tuck.) Fink (Ertz *et al.*, 2016; Jüriado *et al.*, 2022). All molecular phylogenies that include sequences of *Buelliella* (Ertz & Diederich, 2015; Ertz *et al.*, 2016; Hongsanan *et al.*, 2020) show polyphyly of the genus within Dothideomycetes. Two species—*B. minimula* and *B. physciicola*—have been shown to belong to different clades within *Asterotexiales*, but *B. poetschii* belongs to *Asterinales.* Because of this distant phylogenetic position, Hongsanan *et al.* (2020) described the monotypic genus *Neobuelliella* Hongsanan & K.D. Hyde and family *Neobuelliellaceae* for the latter.

In this paper we have two goals. First, we provide phylogenetic information for an additional *Buelliella* species—*B. lecanorae* Suija & Alstrup—based on recently generated sequences. Second, we describe the asexual stage for *B. physciicola* based on observational and molecular data.

MATERIAL AND METHODS

Materials and microscopy

The study is based on fresh specimens of *Buelliella physciicola* and *B. lecanorae* collected by the authors and deposited in TUF (Table 1). For microscopic examination, freehand ascomata sections were mounted in tap water, in potassium hydroxide (KOH; K) c. 10% solution and in Congo red pre- and post-processed with K. All microscopic measurements were made in tap water and given as (minimum–) average ± standard deviation (–maximum)

Table 1. Sequenced specimens (lab ID, voucher ID, collector name and collector ID) and NCBI ID-s for sequenced DNA regions. – = no sequence generated.

Tabla 1. Especímenes secuenciados (ID de laboratorio, ID de voucher, nombre del recolector e ID del recolector) e ID-s del NCBI para las regiones de ADN secuenciadas. – = ninguna secuencia generada.

Taxon name	Lab ID	Voucher	Collector / Country	nuLSU	nuITS	mtSSU
[Buelliella] lecanorae	AS952	TUF091928	Suija / Estonia	PQ847482	PQ847876	PQ847484
[Buelliella] physciicola	AS804	TUF091855	Haldeman 3752 / U.S.A.	–	PQ847874	–
[Buelliella] physciicola	HA512	TUF095350	Haldeman 3735 / U.S.A.	PQ847481	PQ847873	–
[Buelliella] physciicola	AS093	TUF095223	Haldeman 5246 / U.S.A.	PQ847483	PQ847875	–

and followed by the number of measurements (n). Microscropy was done using a Leica M205 A stereomicroscope and a Nikon 80i light microscope. Microscopic structures were measured and photographed using NIS-Elements ver. 5.20.00 imaging software.

DNA extraction, PCR amplification, DNA sequencing and analyses of sequences

DNA extraction and amplification were carried out at Tartu University (TU). For DNA extraction, we removed ascomata or conidiomata from the lichen thallus and placed them into a 1.5 mL test tube. DNA extraction was carried out using High Pure PCR Template Preparation Kit (Roche Applied Science®) and following the protocol provided by the manufacturer.

We amplified two nuclear (internal transcribed spacer [nulTS] and large subunit [nuLSU]) ribosomal DNA regions, and for *Buelliella lecanorae* also mitochondrial small subunit (mtSSU) ribosomal DNA region. To amplify these loci, we used the primer pairs: ITS0F / LA-W (Tedersoo *et al.*, 2008), LR0R / LR7 (Vilgalys & Hester, 1990), and mrSSU1 / mrSSU3r (Zoller *et al.*, 1999), respectively. The details of PCR amplification, DNA purification and sequencing are given e.g. in Suija *et al.* (2018). Both DNA strands were Sanger sequenced in Macrogen Inc. (Amsterdam, the Netherlands). The extracted DNA samples are kept in the DNA and Environmental Sample Collection of the Natural History Museum in Tartu University (TUE).

CodonCode Aligner ver. 8.0.2 (CodonCode Corporation®, Centerville, MA, U.S.A.) was used to check, assemble, and manually adjust the resulting sequence fragments. To avoid misidentifications, we compared consensus sequences with those available in the nucleotide database of the National Center for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih.gov/) using mainly the 'megablast' algorithm (Altschul *et al.*, 1990). After checking, the new sequences were submitted to NCBI (Table 1) and UNITE (Abarenkov *et al.*, 2023) data repositories.

We compiled and analysed both nuLSU and mtSSU datasets, but the phylogeny presented is based only on the nuLSU marker because of the larger taxon selection. The taxon compilation is based mainly on that of Ertz *et al.* (2016) including lichenicolous genera *Hemigrapha*, *Karschia*, *Labrocarpon*, *Neobuelliella* and *Taeniolella*, all belonging to *Asterinales* and *Asterotexiales*. *Capnodium coffeae* (*Capnodiales*), *Dothidea insculpta* (*Dothideales*) and *Preussia terricola* (Pleosporales) were incorporated to root the tree. The final nuLSU dataset contained 66 taxa, and was aligned using the online version of MAFFT ver. 7 (Katoh *et al.*, 2019; https://mafft.cbrc.jp/alignment/server/index.html) applying L-INS-i (Katoh *et al.*, 2005) as an iterative refinement method. The online version of Gblocks ver. 0.91b (Talavera & Castresana, 2007) run at http://molevol.cmima.csic.es/castresana/Gblocks_server.html was used to eliminate poorly aligned positions and divergent regions of the alignment but allowing gap positions within the final blocks. The original alignment contained 1915 nucleotide positions, but after applying Gblocks, the resulting alignment contained 786 sites, of them 412 constant (= 52.4% of all sites) and 273 parsimony informative sites (PIC; = 34.7%).

We used the online version of IQTree ver. 1.6.12. (Nguyen *et al.*, 2015) for reconstruction of the phylogeny. The best-fit nucleotide substitution model selected according to AIC criterion was TIM2+F+I+G4. To estimate branch support, we used ultrafast bootstrapping (Hoang *et al.*, 2018) with 1000 iterations. The log-likelihood of the consensus tree was: -7950.529669. In parallel, we calculated Bayesian based phylogeny implemented in MrBayes ver. 3.2.7. (Ronquist *et al.*, 2012). TIM + I + G was selected as the nucleotide substitution model according to the lowest AIC value. The settings of the Bayesian were as follows: two parallel, simultaneous runs with four incrementally heated chains starting with a random tree; ngen = 700,000 generations, samplefreq and printfreq = 500, diagnfreq = 2000. The mcmc analysis was run until the average standard deviation of split frequencies (SDSF) was 0.01, and the potential scale reduction factor (PSRF) was close to 1 indicating convergence of the chains. The first 25% was discarded as 'burn-in' and a consensus tree and posterior probabilities (PP) were calculated from the remaining tree distribution. The phylogenetic tree was visualised and edited using FigTree ver. 1.4.4 (Rambaut, 2018) and post-processed with Adobe Illustrator CS3® ver. 13.0.0.

RESULTS

Eight sequences (3 nuLSU, 4 nuITS and 1 mtSSU) were generated for this study (Table 1), but only nuLSU sequences were used to generate the phylogeny because here the number of reference sequences was the largest. The phylogeny agrees with that of Ertz and Diederich (2015) and Ertz *et al.* (2016) showing polyphyly of *Buelliella* and other lichenicolous genera

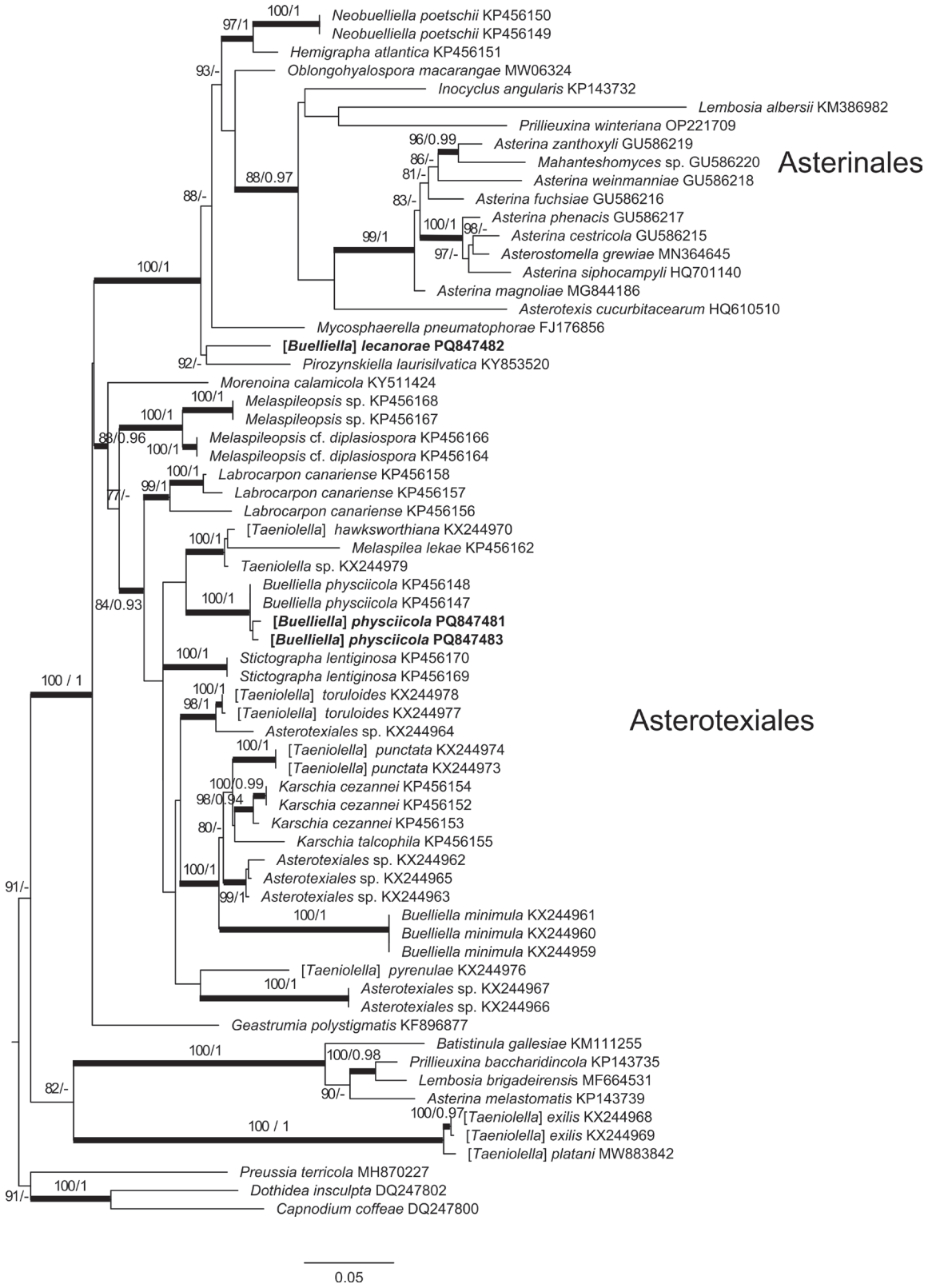

Fig. 1. The nuLSU based ML phylogeny showing position of lichenicolous *Asterinales* and *Asterotexiales* (Dothideomycetes), including newly sequenced *Buelliella lecanorae* and *B. physciicola* (both asexual and sexual stage). New sequences are marked in bold. The clades with bootstrap support (BS) higher than 75 and Bayesian posterior probabilities ➤

(PP) higher than 0.93, indicated above the branch and separated by slash, are considered as supported. Thicker lines show support based on both analyses. NCBI accession codes are at the tips of the tree. The scale bar is proportional to the substitution rate.

Fig. 1. La filogenia ML basada en nuLSU muestra la posición de los líquenícolas *Asterinales* y *Asterotexiales* (Dothideomycetes), incluyendo las nuevas secuencias de *Buelliella lecanorae* y *B. physciicola* (tanto en estado asexual como sexual). Las nuevas secuencias están marcadas en negrita. Los clados con un soporte bootstrap (BS) superior a 75 y probabilidades posteriores bayesianas (PP) superiores a 0,93, indicados sobre el clado y separados por una barra oblicua, se consideran soportados. Las líneas más gruesas muestran el soporte basado en ambos análisis. Los códigos de acceso NCBI están en los extremos del árbol. La barra de escala es proporcional a la tasa de sustitución.

in *Asterinales* and *Asterotexiales* (Dothideomycetes) (Fig. 1). According to the phylogeny, *Buelliella physciicola* and *B. minimula* belong to *Asterotexiales* while *B. lecanorae* comes under *Asterinales* and is sister to the saprophytic hyphomycete *Pirozynskiella laurisilvatica* Hern.-Restr., R.F. Castañeda & Gené (BP = 92; PP = 0.78). *Neobuelliella poetschii* and other lichenicolous species in *Asterinales* are only distantly related to it.

The North American and European specimens of *B. physciicola* form a well-supported clade (BP = 100, PP = 1), that is sister to a clade consisting of two *Taeniolella* species and *Melaspilea lekae* Brackel & Kalb (Fig. 1). The nuLSU sequences of *B. physciicola* specimens from different regions are not one-by-one identical, but there are five parsimony informative sites (0.5 % of 1293 sites; Table 2). There are no nuITS sequences available for European specimens to evaluate the variation in a less-conservative gene locus. Two of the North American specimens (TUF091855 / Haldeman 3752 and TUF095223 / Haldeman 5246) have ascomata, while the third specimen (TUF095350 / Haldeman 3735) has sporodochia superficially resembling *Epithamnolia* (Suija *et al.*, 2018). The comparison of DNA sequences (nuLSU and nuITS) leaves, however, no doubt that this fungus is the asexual stage of *B. physciicola*. The number of variable sites in the alignment of three nuITS sequences is 11 (1.3% of 823 bp). Herewith, we amend the description of *B. physciicola*.

Table 2. Distribution of polymorphisms in nuLSU sequences in European and North American specimens of *Buelliella physciicola*.

Tabla 2. Distribución de polimorfismos en las secuencias nuLSU de especímenes europeos y norteamericanos de *Buelliella physciicola*.

Sequence	Country	Position in the nuLSU alignment				
		59	926	927	946	1006
KP456148	Belgium	C	T	C	G	C
KP456147	Belgium	C	T	C	G	C
PQ847483	U.S.A.	T	C	T	A	T
PQ847481	U.S.A.	T	C	T	A	T

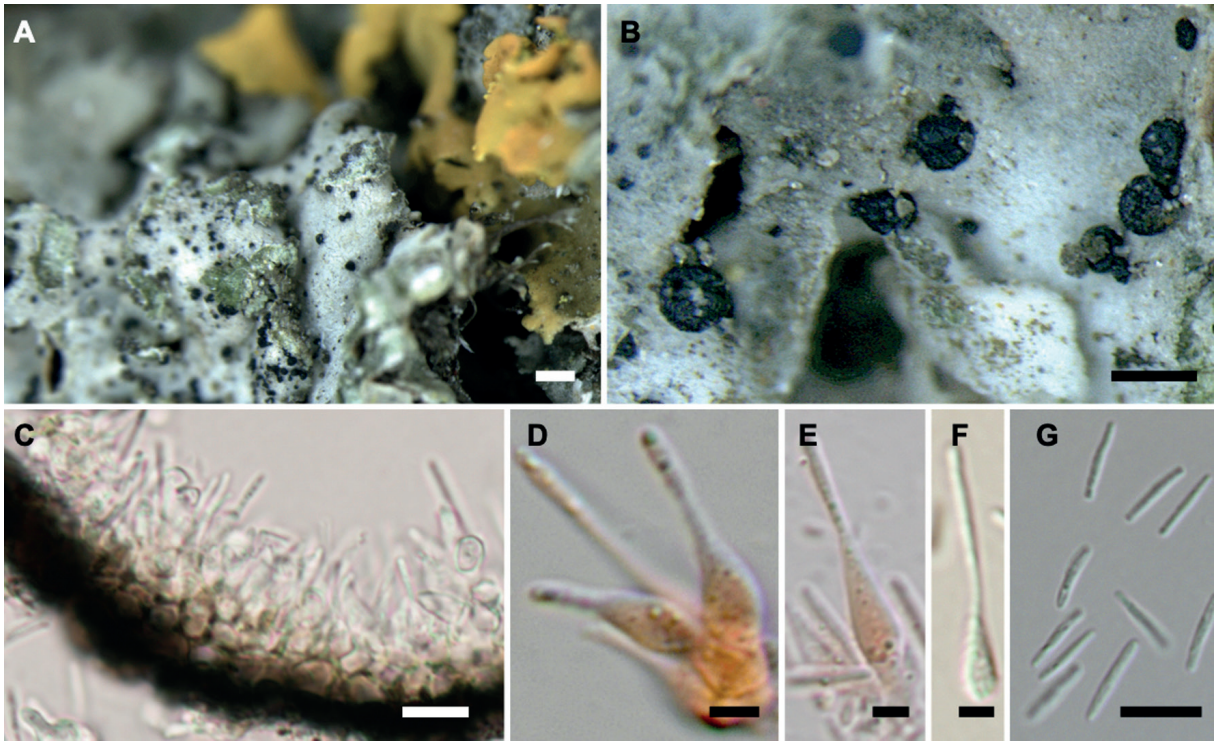

Fig. 2. Asexual stage of *Buelliella physciicola* (Haldeman 3735; TUF095350). A-B) Sporodochia on the thallus of *Phaeophyscia orbicularis.* C) Detail of the conidioma (cross section), conidiogenous cells lining the wall. D-F) Conidiogenous cells with conidia. G) Conidia. Scales: A = 0.5 mm, B = 0.1 mm, C = 5 μm, D, E, F = 2 μm; G = 10 μm. C, F and G in water, D and E in Congo red pre- and post-treated with KOH, respectively.

Fig. 2. Estado asexual de *Buelliella physciicola* (Haldeman 3735; TUF095350). A-B) Esporodoquios en el talo de *Phaeophyscia orbicularis*. C) Detalle del conidioma (corte transversal), células conidiógenas recubriendo la pared. D-F) Células conidiógenas con conidios. G) Conidios. Escalas: A = 0,5 mm, B = 0,1 mm, C = 5 μm, D, E, F = 2 μm; G = 10 μm. C, F y G en agua, D y E en rojo Congo pre y postratados con KOH, respectivamente.

Buelliella physciicola Poelt & Hafellner,
Beih. Nova Hedwigia 62: 155 (1979). (Fig. 2)

Mycelium indistinct. Conidiomata sporodochial, sessile, (40–)49.6–115.6(–135) μm in diameter (n = 20), black, glossy, cupulate (with central depression) when mature, without depression when young, dispersed or loosely aggregated over the lichen thallus. Wall of the conidiomata dark brown, of *textura angularis* type, c. 10 μm in cross section, K–; individual cells (3.0–)3.4–4.9(–5.5) × (2.4–)2.7–3.6(–4.0) μm, l/w = 1.2–2.0 (n = 20). Conidiophores not observed. Conidiogenous cells lining the wall of conidiomata, hyaline, flask-shaped, (6.0–)6.3–8.2(–12) × (1.5–)2.0–3.0 μm, l/w = 2.2–4.5 (n = 11), phialidic, acropetal, determinate. Conidia one-celled, hyaline, smooth-walled, bacilliform to filiform, with one end rounded and the other abruptly truncate, a few also narrowing at one end, straight to slightly curved, (7.5–)8.1–9.9(–11.0) × (0.7–)0.9–1.3(–1.5) μm, l/w = 5.9–13.3 (n=28).

Specimens examined in this study: *Buelliella physciicola*: UNITED STATES, Washington, Asotin County, Hells Canyon area, Grande Ronde River mouth, 46.06209°N 117.0012°W, 327 m asl, outcrop cliff bands on steep grassy slope above river, on *Phaeophyscia orbicularis* and *Physconia enteroxantha* on the base of a small deciduous shrub, 22-I-2021, leg. & det. *M. Haldeman 3735* (TUF095350); Whatcom County, Chuckanut Bay Pocket Estuary, 48.7025°N 122.4992°W, 5 m asl, *Pseudotsuga* and *Alnus rubra* woods on protected estuarine shore, on *P. orbicularis* on sandstone outcrop, 3 m above the barnacles, 28-II-2021, leg. & det. *M. Haldeman 3752c* (TUF091855); Larrabee State Park, between Clayton Beach and Wildcat Cove, 48.6462°N 122.4895°W, 10 m asl, on *P. orbicularis* on exposed sandstone above bay, 25-I-2024, leg. & det. *M. Haldeman 5246* (TUF095223).

Buelliella lecanorae: ESTONIA, Pärnu County, Lääneranna, comm., Kitselaid islet, Varbla Islets Nature Reserve, 58.45437°N 23.6766°E, on *Lecanora saligna* growing on *Juniperus communis*, 23-IX-2022, leg. & det. A. Suija (TUF091928.a); Viljandi county, Põhja-Sakala comm, Suure-Jaani churchyard, 58.53345°N 25.46664°E, on *L. chlarotera* on *Acer platanoides*, 20-VII-1996, leg. I. *Jüriado 421* (TUF008283.a, holotype).

DISCUSSION

In this paper, we do not make any nomenclatural rearrangements although newly sequenced *Buelliella lecanorae* belongs to the order *Asterinales* whereas the type of *Buelliella*, *B. minimula*, belongs to the order *Asterotexiales*. However, at this point, we chose not to introduce nomenclatural changes until more species and specimens are sequenced along with detailed morphological studies.

The asexual stages of *Asterinales* and *Asterotexiales* are structurally variable, being either coelomycetous or hyphomycetous, and the process of conidiogenesis varies between taxa (e.g., Hongsanan *et al*., 2020; Ertz *et al*., 2016). However, many of the asexual species are included in these orders based on observational data without confirmation with sequence data. *Taeniolella* is an asexual fungus in the *Asterotexiales* with many lichenicolous species. It is characterized by a lack of conidiomata, forming dark brown hyphal colonies on the host (Heuchert *et al.*, 2018). This is much different than the asexual stage we describe for *Buelliella physciicola*, which superficially resembles *Epithamnolia* (Zhurbenko, 2012; Suija *et al.*, 2018; Suija *et al.*, 2024). However, the conidiogenous cells in *Buelliella physciicola* are more flask-shaped (Fig. 2), whereas those in *Epithamnolia*, a member of the *Leotiales*, are narrowly lageniform to fusiform (Suija *et al*., 2024).

We also found, that the nuLSU sequences from North American and European *Buelliella physciicola* specimens differ from each other by a few nucleotide positions hinting at a potential speciation event. *Buelliella physciicola* is a globally distributed species reported from Asia (Japan), Canary Islands, Europe (many countries), North America (Canada, Mexico, U.S.A.) and South America (Ecuador, Peru) (Hafellner, 1979; Santesson, 1988, 1998; Hafellner, 2004; Hafellner *et al.*, 2008; Brackel, 2014; Ertz & Diederich, 2015; Etayo, 2017). Therefore, more DNA barcoding markers (nuITS) should be generated, and more detailed microscopic studies should be carried out on a wider global scale to clarify if *B. physciicola* is a single species or belongs to a group of closely related species.

The type specimen of *B. physciicola* was from *Phaeophyscia sciastra* (Hafellner, 1979). That description included other hosts like "*Phaeophyscia orbicularis* and *Physcia* cf. *hirtuosa* (*Phaeophyscia hirtuosa* in Esslinger, 1978: 304). Our sequenced specimens from northwestern U.S.A. (Washington) and Europe (both from Belgium) were also on *Phaeophyscia orbicularis* (Ertz & Diederich, 2015). Hafellner (2004), only listed *Phaeophyscia* spp. as hosts in his account of *B. physciicola*. Almost all published records of *B. physciicola* are from *Phaeophyscia* spp. (see above sources). However, there is one record from Ecuador on *Physcia* sp. (Etayo, 2017). Therefore, in addition to exploring genetic variation geographically, variation on other host species should be explored. Our record Haldeman 3735 was mainly growing on *Phaeophyscia orbicularis*, but was also growing on an intertwined thallus of *Physconia enteroxantha*. We did not sequence the conidiomata from the *Physconia*, but it was morphologically consistent with the conidiomata on *Phaeophyscia*. This may support the idea that *B. physciicola* can inhabit a broader host range within the *Physciaceae*. but *Phaeophyscia* seems to be the preferred host genus.

There are scattered reports of *Buelliella lecanorae*. All previous reports have been from Europe (Estonia, Germany, Switzerland and Ukraine), Asia (Joshi *et al*., 2020) and South America (Flakus & Kukwa, 2012), on corticolous members of the *Lecanora subfusca* group—*L. argentata*, *L. chlarotera* and *L. pulicaris*—(Suija & Alstrup, 2004; Brackel, 2014; Kapetz *et al.*, 2015; Zimmermann, 2022). However, the sequenced specimen reported here was from a member of the *Lecanora varia* group, *L. saligna*. Our phylogeny includes only one European specimen, therefore, similarly to *B. physciicola*, there may be some polymorphisms in DNA sequences when sampled from wider geographic regions.

To conclude, our study is one step forward for understanding phylogeny and heterogeneity of the morphology-based genus *Buelliella.* Increasing sampling and sequencing is necessary to solve phylogenetic placement of several taxa lacking recent collections and to finally make inevitable nomenclatural rearrangements.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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