DOI 10.12905/0380.sydowia79-2027-0027

# Island Icebreaker: first records of Laboulbeniales from Iceland

Felix Heyman[1,*], Renārs Gūts[1], Warre Van Caenegem[1,2,3], Vladimir I. Gusarov[4] & Danny Haelewaters[1,2,3]

[1] Research Group Mycology, Ghent University, 9000 Ghent, Belgium
[2] Department of Zoology, Faculty of Science, University of South Bohemia, 370 05 České Budějovice, Czechia
[3] Biology Centre of the Czech Academy of Sciences, Institute of Entomology, 370 05 České Budějovice, Czechia
[4] Natural History Museum, University of Oslo, NO-0318 Oslo, Norway

* e-mail: felixheyman2002@gmail.com

Heyman F., Gūts R., Van Caenegem W., Gusarov V.I. & Haelewaters D. (2026) Island Icebreaker: First records of Laboulbeniales from Iceland. Sydowia 79: 27–42.

Laboulbeniales (Ascomycota, Pezizomycotina) are a notoriously understudied order of fungi found all over the world, and their presence in Iceland is only now being documented. These microfungi live as ectobiont commensals and ectoparasites on arthropods. In this study, arthropod specimens were collected on the Reykjanes Peninsula, which resulted in two new records of Laboulbeniales. The first record, *Laboulbenia notiophili* was observed on the host *Notiophilus biguttatus* (Coleoptera: Carabidae). A morphological and molecular phylogenetic study confirmed that *Laboulbenia notiophili* shows no morphological or genetical differentiation compared to previous European records on the same host. Our molecular phylogenetic reconstruction supports the hypothesis that *L. notiophili* represents a complex of multiple species differentiated by their host association. The phylogenetic reconstruction based on ITS sequences revealed five clades: one associated with the Lebiini tribe, the second one with *Notiophilus rufipes*, the third one with remaining *Notiophilus* host species and the final two consisting of *L. metableti* and *L. stilicicola*. The second record, *Rickia zanettii*, was found on the host *Omalium excavatum* (Coleoptera: Staphylinidae) of which the first genetic data were generated. The length of *R. zanettii* was smaller compared to previous records of *R. zanettii*, but otherwise the morphology is identical. Additionally, the first Norwegian records of *Rickia huggertii* on *Omalium* cf. *riparium* were included in the phylogenetic analysis. These Icelandic records represent the first-ever observations of Laboulbeniales from the island, revealing gaps in the knowledge of the island's fungal diversity. They also highlight the value of continued sampling, even in well-studied regions, and demonstrate that Wallacean shortfalls are not confined to understudied areas.

Keywords: Ascomycota, *Laboulbenia notiophili*, Laboulbeniomycetes, *Rickia zanettii*, species complex, Wallacean shortfall.

Situated between the North Atlantic and Arctic Oceans in the subarctic zone, Iceland is often referred to as "the land of fire and ice". This informal title reflects the dual forces that have shaped its landscape, which influenced Iceland's biodiversity (Wasowicz et al. 2014, Hågvar et al. 2020). On one side, Iceland lies directly atop the Mid Atlantic Ridge (MAR), which drives substantial geological activity, carving the terrain with faults, lava flows, and volcanic ridges (Sigurgeirsson & Einarsson 2019, Sæmundsson et al. 2020). On the other side, numerous glaciers are scattered across the island. These glaciers are remnants of an ice sheet with an average thickness of 940 meters that covered Iceland during the Last Glacial Maximum (Hubbard et al. 2006). The *tabula rasa* theory hypothesizes that this ice sheet eradicated most terrestrial life of the island. Following its retreat, Iceland was recolonized primarily by palearctic species (Coope et al. 1986, Vickers & Buckland 2015, Bennike & Böcher 2021). Ice rafting from Scandinavia likely facilitated this recolonization (Panagiotakopulu 2014). Of all Icelandic insects, Coleoptera in particular have a clear palearctic distribution and are therefore used to support this hypothesis (Panagiotakopulu 2021). Although Coleoptera host a wide range of parasitic interactions, research on these parasites is still insufficient (Wheeler & Blackwell 1984, Dougherty et al. 2016, Carlson et al. 2020).

Among the parasites that infect beetles are representatives of the fungal class Laboulbeniomycetes (Ascomycota, Pezizomycotina). These are obligate ectobionts and ectoparasites on arthropods (Haelewaters et al. 2022a). Molecular phylogenetic analyses based on three to six loci revealed that Laboulbeniomycetes form a sister clade to the Sordariomycetes (Haelewaters et al. 2019b). The Laboulbeniomycetes class encompasses three formally described orders (Herpomycetales, Laboulbeniales and Pyxidiophorales) in addition to two informal clades (*Chantransiopsis*, *Laboulbeniopsis*). The order Laboulbeniales has the highest species diversity, consisting of 2370 species in 146 genera (Haelewaters et al. 2024). They are reported on every continent except Antarctica. Despite their global presence and diversity, they are still severely understudied (Haelewaters et al. 2024). This is partly attributed to their minute size and inability to grow on an artificial medium. Around 80 % of Laboulbeniales are found on Coleoptera; specifically Carabidae and Staphylinidae host many species (Weir & Hammond 1997). However, the generic diversity differs between the families. Carabidae are host to species of 17 different genera, most of the diversity is contained in the genus *Laboulbenia*. On the contrary, Staphylinidae host species divided over 50 genera (Haelewaters et al. 2019b). In contrast to the understudied Laboulbeniales, these beetle families are well-documented in Iceland: 35 species of Carabidae and 76 species of Staphylinidae have been recorded thus far (Náttúrufræðistofnun 2024). Despite the thorough documentation of their hosts, no Laboulbeniales have ever been reported from Iceland.

Laboulbeniales differ morphologically from the majority of fungi, particularly in their lack of hyphae, which is an apomorphy for the clade. Instead, a thallus is developed. This is a microscopic, hardy and multicellular structure formed through a determinate growth from a two-celled ascospore. The thallus is attached with a specialized foot cell to the exoskeleton of the host. It consists of a receptacle that functions as a platform for the one or more perithecia and the appendages. The perithecium produces the ascospores while the appendages bear the antheridia, who produce spermatia (Majewski 1994). The majority of Laboulbeniomycetes species are monoecious, male and female sexual structures on the same thallus. Only a few species are dioecious, male and female sexual structures on separate thalli. The spores consist of two cells and they are covered by a slime envelope to stick more easily to their host. Spore transmission takes place between individuals through direct contact, whereby host-population density and infection are directly proportional (De Kesel 1993, 1995). New infections mostly arise after mating, grooming and communal hibernating (Huldén 1983). Rossi (2011) observed evidence of accidental transmission when he identified *Laboulbenia davidsonii* W. Rossi on a cicindelid genus *Odontocheila* Laporte, 1834 that was clearly related to a *Laboulbenia* species that parasitize the unrelated carabid genus *Galerita* Fabricius, 1801. Accidental transmission is thought to have played a key role in the speciation of Laboulbeniales (Rossi 2011, De Kesel & Haelewaters 2014).

Speciation of Laboulbeniales is largely determined by host or by habitat. The first main driver, the host, often limits a Laboulbeniales species to a single or a small group of closely related host species (Thaxter 1896, De Kesel 1996). Recently molecular phylogenetic analyses revealed that species, which were once thought to have a wide host distribution, actually are composed of multiple (semi-) cryptic species, each having a stricter host association (Haelewaters et al. 2018, 2019a,b; Van Caenegem et al. 2024). This is the case for *Hesperomyces virescens* Thaxt. and *Laboulbenia flagellata* Peyr., which both have a large geographic distribution and multiple unrelated host species in different higher-level taxa. When cryptic diversity was discovered, the species complexes were split up in multiple closely related species with almost no morphological differences, in general according to host species (Haelewaters et al. 2018, 2019a,b, 2022a,b; Van Caenegem et al. 2024). The second driver, the habitat and the ecological aspect is seen in the closely related species *Laboulbenia slackensis* Cépède & F. Picard and *L. littoralis* De Kesel & Haelew., despite their hosts – *Pogonus chalceus* (Marsham, 1802) (Carabidae) and *Cafius xantholoma* (Gravenhorst, 1806) (Staphylinidae) – being distantly related (De Kesel & Haelewaters 2014). These halobiontic hosts co-occur in accumulations of decomposing seaweed along beaches. The unrelatedness of the hosts indicates that not only host but also ecological specificity play an important role in speciation (De Kesel & Haelewaters 2014, Haelewaters et al. 2019a,b). Yet, many habitats and countries remain understudied or neglected, a phenomenon referred to in conservation biology as the Wallacean shortfall (Haelewaters et al. 2024).

The Wallacean shortfall emphasizes the importance of documenting understudied taxa like Laboulbeniales in regions like Iceland. Understanding the host-parasite specificity of Laboulbeniales in Iceland could provide insights into how isolation and ecological conditions influence coevolutionary dynamics. This study sought to record the first Laboulbeniales from Iceland. Specimens collected during a field trip to the Reykjanes Peninsula near Reykjavík were examined. The Laboulbeniales and coleopteran hosts were identified to species level. Two new records were found, marking the first documentation of these fungi in Iceland and filling a significant knowledge gap.

## Materials and methods

### Study site, collection of arthropods

All arthropods were collected in Iceland on the Reykjanes Peninsula between 3 and 8 September 2023. A standard collecting method was conducted along three 100-m transects with the help of baited pitfalls, Berlese traps, Malaise traps, plant beating, and litter sifting. Additionally, incidental sampling was done using mouth-operated aspirators and by hand. Sampled arthropods were stored in Falcon tubes filled with 96% ethanol. Arthropod specimens were screened using an SZB350 stereoscope (VWR, Radnor, PA) at 45× magnification. Infected specimens were separated in 1.5 ml Eppendorf tubes and assigned unique identifiers.

### Mounting of Laboulbeniales

A hypodermic needle was used to carefully remove thalli of Laboulbeniales from the host at the foot. The thalli were mounted on permanent slides with the double-coverslip technique (Liu et al. 2020). First, a drop of water was placed in the middle of microscope slide, on top of which a 22×22-mm coverslip was placed. A droplet of a 1:1 mixture of Hoyer's medium and glycerol was placed on top of this coverslip, in which a thallus or multiple thalli from a single location on the host's body were placed. An 18×18-mm cover slip with a drop of Amann's medium was flipped upside-down and gently placed on top of the 22×22-mm coverslip. The four corners of the coverslips were sealed using clear nail polish. After the polish had dried, ample Solakryl BMX (Ento Sphinx s.r.o., Pardubice, Czechia) was applied to the smaller coverslip. Both coverslips were turned over and placed on the microscope slide, keeping the orientation of the thalli taken into account (aiming for the foot pointing downward when possible). The Solakryl BMX medium was given time to fill up the area between the microscope slide and the larger coverslip, with the smaller coverslip in between them. Each permanent slide was assigned a unique label and deposited in the Laboulbeniales slide collection of the Herbarium Universitatis Gandavensis (GENT), Ghent, Belgium. Hosts were deposited in the collection of Taxon Expeditions (TXEX), Leiden, The Netherlands.

### Morphological analyses

Thalli were photographed using a Nikon DS-Fi3 camera mounted on an Eclipse Ni-U microscope (Nikon, Melville, NY) equipped with differential interference contrast (DIC) optics to enhance contrast. The thalli were measured using ImageJ (Abràmoff et al. 2004) and measurements were analysed using Excel version 2210 (Microsoft Corporation, Redmont, WA). The method that Haelewaters & De Kesel (2020) presented for reporting measurements in morphological descriptions was also used in this paper: (a–)b–c–d(–e), with "a" and "e" being the extreme values, "b" the average minus standard deviation, "c" the average, and "d" the average plus standard deviation; when b or d is lower or higher than a or e, only the extreme value is kept (without parentheses). Morphological descriptions followed De Kesel et al. (2016) and Van Caenegem et al. (2024).

Principal Component Analysis (PCA) plots were made in R using packages *readxl*, *dplyr*, *ggplot2*, and *factoextra* (Wickham 2016, Kassambara & Mundt 2020, Wickham & Bryan 2023, Wickham et al. 2023). Differences in morphology among the three recovered clades of *L. notiophili* sensu lato (s.l.) were tested using linear mixed models as implemented in the *lme4* package in R (Bates et al. 2015). We tested the assumptions for these models using the *DHARMa* package (Hartig 2022). We used the *emmeans* package to obtain the Estimated Marginal Means (EMM) for each group and to compare the means between groups (Lenth 2023). Measurements and R code can be downloaded at https://github.com/dannyhaelewaters/teamlaboul/tree/main/island_icebreaker.

### DNA extraction, PCR amplification, and sequencing

DNA extractions were performed using the REPLI-g Single Cell Kit (Qiagen, Stanford, CA) following the standard and halved protocols as described previously (Van Caenegem & Haelewaters 2024). Three regions of the ribosomal DNA were amplified: the small subunit (18S), large subunit (28S), and the internal transcribed spacer region (ITS). The 25-µl PCR reactions were composed of 13.3 µl of RedExtract Taq polymerase (Sigma-Aldrich, St. Louis, MO), 2.5 µl of each 10-µM primer, 5.45 µl of ddH2O, and 1 µl of DNA extract. Primer combinations used are shown in Tab. 1. Cycling conditions followed Van Caenegem & Haelewaters (2024). Gel electrophoresis was performed and PCR products were visualized using ethidium bromide staining. Purification of PCR products was done using 1.5 µl of Exo-FAP (0.5 µl Exonuclease I, 1 µl FAST Alkaline Phosphatase) (Thermo Fisher Scientific, Waltham, MA) per 10 µl of PCR product, at 37 °C for 15 min, followed by deactivation at 85 °C

**Tab. 1.** DNA region with associated primer combinations used in this study.

| Region | Forward primer | Reverse primer | Forward primer reference | Reverse primer reference |
|---|---|---|---|---|
| **18S** | NSL1 | NSL2 | Haelewaters et al. (2015) | Haelewaters et al. (2015) |
| **28S** | LR0R | LR5 | Hopple (1994) | Vilgalys & Hester (1990) |
| **28S** | NL1 | NL4 | Kurtzman & Robnett (1997) | Kurtzman & Robnett (1997) |
| **28S** | LIC24R | LR3 | Miadlikowska & Lutzoni (2000) | Vilgalys & Hester (1990) |
| **ITS** | ITS1f | ITS4 | Gardes & Bruns (1993) | White et al. (1990) |

for 15 min. The PCR products were sent to Macrogen (Seoul, South Korea), where they were sequenced using an automated ABI 3730 XL capillary sequencer.

### Molecular phylogenetic analyses

Two DNA datasets were assembled, one with ITS sequences for *Laboulbenia notiophili* s.l. (Tab. 3) and another with 18S, ITS, and 28S sequences for *Rickia zanettii* (Tab. 5). Newly generated sequences were supplemented with sequences downloaded from NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/). Sequences were aligned by locus with the G-INS-i strategy using the online version 7 of MAFFT (Katoh et al. 2019). Aligned sequences were then manually trimmed using BioEdit Sequence Alignment Editor version 7.2.6 (Hall 1999) and concatenated in SequenceMatrix 1.9 (Vaidya et al. 2011). The aligned and concatenated dataset for *L. notiophili* sensu lato included three partitions: ITS1, 5.8S gene, and ITS2. The aligned and concatenated dataset for *R. zanettii* included five partitions: 18S, ITS1, 5.8S gene, ITS2, and 28S. Models for nucleotide substitution were selected for each partition with ModelFinder (Kalyaanamoorthy et al. 2017) according to the corrected Akaike Information Criterion (AICc). Maximum likelihood (ML) analyses were inferred using IQ-TREE (Nguyen et al. 2015) under partitioned models (Chernomor et al. 2016). Ultrafast bootstrapping was performed with 1000 replicates (Hoang et al. 2018). We performed an additional Bayesian analysis for our *L. notiophili* s.l. dataset. Bayesian inference was done using MrBayes (Ronquist et al. 2012), available on the CIPRES Science Gateway web portal (Miller et al. 2010). Four Markov chains were run for 80 million generations, with sampling every 8,000 generations. The aligned and concatenated dataset was partitioned as above. The analysis was performed using a GTR substitution model for each locus, with some sites being invariable and gamma-distributed rate variation across the remaining sites (GTR+I+G) (Abadi et al. 2019). A burn-in of 8000 trees was selected. Phylogenetic trees were visualized in FigTree version 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and edited using Inkscape (http://www.inkscape.org). Final alignments and unedited trees can be downloaded at https://github.com/danny haelewaters/teamlaboul/tree/main/island_icebrea ker.

## Results

### Screening of arthropods

A total of 1019 Icelandic arthropod specimens were screened, resulting in four infected specimens (parasite prevalence = 0.39%). All infected specimens were Coleoptera (beetles). The total number of Coleoptera among screened arthropods was 319, resulting in a parasite prevalence of 1.25% for Coleoptera. Two of the four infected specimens were *Notiophilus biguttatus* (Fabricius, 1779) (Carabidae), infected by *Laboulbenia notiophili* s.l. Cépède & F. Picard. The other two specimens were *Omalium excavatum* Stephens 1834 (Staphylinidae), infected by *Rickia zanettii* W. Rossi & Cesari (Tab. 2).

Please add:

### Molecular phylogenetic analyses

The ITS dataset of *L. notiophili* s.l. consisted of 19 isolates, totaling 678 characters. The selected models for the three partitions in the ITS dataset were as follows: HKY+F for ITS1 (237 bp, -lnL = 768.6663), K3P for 5.8S (143 bp, -lnL = 472.6717), and TPM2+F for ITS2 (298 bp, -lnL = 1462.3184). The concatenated 18S–ITS–28S dataset of *Rickia* consisted of 22 isolates, totaling 1760 characters. The selected models for the five partitions in this concatenated dataset were as follows: GTR+F+G4 for 18S (544 bp, -lnL = 4610.4632), TIM3+F+G4 for ITS1 (136 bp, -lnL = 703.5057), K2P for 5.8S (143 bp, -lnL = 619.9430), TN+F+I for ITS2 (283 bp, -lnL = 2171.8545), and HKY+F for 28S (654 bp, -lnL = 6959.2999).

**Tab. 2.** All Laboulbeniales found in Iceland with their respective host species.

| Collection number | Laboulbeniales species | Host species |
|---|---|---|
| **D. Haelew. 5356** | *Laboulbenia notiophili* s.l. Cépède & F.Picard | *Notiophilus biguttatus* |
| **D. Haelew. 5363** | *Laboulbenia notiophili* s.l. Cépède & F.Picard | *Notiophilus biguttatus* |
| **D. Haelew. 5369** | *Rickia zanettii* W. Rossi & Cesari | *Omalium excavatum* |
| **D. Haelew. 5371** | *Rickia zanettii* W. Rossi & Cesari | *Omalium excavatum* |

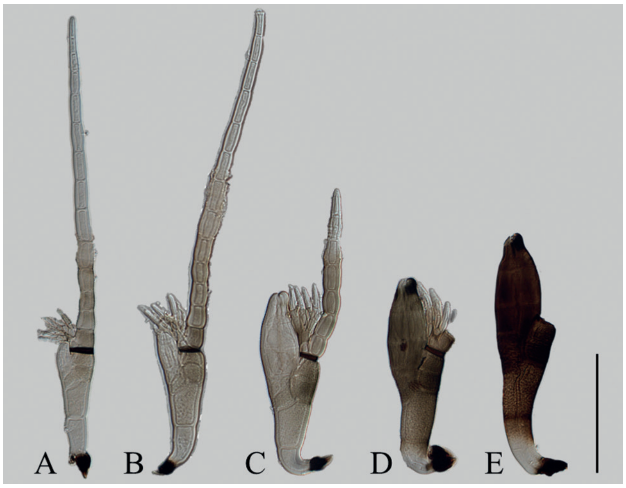

**Fig. 1.** *Laboulbenia notiophili* thalli removed from *Notiophilus biguttatus* (Coleoptera, Carabidae) collected in Iceland. **A.** Juvenile thallus, slide D. Haelew. 5356f. **B.** Subadult thallus, slide D. Haelew. 5356f. **C.** Subadult thallus, slide D. Haelew. 5356f. **D.** Adult thallus, slide D. Haelew. 5356c. **E.** Adult thallus, slide D. Haelew. 5356e. Bar 100 µm.

## Taxonomy

***Laboulbenia notiophili*** Cépède & F. Picard, Bull. Sci. Fr. Belg. 42: 259. 1908. – Fig. 1

Studied material. – ICELAND. Southern Peninsula (Suðurnes), Reykjanesbær, Sólbrekkuskógur, Transect 3, 63.949848 N 22.436438 W, 13 m a.s.l., 5 September 2023, on *Notiophilus biguttatus* (Coleoptera, Carabidae, Nebriinae), D. Haelew. 5356 (TXEX.COL.05006), *leg.* Danny Haelewaters & Warre Van Caenegem, slides D. Haelew. 5356b (GENT, 1 juvenile thallus and 1 subadult thallus from the head), D. Haelew. 5356c (GENT, 3 juvenile, 3 subadult, and 2 adult thalli from prosternum), D. Haelew. 5356d (GENT, 3 juvenile and 2 subadult thalli from right mesocoxa), D. Haelew. 5356e (GENT, 2 subadult and 4 adult thalli from the elytra), and D. Haelew. 5356f (GENT, 2 subadult thalli from the right profemur and protibia); at the shore of Seltjörn, 63.9471069 N 22.4335329 W, 0 m a.s.l., 6 September 2023, on *N. biguttatus*, D. Haelew. 5363 (TXEX.COL.05007), *leg.* Danny Haelewaters & Warre Van Caenegem, slides D. Haelew. 5363b (GENT, 1 adult thallus from the pronotum) and D. Haelew. 5363c (GENT, 1 adult thallus from left protibia).

Material sequenced. – ICELAND. Southern Peninsula (Suðurnes), Reykjanesbær, Sólbrekkuskógur, 100-m transect 3, 30 m at 0 m wide, 63.949848 N 22.436438 W, 13 m a.s.l., 5 September 2023, on *N. biguttatus*, D. Haelew. 5356 (TXEX.COL.05006), *leg.* Danny Haelewaters & Warre Van Caenegem, isolate D. Haelew. 5356a (3 adult thalli from the pronotum), PV448612 (ITS); at the shore of Seltjörn, 63.9471069 N 22.4335329 W, 0 m a.s.l., 6 September 2023, on *N. biguttatus*, D. Haelew. 5363 (TXEX.COL.05007), *leg.* Danny Haelewaters & Warre Van Caenegem, isolate D. Haelew. 5363a (2 adult thalli from the left elytron), PV448613 (ITS).

Description. – Thallus unevenly pigmented, ash grey to dark brown with olivaceous tints. – Cell I 1.8× longer than broad, broadening apically, brownish colored near septum I–II. – Cell II 1.6× longer than broad, rectangular and slightly broadening towards the apex, even slight pigmentation, darker at septum II–III. – Cell III 0.9× longer than broad, rectangular to trapezoidal, slightly broadening towards the apex, dorsally darker. – Cell IV 0.9× longer than broad, trapezoidal, dorsally darker. – Cell V 2.7× longer than broad, small and narrow wedge-shaped to triangular. – Cell VI 0.7× longer than broad, rectangular to trapezoid. – Cell VII 0.8× longer than broad. – Insertion cell 0.3× longer than broad, flattened, attached to the lower fourth of the perithecium, black. – Basal cell of the outer appendage 1.7× longer than broad, rectangular, dorsally darker. – Outer appendage singular, becoming paler to hyaline apically. – Basal cell of the inner appendage 1.3× longer than broad, round to trapezoidal, pale. – Inner appendage two to many branches, becoming pale to hyaline apically. – Antheridia flask-shaped. – Perithecium 2.3× longer than broad, rather slender and broadest in the middle, olivaceous to dark brown, a well-developed dorsal preapical spot and a sometimes present very small ventral preapical spot.

Measurements. – Thallus (187.7–)191.2–214.4–229.5 µm (n = 3) from foot to perithecial tip. – Cell I (27.7–)30.9–38.0–45.1(–47.9) µm × 19.0–21.6–24.5(–26.9) µm (n = 6). – Cell II (40.5–)42.5–46.5–50.3 µm × (24.2–)24.8–29.1–33.3(–36.8) µm (n = 6). – Cell III (15.0–)16.6–18.8–20.9(–21.1) µm × (15.9–)16.3–20.6–24.9(–28.3) µm (n = 6). – Cell IV (13.8–)14.1–16.2–18.4(–19.3) µm × (15.4–)15.5–17.7–20.0(–31.6) µm (n = 6). – Cell V 7.5–9.0–10.5

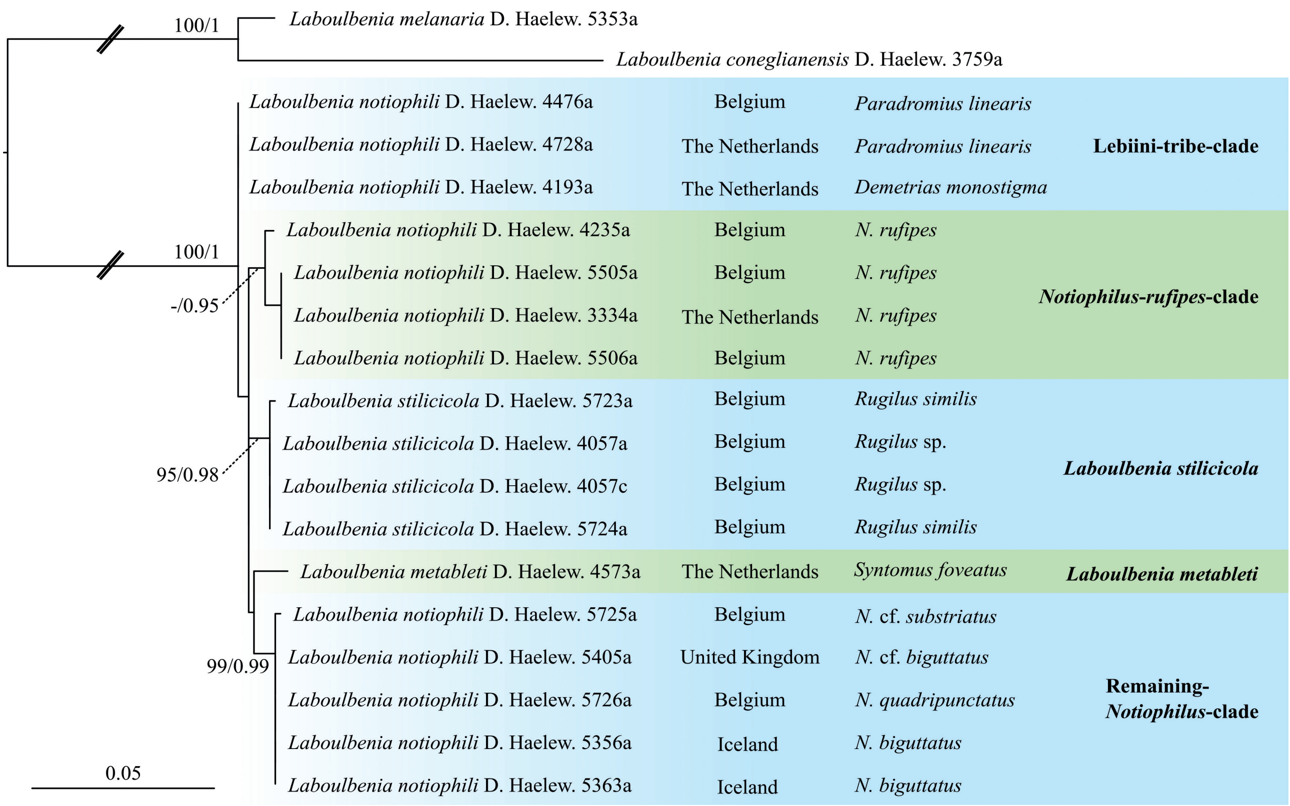

**Fig. 2.** Phylogeny of *Laboulbenia* reconstructed from an ITS dataset. The topology is the result of ML inference performed with IQ-TREE. UFBoot2 ML bootstrap values ≥70 and Bayesian posterior probabilities ≥0.7 are shown at the nodes. Colors indicating different clades of *L. notiophili* sensu lato, *L. metableti* (synonymized with *L. notiophili* by some authors), and *L. stilicicola*. *Laboulbenia coneglianensis* and *L. melanaria* serving as outgroup.

(–11.1) µm × (2.4–)2.5–3.4–4.2(–4.5) µm (n = 6). – Cell VI (11.6–)12.2–13.4–14.6 µm × (16.1–)16.4–20.0–23.5(–24.3) µm (n = 6). – Cell VII 9.9–12.0–14.1(–14.6) µm × 12.2–14.4–16.9(–18.9) µm (n = 6). – Insertion cell 4.0–4.5–5.0(–5.3) µm × 13.5–16.0–18.5(–19.5) µm (n = 4). – Basal cell of the outer appendage 16.7–20.4–26.5(–29.5) µm × 9.8–12.0–14.6(–15.8) µm (n = 4). – Basal cell of the inner appendage 4.8–8.1–11.6(–13) µm × 4.1–8.1–12.9(–14.5) µm (n = 4). – Perithecium 77.3–85.1–94.8(–104.0) µm × 31.0–38.4–47.8(–56.8) µm (n = 6).

Notes. – *Laboulbenia notiophili* was described from *Notiophilus aquaticus* (Linnaeus, 1758) [= *Notiophilus semipunctatus* (Fabricius, 1775)], but the type is lost (Santamaria & Pedersen 2021). It has been suggested that this taxon is a species complex in need of molecular phylogenetic study (De Kesel et al. 2020). However, without sequences of material from the original host species, delimiting *L. notiophili* sensu stricto (s.s.) is impossible. The Icelandic specimens were identified based on morphological characteristics (Fig. 1). In our phylogenetic tree consisting of 19 isolates (Tab. 3, Fig. 2), the Icelandic isolates were placed together with other sequences of *L. notiophili* from *N. biguttatus*, *N. quadripunctatus* Dejean, 1826, *and N.* cf. *substriatus* G.R. Waterhouse, 1833 from Belgium and the UK. This clade was separated from two other groups with material morphologically identified as *L. notiophili* (Lebiini-tribe clade and *Notiophilus-rufipes* clade). A restricted morphological comparison indicated that the length-to-width ratios of cells II, III, and the perithecium, and total thallus length could be potentially used to morphologically distinguish these clades (Tab. 4, Fig. S1).

*Laboulbenia notiophili* differs from *L. calathi* T. Majewski by the combination of the following characteristics: smaller thallus size; smaller ratio of perithecium to total thallus length; pigmentation consistently reaching beyond perithecium and cell III; pigmentation darker in especially the perithecium, outer appendage, and the posterior side of cells III and IV; and the longer outer appendage. *Laboulbenia metableti* Scheloske is different from *L. notiophili* by its slightly smaller thallus size, larger ratio

**Tab. 3.** Overview of *Laboulbenia* species used in our phylogenetic analysis, each with collection number, host species, host classification, country of origin, and Genbank accession number.

| Species | Collection # | Host species | Host classification | Country | Genbank # ITS |
|---|---|---|---|---|---|
| *L. metableti* | D. Haelew. 4573a | *Syntomus foveatus* | Carabidae, Harpalinae, Lebiini | The Netherlands | PP626228 |
| *L. notiophili* s.l. | D. Haelew. 4193a | *Demetrias monostigma* | Carabidae, Harpalinae, Lebiini | The Netherlands | PP626230 |
| *L. notiophili* s.l. | D. Haelew. 5356a | *Notiophilus biguttatus* | Carabidae, Nebriinae, Notiophilini | Iceland | PV448612 |
| *L. notiophili* s.l. | D. Haelew. 5363a | *Notiophilus biguttatus* | Carabidae, Nebriinae, Notiophilini | Iceland | PV448613 |
| *L. notiophili* s.l. | D. Haelew. 5405a | *Notiophilus biguttatus* | Carabidae, Nebriinae, Notiophilini | United Kingdom | PV448614 |
| *L. notiophili* s.l. | D. Haelew. 5725a | *Notiophilus substriatus* | Carabidae, Nebriinae, Notiophilini | Belgium | PV448615 |
| *L. notiophili* s.l. | D. Haelew. 5726a | *Notiophilus quadripunctatus* | Carabidae, Nebriinae, Notiophilini | Belgium | PV448616 |
| *L. notiophili* s.l. | D. Haelew. 4235a | *Notiophilus rufipes* | Carabidae, Nebriinae, Notiophilini | Belgium | PP626231 |
| *L. notiophili* s.l. | D. Haelew. 5505a | *Notiophilus rufipes* | Carabidae, Nebriinae, Notiophilini | Belgium | PV448617 |
| *L. notiophili* s.l. | D. Haelew. 5506a | *Notiophilus rufipes* | Carabidae, Nebriinae, Notiophilini | Belgium | PV448618 |
| *L. notiophili* s.l. | D. Haelew. 3334a | *Notiophilus rufipes* | Carabidae, Nebriinae, Notiophilini | The Netherlands | PV448619 |
| *L. notiophili* s.l. | D. Haelew. 4476a | *Paradromius linearis* | Carabidae, Harpalinae, Lebiini | Belgium | PP626232 |
| *L. notiophili* s.l. | D. Haelew. 4728a | *Paradromius linearis* | Carabidae, Harpalinae, Lebiini | The Netherlands | PP626233 |
| *L. stilicicola* | D. Haelew. 5723a | *Rugilus similis* | Staphylinidae, Paederinae, Lathrobiini | Belgium | PV448620 |
| *L. stilicicola* | D. Haelew. 5724a | *Rugilus similis* | Staphylinidae, Paederinae, Lathrobiini | Belgium | PV448621 |
| *L. stilicicola* | D. Haelew. 4057a | *Rugilus rufipes* | Staphylinidae, Paederinae, Lathrobiini | Belgium | PP626247 |
| *L. stilicicola* | D. Haelew. 4057c | *Rugilus rufipes* | Staphylinidae, Paederinae, Lathrobiini | Belgium | PP626248 |
| Outgroup | | | | | |
| *L. coneglianensis* | D. Haelew. 3759a | *Harpalus griseus* | Carabidae, Harpalinae, Harpalini | Belgium | OR680741 |
| *L. melanaria* | D. Haelew. 5353a | *Diachromus germanus* | Carabidae, Harpalinae, Harpalini | Belgium | PV448622 |

**Tab. 4.** Overview of the Estimated Marginal Means (EMM) and their confidence intervals (C.I.) for the four most contributing variables of the PCA plot for *Laboulbenia notiophili* sensu lato, i.e., the length-to-width ratios of cell II, cell III, and the perithecium, and total thallus length. EMMs in bold are significantly different from each other (if two EMMs are indicated) or from all other (if one EMM is indicated).

| Clade | L/W Cell II | L/W Cell III | L/W Perithecium | Total thallus length (µm) |
|---|---|---|---|---|
| **Lebiini-tribe** | 2.07 [1.67–2.47] | 1.092 [1.000–1.190] | 2.56 [2.20–2.92] | **168** [152–186] |
| **Notiophilus-rufipes** | **2.42** [2.11–2.73] | 1.161 [1.084–1.240] | **2.78** [2.50–3.06] | **201** [186–217] |
| **Remaining-Notiophilus** | **1.92** [1.68–2.16] | **0.951** [0.899–1.000] | **2.21** [1.99–2.43] | 186 [175–197] |

**Tab. 5.** Overview of *Rickia* species used in the phylogenetic analysis with collection numbers, host species, host classification, country of origin and Genbank accession number for each gene used: SSU, LSU and ITS. [a] Margaryan,A.; unpubl.

| **Species** | **Collection #** | **Host species** | **Host classification** | **Country** | **Genbank # SSU** | **Genbank # LSU** | **Genbank # ITS** |
|---|---|---|---|---|---|---|---|
| *R. gigas* | D. Haelew. 1557a | *Tropostreptus hamatus* | Spirostreptida, Spirostreptidae | Tanzania | MT416216 | | |
| *R. gigas* | D. Haelew. 1557b | *Tropostreptus hamatus* | Spirostreptida, Spirostreptidae | Tanzania | MT416217 | | |
| *R. gigas* | No14 | *Tropostreptus hamatus* | Spirostreptida, Spirostreptidae | Tanzania | MT704348[a] | | |
| *R. huggertii* | D. Haelew. 5598a | *Omalium* cf. *riparium* | Coleoptera, Staphylinidae | Norway | PV435119 | PV435124 | PV448624 |
| *R. huggertii* | D. Haelew. 5599a | *Omalium* cf. *riparium* | Coleoptera, Staphylinidae | Norway | PV435120 | | PV448625 |
| *R. huggertii* | D. Haelew. 5601a | *Omalium* cf. *riparium* | Coleoptera, Staphylinidae | Norway | PV435121 | PV435125 | PV448626 |
| *R. laboulbenioides* | SR4s | *Cylindroiulus punctatus* | Julida, Julidae | Denmark | MH040558 | | MH040593 |
| *R. laboulbenioides* | SR5s | *Cylindroiulus punctatus* | Julida, Julidae | Denmark | MN530041 | | MK500060 |
| *R. pachyiuli* | SR13s | *Pachyiulus hungaricus* | Julida, Julidae | Serbia | MN530042 | MK500059 | MK500059 |
| *R. pachyiuli* | SR1s | *Pachyiulus hungaricus* | Julida, Julidae | Serbia | MH040559 | | MH040594 |
| *R. pachyiuli* | SR8s | *Pachyiulus hungaricus* | Julida, Julidae | Serbia | MT604592 | | MK500058 |
| *R. unciger* | SR12s | *Unciger foetidus* | Julida, Julidae | Denmark | | | MK500061 |
| *R. wasmannii* | ADK6272a | *Myrmica sabuleti* | Hymenoptera, Formicidae | Belgium | MN530043 | | MK500050 |
| *R. wasmannii* | DE_Rak4 | *Myrmica scabrinodis* | Hymenoptera, Formicidae | Hungary | KT800037 | KT800021 | KT800050 |
| *R. wasmannii* | D. Haelew. 1234a | *Myrmica sabuleti* | Hymenoptera, Formicidae | The Netherlands | | MF458369 | MF458369 |
| *R. zanettii* | D. Haelew. 5371d | *Omalium excavatum* | Coleoptera, Staphylinidae | Iceland | PV435118 | PV435123 | PV448623 |
| *Rickia* sp. | LG364 | Chrysomelidae sp. | Coleoptera | Costa Rica | MG687389 | MK500050 | |
| *Rickia* sp. | LG484 | Staphylinidae sp. | Coleoptera | Namibia | MG687390 | | |
| Outgroup | | | | | | | |
| *Polyandromyces coptosomalis* | D. Haelew. 313f | *Phoeacia sp.* | Hemiptera, Pentatomidae | Ecuador | KT800035 | KT800020 | |
| *Nycteromyces streblidinus* | D. Haelew. 1324d | *Trichobius joblingi* | Diptera, Streblidae | Panama | MH040556 | MH040591 | |
| *Laboulbenia collae* | D. Haelew. 4308b | *Paranchus albipes* | Coleoptera, Carabidae | Portugal (Azores) | PP620879 | PP620963 | |
| *Hesperomyces halyziae* | D. Haelew. 4209a | *Halyzia sedecimguttata* | Coleoptera, Coccinellidae | The Netherlands | OP933652 | OP933659 | |

of cell II to total thallus length, less rounded perithecium, more heavily pigmentated perithecial base, the lower 4 to 5 cells of the outer appendage more pigmented in their middle, and more and symmetrical branching of the inner appendages. Finally, *L. notiophili* is different from *Laboulbenia stilicicola* Speg. in its more heavily pigmented perithecium, smaller ratio of cell II to total thallus length, outer appendage longer with the 3 most basal cells more elongate without distinct dark septa, and inner appendages proliferating into short branchlets. Also the hosts of these species are different: *L. calathi* is associated with hosts in the genus *Calathus* Bonelli, 1810, *L. metableti* with hosts in the genus *Syntomus* Hope, 1838, and *L. stilicicola* with staphylinid hosts in the genus *Rugilus* Leach, 1819.

### ***Rickia zanettii*** W. Rossi & Cesari, Giorn. Bot. Ital. 112(1–2): 71–73. 1978. – Fig. 3

Studied material. – ICELAND. Southern Peninsula (Suðurnes), Suðurnesjabær, Rockville Air Station, 100-m transect 2, 64.034826 N 22.652025 W, 0 m a.s.l., leaf litter sample, 4 September 2023, on *Omalium excavatum* (Coleoptera, Staphylinidae, Omaliinae), D. Haelew. 5369 (TXEX. COL.05009), *leg.* Danny Haelewaters & Warre Van Caenegem, slides D. Haelew. 5369a (GENT, 3 adult thalli from the right profemur), D. Haelew. 5369b (GENT, 1 adult thallus from right antenna), D. Haelew. 5369c (GENT, 1 adult thallus from right antenna), and D. Haelew. 5369d (GENT, 1 juvenile thallus and 1 adult thallus from the abdomen); *Ibid.*, Rockville Air Station, 100-m transect 2, 64.034826 N 22.652025 W, 0 m a.s.l., 4 September 2023, on *O. excavatum*, D. Haelew. 5371 (TXEX. COL.05008), *leg.* Danny Haelewaters & Warre Van Caenegem, slides D. Haelew. 5371a (GENT, 2 juvenile, 1 subadult, and 2 adult thalli from the prosternum), D. Haelew. 5371b (GENT, 4 adult thalli from left mesocoxa), and D. Haelew. 5371c (GENT, 5 adult thalli from the abdomen).

Material sequenced. – *Ibid.*, isolate D. Haelew. 5371d (3 adult thalli from the abdomen), PV435118 (SSU), PV448623 (ITS), PV435123 (LSU).

Description. – Thallus pale, hyaline at base, except for the black foot; orange pigmentation from the perithecium onwards, deepening to a light brown color apically. – Receptacle one-layered, unbranched, triseriate; basal cell small rhombic; anterior (ventral) series consisting of (4–)5–7 cells, basally more rounded, becoming distinctly broader than long, accompanied by 1 to 2 smaller apical cells; median (axial) series consisting of 9–11(–12) squarish cells, with the basal cell higher than broad, more apically flattening, becoming broader than high; posterior (dorsal) series consisting of (7–)9–11(–12) cells, basal cells rounded, becoming distinctly broader than long, accompanied by 1 to 2 smaller apical cells; apical cells with black insertion septum at the base of the flask-shaped antheridia. – Antheridia tapering apically, hyaline. – Perithecium 1.6× longer than broad, single, ovoid; anterior margin free from the receptacle; posterior margin only apically free; apex tapering and ending in small ostiolar lips. – Ascospores 11.3× longer than broad, fusiliform.

Measurements. – Thallus (84.4–)98.0–118.4–138.8(–161.6) µm (n = 16) from foot to perithecial tip. – Perithecium (40.6–)47.2–56.3–65.4 (–70.1) µm × (20.6–)27.2–35.3–43.4(–50.7) µm (n = 16). – Antheridia (8.1–)8.8–9.7–10.6(–11.9) µm × (2.2–)2.4–2.9–3.4(4.0) µm (n = 24). – Ascospores (24.4–)24.9–27.4–29.9(–36.2) µm × (1.5–)2.1–2.5–2.9 (–3.0) µm (n = 19).

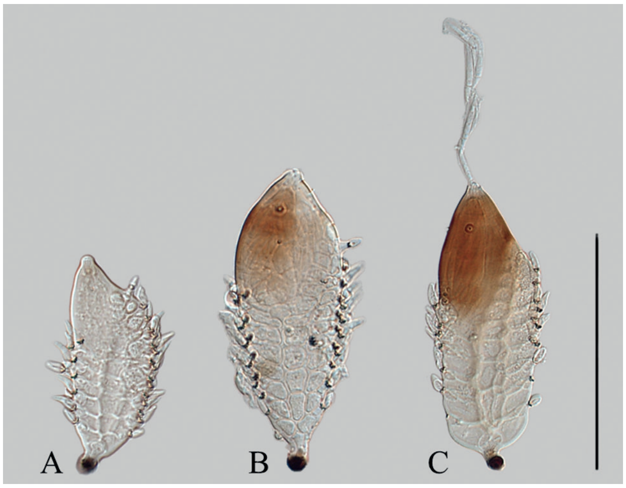

**Fig. 3.** *Rickia zanettii* thalli removed from *Omalium excavatum* (Coleoptera, Staphylinidae) collected in Iceland. **A.** Juvenile thallus, slide D. Haelew. 5371c. **B.** Adult thallus, slide D. Haelew. 5369a. **C.** Adult thallus with ascospores oozing out of the perithecium, slide D. Haelew. 5371c. Bar 100 µm.

Notes. – The Icelandic material studied here is morphologically very similar to *R. zanettii*, apart from the slightly smaller size (Fig. 3). The thalli match those described from Italy on *O. excavatum* (Rossi & Cezari 1978), and from Spain and the UK on *Omalium* sp. (Santamaria 1989, Weir & Beakes 1993). The *R. zanettii* thalli from Iceland were compared to *R. huggertii* Balazuc from Norway (Fig. 4), which is associated with *Omalium* cf. *riparium* C.G.Thomson, 1857. The PCA plot based on morphological data showed two clouds of specimens that occupy a considerable part of the morphospace without overlap (Fig. S2). The phylogenetic analysis with all other available sequences of *Rickia* placed the Icelandic isolates in a clade with other *Rickia* species that parasitize Staphylinidae (Tab. 5, Fig. 5).

*Rickia zanettii* differs from *R. huggertii* in its receptacle with nearly parallel sides, numerous an-

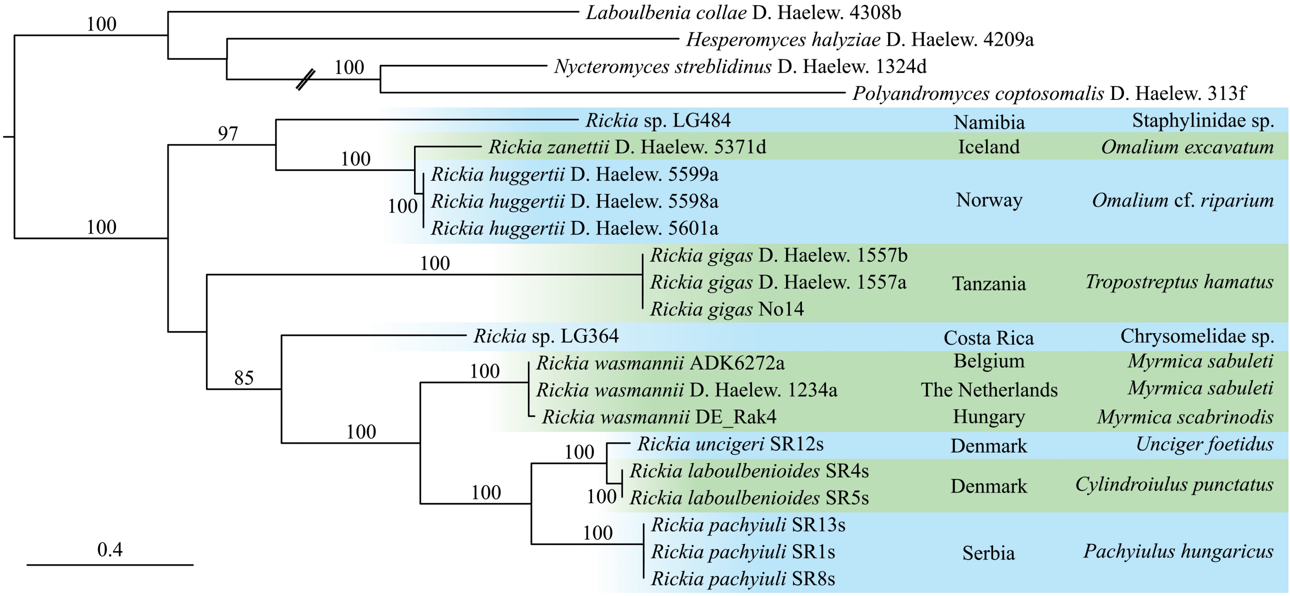

**Fig. 4.** Phylogeny of *Rickia* reconstructed from an 18S–ITS–28S dataset. The topology is the result of ML inference performed with IQ-TREE. UFBoot2 ML bootstrap values ≥70 are shown above or below the branch leading to each node. Colors indicating different clades of *L. notiophili* sensu lato, *L. metableti* (synonymized with *L. notiophili* by some authors), and *L. stilicicola*. *Hesperomyces halyziae*, *Laboulbenia collae*, *Nycteromyces streblidinus*, and *Polyandromyces coptosomalis* serving as outgroup.

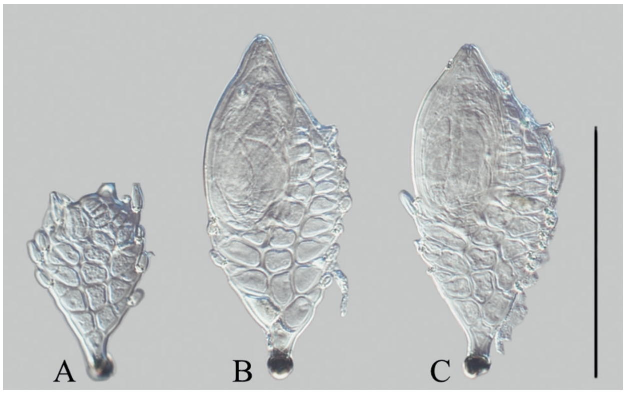

**Fig. 5.** *Rickia huggertii* thalli removed from *Omalium* cf. *riparium* (Coleoptera, Staphylinidae) collected in Norway. **A.** Juvenile thallus, slide D. Haelew. 5599b. **B.** Adult thallus, slide D. Haelew. 5600a. **C.** Adult thallus, slide D. Haelew. 5600a. Bar 100 µm.

theridia on both the anterior and posterior sides, and the perithecium with strong pigmentation (Figs. 3, 4).

## Discussion

### Fungi in Iceland

A total of 543 fungal species were recorded in the first fungal Icelandic checklist by Rostrup (1903). This number has increased to at least 2743 according to Hallgrímsson & Eyjólfsdóttir (2004), around a third of them are lichen-forming or associated with lichens (Brackel 2010). Most species belong to Ascomycota and Basidiomycota. The remaining species belong to smaller clades: Blastocladiomycota, Chytridiomycota, Entomophthoromycota, Kickxellomycota, Mucoromycota, Olpidiomycota and Zoopagomycota. Specific fungal research topics from Iceland include: aquatic fungi (Johnson 1968, 1971; Johnson & Howard 1968; Howard et al. 1970), arbuscular mycorrhizal fungi (Greipsson et al. 2002), coprophilous fungi (Richardson 2004) and soil fungi (Eyjólfsdóttir 1995).

Despite these advancements in Icelandic mycology, this paper is the first that mentions Icelandic Laboulbeniomycetes and with that add two new species, namely *Laboulbenia notiophili* and *Rickia zanettii*, to the record. These species probably hitchhiked with their palearctic coleopteran hosts according to the *tabula rasa* theory (Panagiotakopulu 2014, 2021). The Wallacean shortfall describes the lack of comprehensive distribution records for species that have already been discovered. It is particularly pronounced in understudied taxa such as Laboulbeniomycetes, underscoring the importance of documenting their distributions in underexplored regions like Iceland (Haelewaters et al. 2024).

### *Laboulbenia notiophili*

Cépède & Picard (1908) described *Laboulbenia notiophili* from *Notiophilus aquaticus*, but the type is lost (Santamaria & Pedersen 2021). This Laboulbeniales species is very common in Europe. This was already made apparent 60 years after its description by Scheloske (1969), who reported the species in France, Germany, Hungary, Poland, and Switzerland. The distribution of the species has been expanded by records all over Europe (Santamaria et al. 1991, Rossi & Santamaria 2006, Santamaria & Pedersen 2021). The host range is mainly restricted to the genus *Notiophilus* and the tribus Lebiini (Tab. S1). These are not particularly closely related. In the past, *L. notiophili* was split based on the host range into two species: *L. notiophili* and *L. casnoniae* Thaxt., infecting the genus *Notiophilus* and the tribus Lebiini respectively (Rossi & Santamaria 2006). *Laboulbenia casnoniae* was first described by Thaxter (1891), from *Colliuris pensylvanica* (Linnaeus, 1758) (Carabidae, Lebiinae, Odacanthini) from Connecticut, USA. He included the first drawings of this species in his first monograph and compared it with *L. polyphaga* Thaxt. (Thaxter 1896). This latter species has a wide host range and is currently considered ill defined. In Thaxter's second monograph, he allocated even more specimens to *L. casnoniae* from all over the world, including the first record in Europe, from the United Kingdom (Thaxter 1908).

The European records of *L. casnoniae* were later associated with *L. notiophili* based on morphology (Rossi & Santamaria 2006). Previous to this, six other species were synonymized with *L. casnoniae* (Balazuc 1974; Balazuc et al. 1982; Santamaria 1989, 1998; Santamaria et al. 1991; Majewski 1994; De Kesel 1998; Rossi & Santamaria 2006). When *Laboulbenia blanchardii* Cépède was described by Cépède (1914), he mentioned the close similarity with *L. casnoniae*. However, he noted the difference in the inner appendages, so he argued that it warranted a new name. This difference was not picked up by others and *L. blanchardii* was never reported afterwards. Balazuc et al. (1982) caused some controversy by synonymizing *L. metableti* Scheloske, a morphologically well-defined species, with *L. casnoniae*. When Rossi & Santamaria (2006) synonymized everything with *L. notiophili*, this also included *L. metableti*. De Kesel et al. (2020) eventually separated *L. metableti* from *L. notiophili* based on its unique morphology and pigmentation of the appendages. They also mentioned that the *L. notiophili* specimens from *Demetrias* were slightly different and they suggested to maybe reinstate *L. blanchardii* as well.

Our phylogenetic analysis resolved five distinct clades (Figure 2). This makes the species *Laboulbenia notiophili* paraphyletic and a species complex, which was hypothesized by Haelewaters & De Kesel (2020). The first *L. notiophili* clade infects the members of the Lebiini tribus. This clade will be referred to as the Lebiini-tribe clade and it currently includes sequences coming from two host species: *Demetrias monostigma* Samouelle, 1819 and *Paradromius linearis* (G. A. Olivier, 1795) (Tab. 3). The hosts in this clade prefer coastal dunes and to a lesser extent also swampy banks with a dense border of reeds and sedges, yet they are also frequently found more inland (Turin 2000). Most other host species in these genera are also considered hydrophilic or dune species. The second clade, named the *Notiophilus-rufipes* clade, encompasses all *L. notiophili* specimens on *Notiophilus rufipes*. This host is rather eurytope and mostly linked to closed vegetation, especially oak-birch forests (Turin 2000). The remaining *Notiophilus* specimens form a third clade, the remaining-*Notiophilus* clade. This clade infects other *Notiophilus* species, apart from *N. rufipes*. These *Notiophilus* species prefer a more open habitat compared with *N. rufipes*, with *N. biguttatus* as an exception. It is more generalist species that is also present in deciduous forests (Turin 2000). The ecological preference of *N. rufipes* could have played a role in the differentiation of the *Notiophilus-rufipes*-clade and the remaining-*Notiophilus*-clade. The last two lineages are clearly delineated based on morphology and ecology. The first is *Laboulbenia metableti*, a species restricted to the genus *Syntomus* (Carabidae). This species was long considered a synonym of *L. notiophili* until it was reinstated by De Kesel et al. (2020). The hosts prefer rather dry habitats (Turin 2000). The second species, *Laboulbenia stilicicola*, found on *Rugilus* species (Staphylinidae). One of the most common hosts is *Rugilus similis*, a generalist that occupies forests, meadows and wastelands (Drugmand, 1989).

According to our phylogenetic analysis, *L. notiophili* should be split into three clades corresponding to host association. It remains unclear which clade should carry the name *Laboulbenia notiophili*, because no genetic data are available from thalli associated with the original host species, *Notiophilus aquaticus*. Based on the typical habitat of this beetle, we hypothesize that *L. notiophili* from *N. aquaticus* is most likely conspecific with the remaining-*Notiophilus* clade, although it may also form a separate clade within this species complex. Due to this uncertainty, we report this record from Iceland as *L. notiophili* sensu lato. The clustering of Icelandic specimens within the European remaining-*Notiophilus* clade suggests a relatively recent colonization event, potentially linked to host migration patterns. Alternatively, infected *Notiophilus* specimens may have been introduced from mainland Europe—either by early settlers or through more recent human-mediated transport. Such introductions could explain the absence of previous records, the low prevalence, and the identical ITS sequences, which together suggest that *L. notiophili* does not form stable populations in Iceland and that its occurrence relies on sporadic introductions.

Our morphological analysis revealed that the length to width ratios of cell II, III, and the perithecium, and the total length of the thallus could be potentially used to distinguish these three clades within *L. notiophili* s.l. (Tab. 4). An important note to make here is that we could only use a limited number of thalli coming from different body parts, from a limited number of host specimens. We hope this analysis stimulates future students and researchers of Laboulbeniales to incorporate statistical analyses to distinguish (semi-)cryptic species. We suggest that more analyses are needed, with larger amounts of measurements coming from different hosts and body parts to account for intraspecific variation.

### *Rickia zanettii*

Rossi & Cezari (1978) described *Rickia zanettii* on *Omalium excavatum*. The host specimen was collected in Verona, Italy. Thalli were found on the legs and abdomen of the host. The species has a total length of 150–200 µm, bearing a pear-shaped and rust colored perithecium. The hyaline receptacle is composed of an anterior series with 9–13 cells, a median series with 12–14 cells and a posterior series with 12–14 cells. The anterior and posterior series bear many hyaline antheridia.

*Rickia zanettii* is distributed across Europe but appears to be very rare, with previous records only from Italy, Spain, and the UK (Rossi & Cezari 1978, Santamaria 1989, Weir & Beakes 1993). The descriptions of previous studies showed variation in total length and in the number of cells for each series, which are shown in Tab. 6. The Icelandic specimens found in this study were identified based on morphological characteristics and comparison with the original description (Rossi & Cezari 1978). The cell series of the Icelandic specimens consist of fewer cells compared to Santamaria (1989), but the values align closely with the British records from Weir & Beakes (1993), though the British specimens were generally larger.

Compared with the Italian specimens, a clear size difference is observed. There might be a latitudinal gradient, whereby the size of the specimens gradually reduces towards the poles. Still, this would not explain the size difference of the Spanish specimens. The exact host is not known, so this particular host species may have influenced the growth of *R. zanettii*. Another hypothesis could be that particular local environmental pressures impact the growth of *R. zanettii* and so different sizes are observed depending on the locality. Perhaps, the colder climate, the humidity, the suboptimal habitat, the limited host diversity or a combination of those, may constrain the parasite's growth in places like Iceland (De Kesel 1997). Nevertheless, great care should be taken before such hypotheses can be accepted so that taxonomic drift is prevented. More specimens from all over Europe and more genetic data are required.

*Rickia zanettii* is morphologically most similar to *Rickia huggertii* Balazuc. *Rickia zanettii* is distinguished from *R. huggertii* by Balazuc (1980) based on several characteristics. It has a generally larger total length of 150–200 µm, compared to the 115 µm of *R. huggertii*. The receptacle has nearly parallel sides, and numerous antheridia on both the anterior and posterior sides. Additionally, Balazuc (1980) observed that the perithecium of *R. zanettii* exhibits strong pigmentation and has a more globular shape. Despite these clear morphological characteristics, Weir & Beakes (1993) argued that the two species might be conspecific. They examined a *Rickia* species, found on *Omalium laeviusculum*

**Tab. 6.** All *Rickia zanettii* descriptions, including country, total thallus length, and amount of cells in each series of the receptacle.

| | Country | Total length (µm) | Anterior series | Median series | Posterior series | ***Omalium* species** |
|---|---|---|---|---|---|---|
| **Rossi & Cezari (1978)** | Italy | 150–200 | 9–13 | 12–14 | 12–14 | *O. excavatum* |
| **Santamaria (1989)** | Spain | 100–118 | 6–13 | 10–14 | 10–14 | *O.* sp. |
| **Weir & Beakes (1993)** | Scotland (United Kingdom) | 120–160 | 4–6 | 9–10 | 9–11 | *O. laeviusculum* |
| **This paper** | Iceland | 98–138 | 5–7 | 9–11 | 9–11 | *O. excavatum* |

Gyllenhal, 1827, and concluded that the species most closely resembled the description of *R. zanettii,* but that they shared a lot of morphological characteristics with *R. huggertii* as well. The parallel- to elliptical-shaped receptacle and the intermediate size of the thallus were highlighted as reasons for reaching this conclusion. They did acknowledge the fact that more material is needed to reasonably support this conclusion. The arguments that they bring up, like the smaller size and more parallel sided receptacle are also visible in some of the *R. zanettii* specimens from Iceland. Upon closely examining the original drawings of *R. zanettii* in Rossi & Cezari (1978), *R. huggertii* in Balazuc (1980), and specimens from other studies, we observed that the globular shape of the perithecium of *R. zanettii* described by Balazuc (1980) is not as pronounced and varies between specimens, suggesting it may not be a well-defined and useful characteristic (Santamaria 1989, Weir & Beakes 1993, Santamaria & Pedersen 2021). Here we show that the Icelandic *R. zanettii* specimens form a clade, distinct from the closely related *R. huggertii* from Norway (Fig. 4).

### Additional records from Norway

Finally, we presented here the first records of *Rickia huggertii* in Norway, found on *Omalium* cf. *riparium* (Fig. 5). The thalli were identified based on morphological characteristics. Molecular data were successfully generated for our material. However, no other sequences are available for *R. huggertii*; to be able to delimit species boundaries for this species, sequences should be generated of thalli removed from *O. riparium* collected in France, where the species was described (Balazuc 1980). This species was previously reported in Denmark, France, Italy, and Sweden (Balazuc 1980, Santamaria & Pedersen 2021).

NORWAY. Østfold, Moss, Søndre Jeløy, 59.419100 N 10.606950 E, 0 m a.s.l., piles of *Fucus* on beach, pebbles, and coarse sand, 7 June 2024, on *Omalium* cf. *riparium* Thomson, 1857 (Coleoptera, Staphylinidae), D. Haelew. 5598 [host label], *leg.* Vladimir I. Gusarov & Warre Van Caenegem, slides D. Haelew. 5598b (GENT, 1 adult thallus, elytra) and D. Haelew. 5598c (GENT, 2 adult thalli, mesosternum), isolate D. Haelew. 5598a (2 adult thalli from the mesosternum), PV435119 (SSU), PV448624 (ITS), PV435124 (LSU); *Ibid.*, D. Haelew. 5599 [host label], *leg.* Vladimir I. Gusarov & Warre Van Caenegem, slide D. Haelew. 5599b (GENT, 2 juvenile and 18 adult thalli, 4th sternite), isolate D. Haelew. 5599a (3 adult thalli from the 4th sternite), PV435120 (SSU), PV448625 (ITS); *Ibid.*, D. Haelew. 5600 [host label], *leg.* Vladimir I. Gusarov & Warre Van Caenegem, slide D. Haelew. 5600a (GENT, 7 adult thalli from the left protibia); *Ibid.*, D. Haelew. 5601 [host label], *leg.* Vladimir I. Gusarov & Warre Van Caenegem, isolate D. Haelew. 5601a (3 adult thalli from the right eye): PV435121 (SSU), PV448626 (ITS), PV435125 (LSU).

## Conclusion

Based on morphology, we report the first two records of Laboulbeniales from Iceland: *Laboulbenia notiophili* and *Rickia zanettii*. *Laboulbenia notiophili* was found to be a species complex. Five clades were observed, including two morphologically distinct species, *Laboulbenia metableti* and *L. stilicicola*, and *L. notiophili* s.l., which is composed of three clades, each associated with different hosts: Lebiini-tribe clade, *Notiophilus-rufipes* clade, and the remaining-*Notiophilus* clade. Our limited statistical analysis indicated significant differences in the ratios of cell II, III and the perithecium, and the total length of the thalli to distinguish these three clades. These differences and the use of statistical analyses in Laboulbeniales research should be further explored. Sequencing of thalli coming from the original host, *Notiophilus aquaticus*, should resolve the position of the 'true' *Laboulbenia notiophili*. The second species was identified as *Rickia zanettii*. We based this on the similar morphological characteristics of the specimens, compared with other specimens from Europe. As long as there is no genetic data from the original host and locality, *Omalium excavatum* from Northern Italy, we cannot confirm that all these specimens belong to the same species. The *Laboulbenia notiophili* of Iceland were situated in the same clade as the specimens from the European mainland, without any differences in the ITS region. This suggests that these Laboulbeniales hitchhiked with their palearctic coleopteran hosts, likely facilitated by post-glacial recolonization routes or through recent human-mediated transport. This study revealed the importance of researching understudied groups in underexplored regions and the importance of molecular phylogenetic data in species delimitation and identification of Laboulbeniales.

## Acknowledgements

Fieldwork in Iceland was supported by the European Union's Horizon 2020 project INTERACT, under grant agreement No. 871120. Fieldwork in Norway and W.V.C.'s employment at Ghent University were supported by a grant from the Norwegian Biodiversity Information Centre (project 7-23: iNoLa - Inventory of the Norwegian species of thallus-forming Laboulbeniales associated with beetles, with particular focus on the superfamily Staphylinoidea). We would like to thank Michiel de Groot for proofreading the manuscript and Prof. Dr. Menno Schilthuizen for helping with the identification of host specimens.

## References

Abràmoff D.M., Magalhães P.C., Ram S.J. (2004) Image processing with ImageJ. Biophotonics International.

Balazuc J. (1974) Laboulbéniales de France (suite). *Bulletin Mensuel de la Société Linnéenne de Lyon* **43**: 295–315.

Balazuc J. (1980) Laboulbéniales nouvelles (Ascomycètes), parasites de Coléoptères et de Diptères. *Bulletin du Muséum National d'Histoire Naturelle* **2**: 209–219.

Balazuc J. (1990) Catalogue actuel des Laboulbéniales (Ascomycètes parasites) de la France métropolitaine. *l'Entomologiste* **45**: 219–232.

Balazuc J., Espadaler X., Girbal J. (1982) Laboulbenials (Ascomicets) ibériques. *Collectanea Botanica (Barcelona)* **13**: 403–421.

Bánhegyi J. (1940) Elomunkálatok a magyarországi *Laboulbenia*–félek monografiájához. Etudes préliminaires sur les Laboulbéniales de la Hongrie. *Index Horti Botanici Universitatis Budapestinensis* **4**: 39–59.

Bánhegyi J. (1949) Les Laboulbéniales de la Transylvanie. *Index Horti Botanici Universitatis Budapestinensis* **7**: 93–101.

Bánhegyi J. (1950) Ritka Laboulbeniák a Kárpát Medencében. *Annales Biologicae Universitatis Budapestinensis* **1**: 189–196.

Bánhegyi J. (1960) Contributions à la connaissance des Laboulbéniales de la péninsule des Balkans. *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös, Sectio Biologica* **3**: 49–67.

Bates D., Maechler M., Bolker B., Walker S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48.

Baumgartner R. (1923) Contribution à l'étude des Laboulbéniales de la Suisse. *Jahrbuch der Philosophischen Fakultät II der Universität Bern* **3**: 257–265.

Bennike O. Böcher J. (2021) Interglacial biotas from the North Atlantic Islands. In: *Biogeography in the Sub-Arctic: The Past and Future of North Atlantic Biota* (eds. Panagiotakopulu E., Sadler, J.P.). John Wiley & Sons, Hoboken, NJ: 51–82.

Brackel W. (2010) Some lichenicolous fungi and lichens from Iceland, including *Lichenopeltella uncialicola* sp. nov. *Herzogia* **23**(1): 93–109.

Carlson C.J., Dallas T.A., Alexander L.W., Phelan A.L., Phillips A.J. (2020) What would it take to describe the global diversity of parasites? *Proceedings of the Royal Society B* **287**: 20201841.

Cépède C. (1914) Étude des Laboulbéniacées européennes, *Laboulbenia blanchardii* n. sp. et son parasite *Fusarium Laboulbeniae* n. sp. *Archives de Parasitologie* **16**: 373–403.

Cépède C., Picard F. (1908) Contribution à la biologie et à la systématique des Laboulbéniacées de la flore française. *Bulletin Scientifique de la France et de la Belgique* **42**: 247–268.

Chernomor O., von Haeseler A., Minh B. Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology* **65**(6): 997–1008.

Colla S. (1926) Laboulbeniales osservati nelle collezioni del R. Museo Zoologico di Torino. *Memorie della Reale Accademia nazionale dei Lincei, Classe di Scienze Fisiche, Matematische e Naturali* **2**: 153–193.

Coope G.R., Moore P.D., Gibbs A. (1986) The invasion and colonization of the North Atlantic islands: a palaeoecological solution to a biogeographic problem. *Philosophical Transactions of the Royal Society of London B* **314**: 619–635.

De Kesel A. (1993) Relations between host population density and spore transmission of *Laboulbenia slackensis* (Ascomycetes, Laboulbeniales) from *Pogonus chalceus* (Coleoptera, Carabidae). *Belgian Journal of Botany* **126**: 155–163.

De Kesel A. (1995) Relative importance of direct and indirect infection in the transmission of *Laboulbenia slackensis* (Ascomycetes, Laboulbeniales). *Belgian Journal of Botany* **128**: 124–130.

De Kesel A. (1996) Host specificity and habitat preference of *Laboulbenia slackensis*. *Mycologia* **88**: 565–573.

De Kesel A. (1997) Contribution towards the study of the specificity of Laboulbeniales (Fungi, Ascomycetes), with particular reference to the transmission, habitat preference and host-range of *Laboulbenia slackensis*. PhD thesis, Universiteit Antwerpen, Antwerp.

De Kesel A. (1998) Identificatie en gastheerspectrum van het genus *Laboulbenia* in België (Ascomycetes, Laboulbeniales). *Sterbeeckia* **18**: 13–31.

De Kesel A., Gerstmans C., Haelewaters D. (2020) Catalogue of Laboulbeniales of Belgium. *Sterbeeckia* **36**: 3–143.

De Kesel A., Haelewaters D. (2014) *Laboulbenia slackensis* and *L. littoralis* sp. nov. (Ascomycota, Laboulbeniales), two sibling species as a result of ecological speciation. *Mycologia* **106**: 407–414.

De Kesel A., Haelewaters D., Dekoninck W. (2016) Myrmecophilous Laboulbeniales (Ascomycota) in Belgium. *Sterbeeckia* **34**: 3–6.

De Kesel A., Rammeloo J. (1991) Checklist of Laboulbeniales (Ascomycetes) of Belgium. *Belgian Journal of Botany* **124**: 204–214.

Dougherty E.R., Carlson C.J., Bueno V.M., Burgio K.R., Cizauskas C.A., Clements C.F., Seidel D.P., Harris N.C. (2016) Paradigms for parasite conservation. *Conservation Biology* **30**: 724–733.

Drugmand D. (1989) Distribution et phénologie des Paederinae de Belgique (Coleoptera, Staphylinidae). *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* **55**: 3–52.

Eyjólfsdóttir G. (1995) Soil fungi isolated from Icelandic farmland. *Acta Botanica Islandica* **12**: 53–62.

Gardes M., Bruns T.D. (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

GBIF. (2024) GBIF Occurrence Download. https://doi.org/10.15468/dl.kaq54m (accessed 11 December 2024).

Greipsson S., El-Mayas H., Vestberg M., Walker C. (2002) Arbuscular mycorrhizal fungi in sandy soils in Iceland. *Arctic, Antarctic, and Alpine Research* **34**: 419–427.

Haelewaters D., De Kesel A. (2020) Checklist of thallus-forming Laboulbeniomycetes from Belgium and the Netherlands, including *Hesperomyces halyziae* and *Laboulbenia quarantenae* spp. nov. *MycoKeys* **71**: 23–86.

Haelewaters D., De Kesel A., Gorczak M., Bao K., Gort G., Zhao S.Y., Pfister D.H. (2019a) Laboulbeniales (Ascomycota) of the Boston Harbor Islands II (and other localities): species parasitizing Carabidae, and the *Laboulbenia flagellata* species complex. *Northeastern Naturalist* **25**: 110–149.

Haelewaters D., De Kesel A., Pfister D.H. (2018) Integrative taxonomy reveals hidden species within a common fungal parasite of ladybirds. *Scientific Reports* **8**: 15966.

Haelewaters D., Gorczak M., Pfliegler W.P., Tartally A., Tischer M., Wrzosek M., Pfister D.H. (2015) Bringing Laboulbeniales into the 21st century: enhanced techniques for extraction and PCR amplification of DNA from minute ectoparasitic fungi. *IMA Fungus* **6**: 363–372.

Haelewaters D., Lubbers M., De Kesel A. (2022a) The haustorium as a driving force for speciation in thallus-forming Laboulbeniomycetes. *IMA Fungus* **13**: 1.

Haelewaters D., Matthews T.J., Wayman J.P., Cazabonne J., Heyman F., Quandt C.A., Martin T.E. (2024) Biological knowledge shortfalls impede conservation efforts in poorly studied taxa—A case study of Laboulbeniomycetes. *Journal of Biogeography* **51**: 29–39.

Haelewaters D., Pfliegler W.P., Gorczak M., Pfister D.H. (2019b) Birth of an order: Comprehensive molecular phylogenetic study excludes *Herpomyces* (Fungi, Laboulbeniomycetes) from Laboulbeniales. *Molecular Phylogenetics and Evolution* **133**: 286–301.

Haelewaters D., Van Caenegem W., De Kesel A. (2022b) *Hesperomyces harmoniae*, a new name for a common ectoparasitic fungus on the invasive alien ladybird *Harmonia axyridis*. *Sydowia* **75**: 53–74.

Hågvar S., Gobbi M., Kaufmann R., Ingimarsdóttir M., Caccianiga M., Valle B., Pantini P., Fanciulli P.P., Vater A. (2020) Ecosystem birth near melting glaciers: a review on the pioneer role of ground-dwelling arthropods. *Insects* **11**: 644.

Hall T. A. (1999) BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95– 98.

Hallgrímsson H., Eyjólfsdóttir G.G. (2004) Íslenskt sveppatal. Checklist of Icelandic fungi. 1, Microfungi. *Fjölrit Náttúrufræðistofnunar* **45**: 1–189.

Hartig F. (2022) DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.7. https://cran.r-project.org/web/packages/DHARMa/index.html (accessed 24 May 2025).

Hoang D.T., Chernomor O., von Haeseler A., Minh B.Q., Vinh L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* **35**(2): 518–22.

Høier J. (2009) Laboul-speciale. *Heterocerus. Nyhedsbrev for Danske Coleopterologer* **19**: 11–16.

Hopple J. (1994) Phylogenetic investigations in the genus *Coprinus* based on morphological and molecular characters. PhD thesis, Duke University, Durham, North Carolina.

Howard K.L., Seymour R., Johnson T.W. (1970) Aquatic fungi of Iceland: Saprolegniaceae. *Journal of the Elisha Mitchell Scientific Society* **86**: 63–79.

Hubbard A., Sugden D., Dugmore A., Norddahl H., Pétursson H.G. (2006) A modelling insight into the Icelandic Last Glacial Maximum ice sheet. *Quaternary Science Reviews* **25**: 2283–2296.

Huldén L. (1983) Laboulbeniales (Ascomycetes) of Finland and adjacent parts of the U.S.S.R. *Karstenia* **23**: 31–136.

Huldén L. (1985) Floristic notes on Palaearctic Laboulbeniales (Ascomycetes). *Karstenia* **25**: 1–16.

Johnson T.W. (1968) Aquatic fungi of Iceland: introduction and preliminary account. *Journal of the Elisha Mitchell Scientific Society* **84**: 179–183.

Johnson T.W. (1971) Aquatic fungi of Iceland: *Pythium*. *Mycologia* **63**: 517–536.

Johnson T.W., Howard K.L. (1968) Aquatic fungi of Iceland: species associated with algae. *Journal of the Elisha Mitchell Scientific Society* **84**: 305–311.

Kalyaanamoorthy S., Minh B.Q., Wong T.K.F., von Haeseler A., Jermiin L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* **14**(6): 587–89.

Kassambara A., Mundt F. (2020) factoextra: extract and visualize the results of multivariate data analyses. R package 1.0.7. https://cran.r-project.org/web/packages/factoextra/index.html (accessed 24 May 2025).

Katoh K., Rozewicki J., Yamada K.D. (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**(4): 1160–66.

Kurtzman C.P., & Robnett C.J. (1997) Identification of clinically important ascomycetous yeasts based on nucleotide divergence in the 5' end of the large-subunit (26S) ribosomal DNA gene. *Journal of Clinical Microbiology* **35**: 1216–1223.

Lenth R. (2025) emmeans: estimated marginal means, aka least-squares means. R package version 1.11.1. https://cran.r-project.org/web/packages/emmeans/index.html (accessed 24 May 2025).

Liu J., Haelewaters D., Pfliegler W.P., Page R.A., Dick C.W., Aime M.C. (2020) A new species of *Gloeandromyces* from Ecuador and Panama revealed by morphology and phylogenetic reconstruction, with a discussion of secondary barcodes in Laboulbeniomycetes taxonomy. *Mycologia* **112**: 1192–1202.

Maire R. (1920) Troisième contribution à l'étude des Laboulbéniales de l'Afrique du Nord. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* **11**: 123–138, 143–170.

Majewski T. (1971) Rare and new Laboulbeniales from Poland. *Acta Mycologica* **7**: 269–277.

Majewski T. (1973) Rare and new Laboulbeniales from Poland. III. *Acta Mycologica* **9**: 111–124.

Majewski T. (1994) The laboulbeniales of Poland. *Polish Botanical Studies* **7**: 1–466.

Miadlikowska J., Lutzoni F. (2000) Phylogenetic revision of the genus *Peltigera* (lichen-forming Ascomycota) based on morphological, chemical, and large subunit nuclear ribosomal DNA data. *International Journal of Plant Sciences* **161**: 925–958.

Middelhoek A. (1943) Enige nieuwe Laboulbeniales voor ons land (vervolg). *Fungus* **14**: 71–72.

Miller M.A., Pfeiffer W., Schwartz T. (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. *2010 Gateway Computing Environments Workshop (GCE),* 1–8.

Mishustin R.I., Khodosovtsev A.Y., Rossi W. (2024) New species and new records of Laboulbeniales (Ascomycota) from countries surrounding the Black Sea. *Cryptogamie, Mycologie* **45**: 139–149.

Mishustin R.I., Khodosovtsev A.Y. (2023) More Laboulbeniales (Ascomycota) from Ukraine. *Czech Mycology* **75**: 1–14.

MyCoPortal. (2024) MyCoPortal Portal. https://www.mycoportal.org/portal/collections/individual/index.php?occid=10145017&clid=0 (accessed 24 May 2025).

Náttúrufræðistofnun. (2024) Tegundaskrá smádýra. https://www.ni.is/sites/default/files/2024-12/tegundaskra_smadyra_vefur.pdf (accessed 16 December 2024).

Nguyen L.-T., Schmidt H.A., von Haeseler A., Minh B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**(1): 268–74.

Panagiotakopulu E. (2014) Hitchhiking across the North Atlantic – Insect immigrants, origins, introductions and extinctions. *Quaternary International* **341**: 59–68.

Panagiotakopulu E. (2021) North Atlantic insect faunas, fossils and pitfalls. In: *Biogeography in the Sub-Arctic* (eds. Panagiotakopulu E., Sadler J.P.), © 2021 John Wiley & Sons, Hoboken, NJ: 161–184.

Picard F. (1913) Contribution à l'étude des Laboulbeniales d'Europe et du nord de l'Afrique. *Bulletin de la Société Mycologique de France* **29**: 503–571.

Picard F. (1916) Sur quelques Laboulbéniales d'Europe. *Bulletin de la Société Mycologique de France* **50**: 440–460.

Richardson M. (2004) Coprophilous fungi from Iceland. *Acta Botanica Islandica* **14**: 77–102.

Ronquist F., Teslenko M., Van Der Mark P., Ayers D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. (2012) MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**(3): 539–42.

Rossi W. (2011) New species of *Laboulbenia* from Ecuador, with evidence for host switch in the Laboulbeniales. *Mycologia* **103**: 184–194.

Rossi W., Cezari Rossi M.G. (1976) Contributo alla conoscenza delle Laboulbeniali (Ascomycetes) parassite di Carabidi italiani (Insecta, Coleoptera). *Giornale Botanico Italiano* **110**: 145–153.

Rossi W., Cezari Rossi M.G. (1978) Contributo alla conoscenza delle Laboulbeniali (Ascomycetes) parassite di Stafilinidi italiani (Insecta, Coleoptera). *Giornale Botanico Italiano* **112**: 63–74.

Rossi W., Máca J. (2006) Notes on the Laboulbeniales (Ascomycetes) from the Czech Republic. *Sydowia* 58: 110–124.

Rossi W., Santamaria S. (2006) *Laboulbenia casnoniae* (Ascomycota, Laboulbeniales) and allied species. *Nova Hedwigia* **82**: 189–204.

Rostrup E. (1903) Islands svampe. *Botanisk Tidsskrift* **25**: 281–335.

Sæmundsson K., Sigurgeirsson M.Á., Friðleifsson G.Ó. (2020) Geology and structure of the Reykjanes volcanic system, Iceland. *Journal of Volcanology and Geothermal Research* **391**: 106501.

Santamaria S. (1986) Contribución al conocimiento de los Laboulbeniales (Ascomycotina) ibéricos, I: Género *Laboulbenia*. *Anales del Jardín Botánico de Madrid* **42**: 271–283.

Santamaria S. (1989) El orden Laboulbeniales (Fungi, Ascomycotina) en la Peninsula lberica e lslas Baleares. *Edicions Especials de la Societat Catalana de Micologia* **3**: 1–396.

Santamaria S. (1992) Laboulbeniales (Ascomycotina) ibéricos. Nuevos datos corológicos. *Nota Micologica* **7**: 139–144.

Santamaria S. (1998) Laboulbeniales, I. *Laboulbenia*. *Flora Mycologica Iberica* **4**: 1–186.

Santamaria S., Balazuc J., Tavares I.I. (1991) Distribution of the European Laboulbeniales (Fungi, Ascomycotina) an annotated list of species. *Treballs de l'Institut Botanic de Barcelona* **14**: 1–123.

Santamaria S., Pedersen J. (2021) Laboulbeniomycetes (Fungi, Ascomycota) of Denmark. *European Journal of Taxonomy* **781**: 1–425.

Scheloske H.W. (1969) Beiträge zur Biologie, Ökologie und Systematik der Laboulbeniales (Ascomycetes) unter besonderer Berücksichtigung des Parasit-Wirt-Verhältnisses. *Parasitologische Schriftenreihe* **19**: 1–176.

Siemaszko J., Siemaszko W. (1928) Owadorosty polskie i palearktyczne. *Polskie Pismo Entomologiczne* **6**: 188–211.

Siemaszko J., Siemaszko W. (1932) Owadorosty polskie i palearktyczne. II. *Polskie Pismo Entomologiczne* **10**: 149–188.

Sigurgeirsson M., Einarsson S. (2019) Catalogue of Icelandic Volcanoes - Reykjanes and Svartsengi volcanic systems. Icelandic Meteorological Office, Institute of Earth Sciences at the University of Iceland, Civil Protection Department of the National Commissioner of the Iceland Police. https://icelandicvolcanoes.is/?volcano=REY (accessed 24 May 2025).

Spegazzini C. (1914) Primo contributo alla conoscenza delle Laboulbeniales Italiane. *Redia* **10**: 21–75.

Spegazzini C. (1915) Laboulbeniali ritrovate nelle collezioni di alcuni musei italiani. *Anales del Museo Nacional de Historia Natural de Buenos Aires* **26**: 451–511.

Thaxter R. (1891) Supplementary note on North American Laboulbeniaceaee. *Proceedings of the American Academy of Arts and Sciences* **25**: 261–270.

Thaxter R. (1896) Contributions toward a monograph of the Laboulbeniaceae. *Memoirs of the American Academy of Arts and Sciences, New Series* **12**: 189–429.

Thaxter R. (1908) Contribution towards a monograph of the Laboulbeniaceae: Part II. *Memoirs of the American Academy of Arts and Sciences, New Series* **13**: 219–469.

Turin H. (2000) De Nederlandse loopkevers—verspreiding en oecologie. *Nationaal Natuurhistorisch Museum Naturalis*, Leiden.

Vaidya G., Lohman D.J., Meier R. (2011) SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* **27**(2): 171–80.

Van Caenegem W., Boeken M., Dees A.J., Lubbers M., Moereels L., Schilthuizen M., van Wielink P.S., van Zuijlen J.W., Vandeputte A., Verbeken A., Haelewaters D. (2024) New and interesting Laboulbeniales (Fungi, Ascomycota) from the Netherlands, II. *Nova Hedwigia* **119**: 387–418.

Van Caenegem W., Haelewaters D. (2024) New insights into the DNA extraction and PCR amplification of minute ascomycetes in the genus *Laboulbenia* (Pezizomycotina, Laboulbeniales). *IMA Fungus* **15**: 14.

Vickers K., Buckland P.I. (2015) Predicting island beetle faunas by their climate ranges: the tabula rasa/refugia theory in the North Atlantic. *Journal of Biogeography* **42**: 2031–2048.

Vilgalys R., Hester M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

Wasowicz P., Pasierbiński A., Przedpelska-Wasowicz E.M., Kristinsson H. (2014) Distribution patterns in the native vascular flora of Iceland. *PLoS One* **9**: e102916.

Weir A. (1994) Further records of Laboulbeniales from collections of British Coleoptera. *Mycological Research* **98**: 433–444.

Weir A., Beakes G.W. (1993) New British Laboulbeniales. *Mycological Research* **97**: 1045–1055.

Weir A., Hammond P.M. (1997) Laboulbeniales on beetles: host utilization patterns and species richness of the parasites. *Biodiversity and Conservation* **6**: 701–719.

Wheeler Q.D., Blackwell M. (1984) Fungus–insect relationships: perspectives in ecology and evolution. Columbia University Press, New York.

White T.J., Bruns T., Lee S., Taylor J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols: a guide to methods and applications* (eds. Innis M.A., Gelfand D.H., Sninsky J.J., White T.J.), Academic Press, New York: 315–322.

Wickham H. (2016) ggplot2: elegant graphics for data analysis. Springer Nature, Berlin, Germany.

Wickham H., Bryan J. (2023) readxl: read excel files. https://cran.r-project.org/web/packages/readxl/index.html (accessed 25 May 2025).

Wickham H., François R., Henry L., Müller K. (2023) dplyr: a grammar of data manipulation. https://cran.r-project.org/web/packages/dplyr/index.html (accessed 25 May 2025).

*(Manuscript accepted 19 November 2025; Corresponding Editor: I. Krisai-Greilhuber)*