Phytotaxa 733 (2): 155–171
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.733.2.1

A new species and a new record of *Bolbitius* (Bolbitiaceae, Agaricales) from Scotland and Britain, respectively

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Abstract

A new coprophilous species of *Bolbitius*, *B. corrugatus sp. nov.*, is described and illustrated based on collections from Scotland. The new species is characterised by its yellow, corrugated pileus, hexagonal spores, and coprophilous habitat. A phylogenetic analysis based on ITS and LSU was conducted to support morphological data. A link to a time-lapse video showing the growth of basidiocarps in the type collection is included as part of the description. Another coprophilous species, *B. excoriatus,* is introduced as new to Britain and is included in the phylogenetic analysis. Morphological descriptions, illustrations, and phylogenetic analysis results of the two species are provided. A competition-based hypothesis is proposed for the variation in basidiocarp size among coprophilous fungi.

Key words: Basidiomycota, coprophilous, ITS, LSU, new taxon, phylogeny, taxonomy

Introduction

The genus *Bolbitius* Fr. (1838: 253) comprises species that grow on a range of substrates, such as dung, sawdust, humus, decayed wood, and soil (Watling 1982, Arnolds 2005, Malysheva *et al*., 2015). About 60 species are known worldwide (https://www.catalogueoflife.org, accessed October 21, 2025). In Europe, there are currently only three species of *Bolbitius* that are known to be strictly coprophilous: *B. coprophilus* (Peck) Hongo (1959: 82), *B. excoriatus* Dähncke, Hauskn., Krisai, Contu & Vizzini (2010: 122) and *B. elegans* E. Horak, G. Moreno, A. Ortega & Esteve-Rav. (2002: 615). The *B. titubans* (Bull.) Fr. (1838: 254) species complex has been studied in detail by Malysheva *et al*. (2015). The authors identified four subclades, two of which (subclades one and three) are reported to grow on dung. However, the complex remains unresolved, and the species limits are unclear.

Most of the specimens examined in this study were found by incubating herbivore dung indoors in damp chambers. This method enables a more comprehensive study of the mycobiota on dung than would be possible through chance encounters in the field. Although this method is not new (see Richardson 2003, for example), taxonomic studies of coprophilous Basidiomycota grown under these conditions have traditionally been founded on macro- and micromorphological analyses. With molecular analysis becoming more accessible, it is now possible to clarify and delimit species that were previously difficult to distinguish due to morphological overlap. The genus *Bolbitius* is no exception. This study adds a further coprophilous member to the genus *Bolbitius* with the description of a new species, *B. corrugatus*, and increases the geographic range of *B. excoriatus*.

Accepted by Entaj Tarafder: 3 Nov. 2025; published: 11 Dec. 2025

This study also introduces an additional form of taxonomic documentation: time-lapse footage. Although not a replacement for written morphological descriptions, it serves as a useful medium for illustrating basidiocarp development across the full range of maturity.

Materials and methods

Morphological observations

Cow dung was collected between August 2024 and January 2025 and incubated indoors in damp chambers. These chambers were opaque plastic boxes measuring 20 × 15 × 11 cm. The boxes were covered with a layer of food-grade plastic wrap, but they were not airtight. They were kept out of direct sunlight. Ambient temperature ranged between approximately 15–20 degrees Celsius. The dung was misted with tap water every 2–4 days. This method accounted for all but one of the specimens observed in this study; one specimen of *B. corrugatus* (K-M001445335) was found on cow dung *in situ*. This collection was made in the same location where the incubated dung was collected.

Macroscopic descriptions were based on fresh material. Macroscopic dimensions were measured using a ruler marked in 0.5 mm increments immediately after picking. Photographs were taken with an Olympus OM–D E–M10 Mark II camera, equipped with an M.Zuiko Digital ED 30 mm F/3.5 Macro lens and an M.Zuiko Digital ED 60 mm F/2.8 Macro lens. The diameter of the pileus and the length of the stipe for the single *B. excoriatus* basidiocarp studied were estimated based on measuring the dried sample with a ruler and multiplying the result by 1.5. This is because the specimen was not measured when it was fresh. Therefore, these dimensions are given approximately, based on dried samples and adjusted for shrinkage.

Micromorphological measurements were conducted using a Meiji light–field microscope (Meiji Techno, USA). Most measurements were taken from dried material, but some (c. 30%) were of fresh material. No significant differences were observed between measurements from dried and fresh material. The holotype material was mounted in a 3% Potassium Hydroxide (KOH) solution, while the other specimens were mounted in a 5% KOH solution. The notation [30, 1] indicates that measurements were taken from 30 basidiospores in one collection. The following formula is used to express basidiospore measurements: (lowest length) 5th percentile–95th percentile (highest length) × (lowest width) 5th percentile–95th percentile (highest width). Measurements of other microstructures are expressed on the basis of the 5th percentile–95th percentile for length and width. Q indicates the basidiospore length/width ratio (and uses the same formula as for basidiospores). Qav denotes the average Q of all basidiospores. The studied specimens were deposited at the Royal Botanic Garden Edinburgh.

Time-lapse footage of the type collection was recorded in February and March 2025. Images were recorded with an Olympus OM–D EM–10 Mark II camera and a M.Zuiko Digital ED 60 mm F/2.8 Macro lens. Dung bearing *B. corrugatus* primordia was placed in a glass terrarium containing vegetation from the same collection site. Images were captured at 30-second intervals. Footage was compiled and processed in DaVinci Resolve 19 (Blackmagic Design, 2024).

DNA extraction, amplification, and sequencing

We performed DNA extraction from a small part of the dried basidiocarps using a 1:50 dilution of NaOH and a 1:10 dilution of Tris 8.0 pH buffer, following a modified version of the protocol developed by Osmundson *et al*. (2012). We used the primers ITS1 and ITS4 (White *et al.* 1990) and LR0R–LR5 (Cubeta *et al.* 1991, Vilgalys & Hester 1990) for sequencing the ITS and 28S (LSU) regions of nuclear ribosomal DNA, respectively. PCR reactions (Mullis & Faloona 1987) consisted of 30 cycles at an annealing temperature of 59.5°C. We checked PCR products on 2% agarose gels and SeeGreen nucleic acid stain. Sanger sequencing was performed by Molecular Cloning Laboratories (MCLAB), South San Francisco, California, USA, using ABI 3730XL sequencers. Chromatograms were manually checked and corrected using SnapGene 8.0.1 software (Dotmatics, Boston, MA).

Phylogenetic analyses

For this study, 6 ITS and 4 LSU sequences were newly generated. In addition, 54 ITS sequences and 37 LSU sequences of *Bolbitius* species, and sequences of *Conocybe apala* as an outgroup, were downloaded from the GenBank database

(www.ncbi.nlm.nih.gov/genbank/) for molecular analyses. The sequences of both genetic markers were aligned using MAFFT version 7 (https://mafft.cbrc.jp/alignment/server/index.html; Katoh *et al.* 2019) with the FFT-NS-i option, and were improved where necessary using MEGA11 (Tamura *et al*. 2021).

Phylogenetic analyses were performed with Maximum Likelihood (ML) and Bayesian Inference (BI) methods for the combined ITS+LSU dataset. The best-fit model of evolution was determined through the Akaike information criterion (AIC) function in the FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). In both ML and BI analyses, the GTR+G model was employed for the combined dataset. Maximum likelihood analysis was performed on the IQ-Tree web server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos *et al.* 2016) with 1,000 ultrafast bootstrap replicates. BI analysis was performed using MrBayes 3.2.7 software (Ronquist *et al.* 2012), with two independent runs each consisting of 7 million generations under the described model and four chains, sampling every 100 generations. To check for convergence of MCMC analyses and obtain estimates of the posterior distribution of parameter values, Tracer v1.7.1 was used (Rambaut *et al.* 2018). We accepted the result where the ESS (Effective Sample Size) was above 200 and the PSRF (Potential Scale Reduction Factor) was close to 1. Branches with bootstrap support (BS) and posterior probability (PP) values greater than or equal to 70% and 0.90, respectively, were considered significantly supported (Hillis & Bull 1993, Alfaro *et al.* 2003). Tree topologies were then edited and visualized in iTOL (Letunic & Bork 2019). Newly generated sequences were deposited in GenBank, each with a corresponding accession number.

Results

Molecular phylogeny

The combined dataset of ITS+LSU sequences for members of the genus *Bolbitius* contained 1506 characters, including gaps (ITS: 1–678 and LSU: 679–1506). Both Maximum likelihood and Bayesian analyses produced the same topology. Therefore, we present only the ML tree with both BS and PP values (Fig. 1).

Most clades on the tree are well-supported and correspond to known morphological species of the genus (Fig. 1). In particular, the *B. excoriatus* clade, including sequences from the holotype, has the maximal support (BS = 100 % and PP = 1), and sequences of our Scottish collection are nested within it. However, the results of our phylogenetic analysis also provide additional evidence of considerable intraspecific variability in the group of *B. titubans* and closely related species (Malysheva *et al*. 2015). Difficulties in species delimitation within this species complex and the identification of correspondence between phylogenetic lineages and morphological groups necessitate further studies and additional data.

According to the phylogenetic analysis, the sequences of *B. corrugatus* form an independent and highly supported (BS = 100 % and PP = 1) monophyletic clade that is sister to the *B. excoriatus* clade and apparently represents a distinct taxon. Morphological data also support the recognition of the studied collections as a new species (see Discussion section below).

Taxonomy

Bolbitius corrugatus A. Drummond-Herdman & E.F. Malysheva, *sp. nov.* (Figs. 2–6)
MycoBank: MB: 859598

Diagnosis:—*Bolbitius corrugatus* differs from *B. excoriatus* by having a yellow, not brown, pileus; from *B. titubans* sensu lato, its smaller, more angular and hexagonal basidiospores; from *B. coprophilus* by its yellow turning to pale buff pileus and slightly smaller, more angular and hexagonal basidiospores; and from *B. elegans* by being non-gasteroid, having stouter basidiocarps and having hexagonal basidiospores.

Holotype:—SCOTLAND. Midlothian, Edinburgh, growing on incubated highland cow dung collected on the north–west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 27 February 2025, *A. Drummond–Herdman* (E01528038). GenBank: PV021289 (ITS); PV021294 (LSU).

Etymology:—The specific epithet '*corrugatus*' refers to the species' corrugated pileus.

Time-lapse:—Available at https://youtu.be/AvJDKkuPvG8

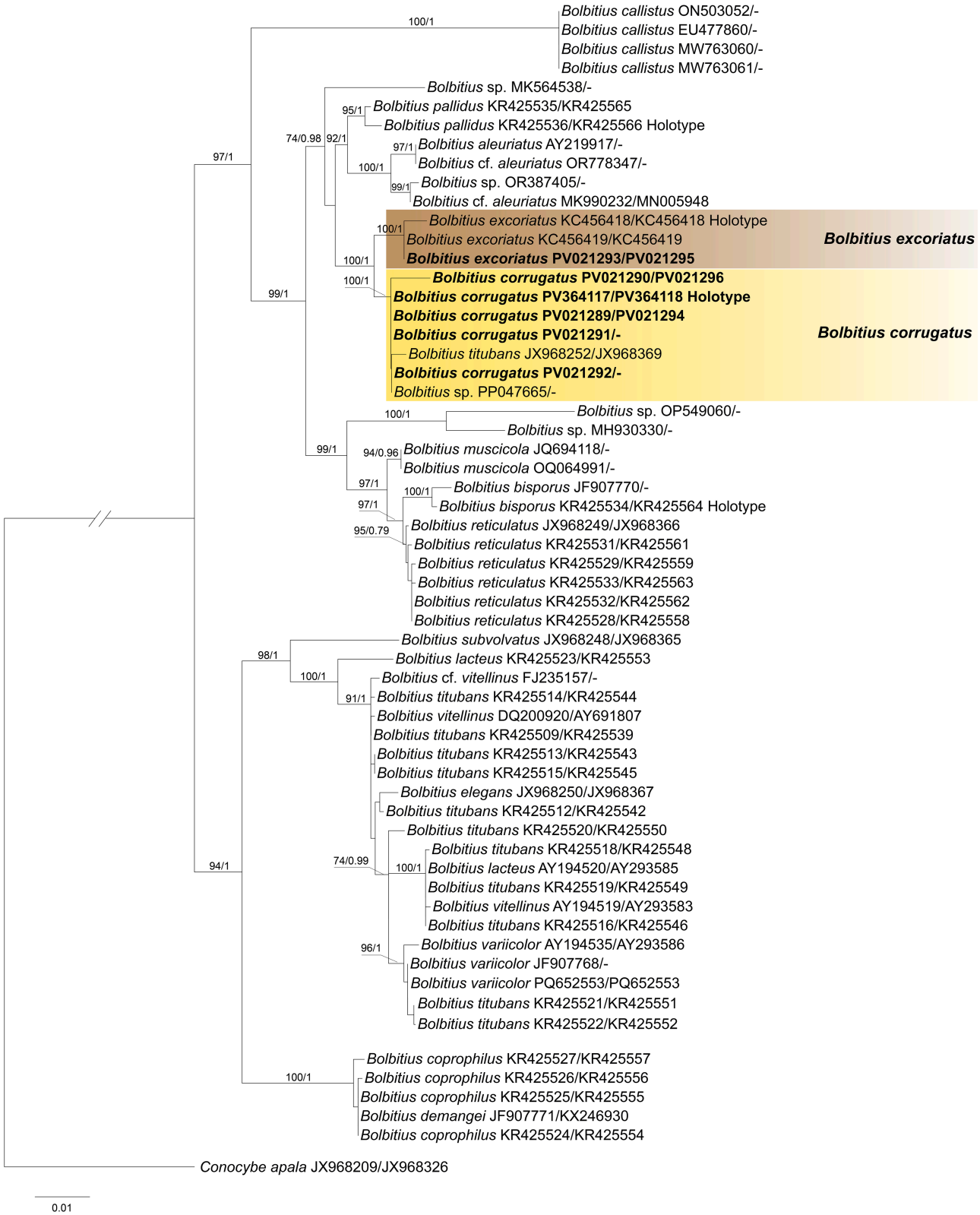

FIGURE 1. Maximum likelihood tree generated from the combined ITS-LSU dataset of the *Bolbitius* species. Bootstrap support and Posterior probability values (BS/PP) are shown above the branches. All sequences are labelled with taxon name and GenBank accession numbers (ITS/LSU). The scale bar indicates the expected changes per site. The sequences newly generated for this study are indicated in bold. Clades of *B. corrugatus* and *B. excoriatus* species are highlighted in colour.

FIGURE 2. Morphological characteristics of *Bolbitius corrugatus* basidiocarp (holotype, E01528038). **A–D.** Various stages of growth. **E.** Gill edge. **F.** Base of stipe.

FIGURE 3. Morphological characteristics of *Bolbitius corrugatus* basidiocarp (K-M001445335). **A–D.** In its natural habitat. **E–F.** The same specimen 2 hours after collection.

Description:—Pileus 4–25 mm wide and 1–4.5 mm high when mature; campanulate when young, expanding to plano–convex, broadly umbonate; surface wrinkled and covered in a gelatinous layer when immature, developing to corrugated from the margin to start of the broad umbo, disk with protruding vein-like reticulum at maturity; margin crenate; predominantly lemon yellow, drying to pale–cream from the margin inwards, finally pale olive at the edge with the centre dark yellow; surface viscid with a glutinous top layer particularly in humidity, excoriate with drying. *Lamellae* free or narrowly adnexed, subdistant, thin, with one series of lamellulae extending to approximately 20% to 50% of the gill; whitish when young, maturing to orange, then light brown; edge white, crisped to finely serrate. *Stipe* 8.5–71 × 0.5–1.7 mm, equal, flocculose, with a bulbous base up to 3 mm wide, sometimes shortly tapering but not rooting; pale white, with a yellow–green tint which concentrates at the base, drying to pale buff. *Odour* and *Taste* not distinctive.

Basidiospores [151, 4] (7.8)9.0–10.5(12.0) × (5)6–7(8) µm, mean: 9.9 × 6.4 µm, width in front view: 5–6.5(6.6) um, Q = (1.25)1.37 × 1.75(1.83), Qav = 1.67; variable in shape, angular or subhexagonal, lentiform-oblong, often slightly irregular in side view, irregular in front-view, yellow-brown in KOH, thick-walled, with central or slightly eccentric germ pore 2.2–3.5 µm wide. *Basidia* 2-, 3- and 4-spored, 19–25 × 9–12 µm, clavate. *Pseudoparaphyses* present, clavate. *Cheilocystidia* 20–39 × 9–21 µm, variable in shape: broadly fusiform, utriform, lageniform with a long or short neck, clavate, rarely sphaeropedunculate, hyaline, thin-walled, intermixed with basidia. *Pleurocystidia* absent. *Pileipellis* hymeniform, consisting of pyriform, subglobose, broadly clavate to sphaeropedunculate elements (15–35 × 11–23 µm), covered in a gelatinous layer (but this may not show on dried basidiocarps). *Stipitipellis* a cutis, consisting of cylindrical hyaline hyphae, with caulocystidia singularly, in small groups, or in dense clusters of up to ten. *Caulocystidia* variable in shape: oblong-reniform, utriform, broadly lageniform or narrowly lageniform with slightly incurved walls (1–3 incurves), 20–39 × 10–19 µm. *Clamp connections* not observed.

FIGURE 4. Basidiocarps of *Bolbitius corrugatus*. All photographs were taken immediately after basidiocarps were picked. **A, D, E, F, H, I.** Holotype (E01528038). **B, C, G.** Epitype (BX7). Note: the pileus in section H is darkened by another's spore deposit.

Habitat and distribution:—Solitary or in small groups on old cow dung in upland grassland.

Additional specimens examined:—**SCOTLAND**: Midlothian, Edinburgh, mixed acidic upland grassland, growing on incubated highland cow dung collected on the north–west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 31 August 2024, *A. Drummond–Herdman* (K-M001445334), GenBank: PV021292 (ITS); ibid., growing on highland cow dung on the north–west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 8 September 2024, *A. Drummond–Herdman* (K-M001445335), GenBank: PV021291 (ITS); ibid., growing on incubated highland cow dung collected on the north-west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 11 September 2024, A. Drummond–Herdman (K-M001445336), GenBank: PV021289 (ITS); PV021294 (LSU); ibid., growing on incubated highland cow dung collected on the north-west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 16 September 2024, *A. Drummond–Herdman* (K-M001445337). GenBank: PV021290 (ITS); PV021296 (LSU); **HUNGARY**: Hortobágy, on cow dung, 14 June 2007, *László Nagy* (NL-1994), GenBank: JX968252 (ITS); JX968369 (LSU).

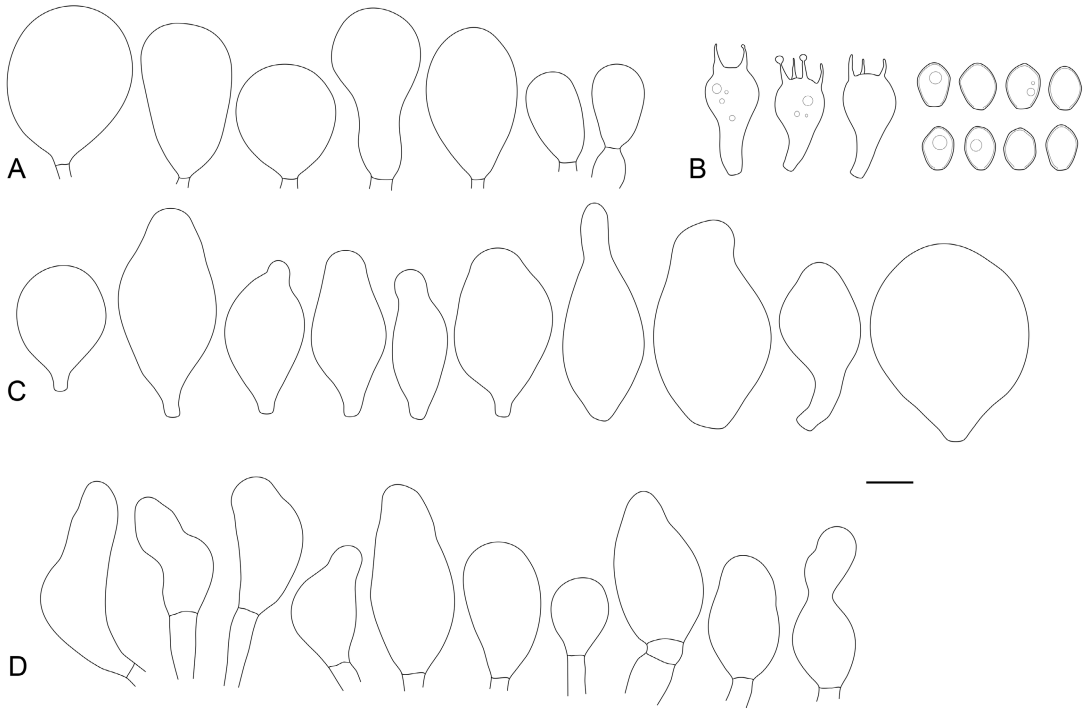

FIGURE 5. Microscopic structures of *Bolbitius corrugatus* (**Holotype**). **A**. Elements of pileipellis. **B**. Basidia and spores. **C**. Cheilocystidia. **D**. Caulocystidia. Scale bar = 10 µm.

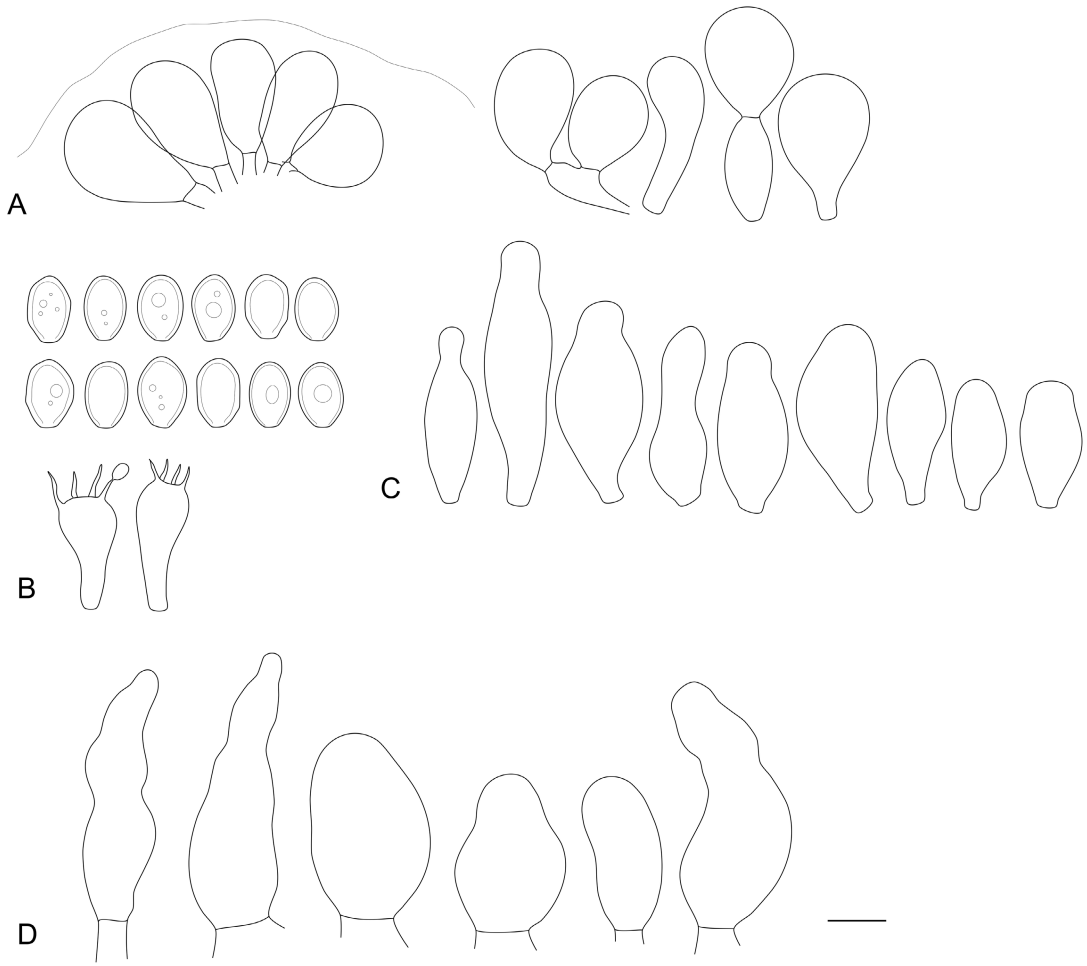

FIGURE 6. Microscopic structures of *Bolbitius corrugatus* (K-M001445334; K-M001445335; K-M001445336; K-M001445337; E01528038). **A.** Elements of pileipellis. **B.** Spores and basidia. **C.** Cheilocystidia. **D.** Caulocystidia. Scale bar = 10 µm.

Bolbitius excoriatus Dähncke, Hauskn., Krisai, Contu & Vizzini, Österreichische Zeitschrift für Pilzkunde 19: 122 (2010) (Figs. 7, 8)
MycoBank MB: 519280

Pileus approximately 6 mm diam., oviform-parabolic when young, convex with maturity; viscid pellicle, drying with age; excoriate margin at all stages; brown with light tints in the centre and edge. *Lamellae* free, close, slightly ventricose; pale when young, speckled light brown with age; edge slightly crystalline in appearance; not deliquescing. *Stipe* approximately 10 mm long, white with a yellowish green tint, flocculose and pruinose. *Odour and Taste*: not observed.

Basidiospores [30, 1] 8–9(10) × 5–6(6.5) µm, mean: 8.9 × 5.9 µm, Q = 1.33 × 1.71(1.80), Qav = 1.53; variable in shape, angular to hexagonal, mitriform, lentiform-oblong; yellow-brown in KOH; thick-walled, with central or slightly eccentric germ pore. *Basidia* 2- and 4-spored, 21.4–28.3 × 8.9–10.0 µm, clavate or narrowly clavate, sometimes slightly irregular. *Pseudoparaphyses* present, clavate. *Cheilocystidia* 29–40 × 15–23 µm, variable in shape: broadly utriform, often asymmetrical; clavate; irregularly oblong. *Pleurocystidia* absent. *Pileipellis* hymeniform, consisting of clavate, subglobose, broadly clavate to sphaeropedunculate elements 16–25 × 6–11 µm, covered in a gelatinous layer (but this may not show on dried basidiocarps). *Stipitipellis* a cutis. *Caulocystidia* variable in shape: broadly lageniform, utriform, clavate, subcylindrical, 22–31 × 8–13 µm. *Clamp connections* not observed.

Material examined:—**SCOTLAND**: Midlothian, Edinburgh, mixed acidic upland grassland, growing on incubated highland horse or cow dung collected on the north–west slopes of Caerketton Hill, 55.888, -3.226, elev. 331 m, 18 October 2024*, A. Drummond–Herdman* (E01528037). GenBank: PV021293 (ITS); PV021295 (LSU).

FIGURE 7. Basidiocarp of *Bolbitius excoriatus* (E01528037). **A.** Immature. **B–D.** Mature, displaying its excoriate pileus.

Discussion

Taxonomic position

This study was initiated by the first author after he was unable to identify the first Scottish collection using macro- and micromorphological characteristics. The following literature was referred to: Richardson & Watling (1997), Horek *et al*. (2002), Arnolds (2003), Doveri (2004), Arnolds in Noordeloos *et al*. (2005), Hausknecht & Vesterholt in Knudsen & Vesterholt (2008), and Malysheva *et al*. (2015). The collection evidently belonged to the *Bolbitius titubans* species complex due to its coprophilous habitat, yellow pileus, whitish stipe, and rusty brown spore print.

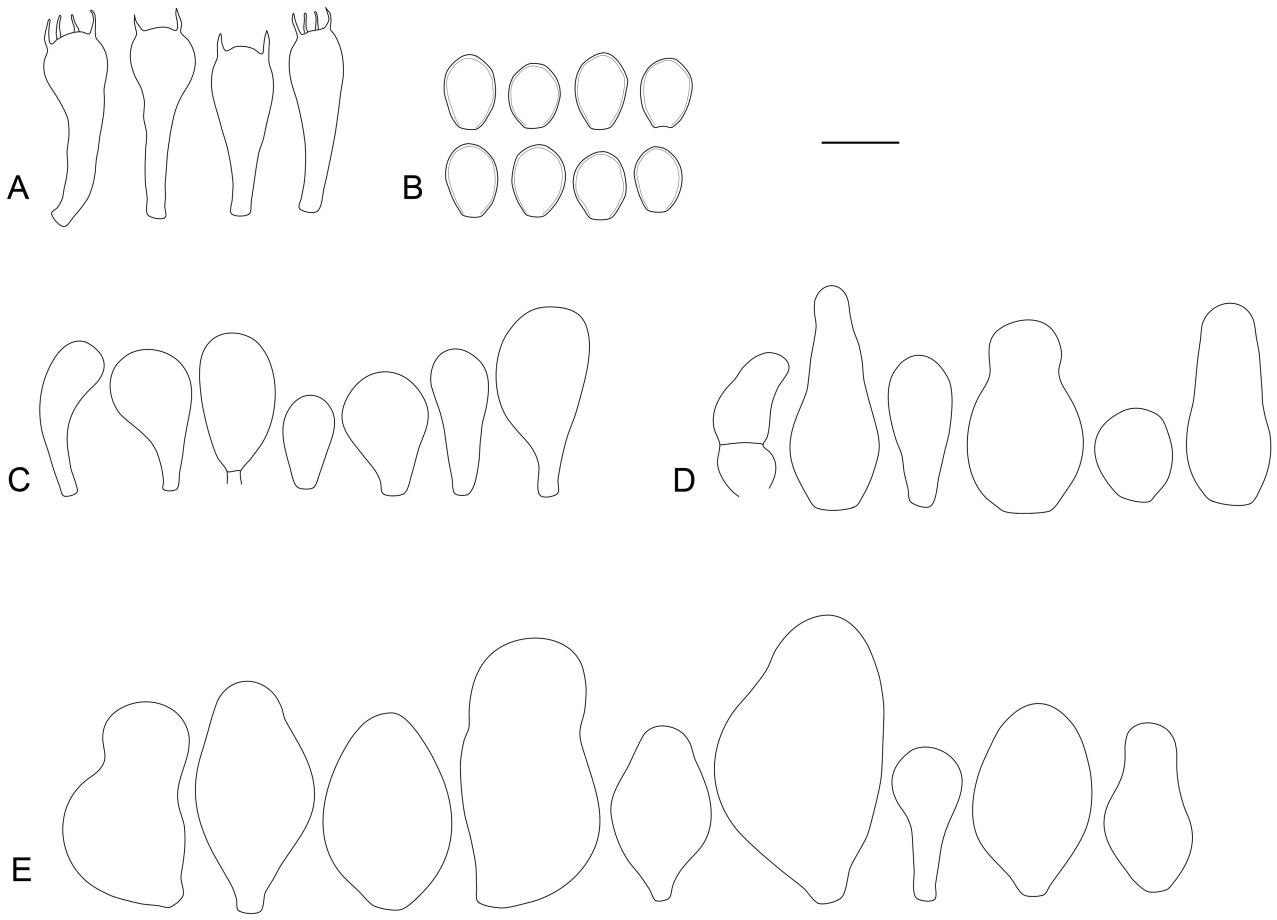

FIGURE 8. Microscopic structures of *Bolbitius excoriatus* (E01528037). **A**. Basidia. **B**. Spores. **C**. Elements of pileipellis. **D**. Caulocystidia. **E**. Cheilocystidia. Scale bar = 10 µm.

Over the years, multiple taxa (at various ranks) have been described under what we now refer to as the *B. titubans* species complex. However, all such taxa are described as having ellipsoid, ovoid, or amygdaloid spores, or other morphologically similar forms. We found no description of a taxon with a yellow pileus, growing on dung, which has hexagonal or distinctly angular spores.

Why, then, has *B. corrugatus* remained undetected until now? Perhaps this is partly because there has not been a widespread drive to study yellow coprophilous *Bolbitius* specimens under the microscope due to a presumption that microcharacters overlap and that, in any event, the taxa can be easily distinguished macroscopically. Doveri (2004) says, 'in *Bolbitius* the distinction between one species and another is based especially on the habitat and macroscopic characteristics, as microscopic features are often very similar'. With a similar effect, Arnolds in Noordeloos *et al*. (2005) says '*Bolbitius titubans* var. *titubans* is easily recognised by the bright yellow viscid pileus and the fragile, deliquescent nature of the basidiocarps with free, orange-brown lamellae'. This explanation may help clarify why *B. corrugatus*, with its hexagonal spores, has remained undetected until now.

Another explanation for the lack of observations is that *B. corrugatus* is genuinely rare, rather than merely under-recorded. It may be restricted to a narrow range of habitats. The Scottish collections grew in U4 grassland, subcommunities U4a, U4b, and U4e (Averis *et al*. 2004). The soil is classified as ranker, specifically subgroup brown ranker, which means it is shallow soil overlaying noncalcareous rock or rock rubble with a mineral A horizon and occasionally a thin, weakly developed B horizon (Scottish Soil Classification 2013). Being coprophilous, the species only grows in ecosystems that contain grazing herbivores. All the specimens of the Scottish collections grew on dung from a herd of highland cattle, which live and graze year-round in 300 acres of upland grassland. The only human input is locally sourced hay in winter; otherwise, they are entirely free-range. This means the cattle have a varied diet of a broad range of plant species. Subsequently, their dung has a greater capacity to support a wide range of coprophilous fungi species due to its higher lignin content (Kuyper 2021). This is in contrast to, for example, herbivores fed on concentrated feeds and monocultures of ryegrass (*Lolium perenne*), which, while easier to digest for the animal, results

in dung of reduced quality from the perspective of coprophilous fungi (Kuyper 2021). As Richardson (2001) noted, it is highly likely that the diversity and species occurrence of coprophilous fungi are influenced by the nutritional quality of different dung types. Therefore, we suggest that if *B. corrugatus* has not been readily observed until now due to genuine rarity—rather than misidentification—it may be because it is restricted to a narrow range of habitats: grasslands of, or similar to, the type described above: grasslands of, or similar to, the type described above where large herbivores, particularly cattle, graze freely.

Collections studied

This study is based on seven collections of *B. corrugatus*, all of which were grown on cow dung: six from Scotland and one from Hungary. The Hungarian collection was made by the last author in June 2007, in Hortobágy, eastern Hungary. This is a dry grassland steppe region, traditionally focused on raising cattle.

Phylogenetic analysis also showed that the ITS sequence PP047665, designated in GenBank as *Bolbitius* sp. (voucher MO527422), is nested within the *B. corrugatus* clade. The collection was made by Terri Clements in August 2023, in Arizona, USA (Clements 2023). We did not have the opportunity to conduct a microscopic examination of this specimen; however, it is macroscopically similar to the collections studied (mushroomobserver.org/527422). The American specimens were growing on cow dung in grassy subalpine meadows at an elevation of approximately 2,800 m.

The first four collections were the trigger for this study. They were made by the first author between August and September 2024. A total of three basidiocarps grew from a few pieces of cow dung (all originally from the same deposit). A fourth specimen was found growing on cow dung in the wild, at the same location where the dung for the previous four had been collected. The ambient temperature for those grown indoors was approximately 15–20 °C, and the dung was kept moist by light misting with tap water every 2–4 days.

Two further collections were made between February and March 2025. This consisted of multiple basidiocarps (10+) over approximately four weeks. They grew on incubated dung collected from the same location as the first Scottish collection. In contrast to the first Scottish collection, these basidiocarps often grew in groups. Indoor conditions were broadly consistent between the two collections, although ambient temperatures were slightly cooler during the second collection, due to the time of year.

Microscopic features of the Hungarian collection and clarification of morphology

In general, the micromorphology of the Hungarian specimen (NL-1994) corresponded with that of the Scottish collections. The spores were mostly hexagonal, oblong to lentiform, and slightly irregular. Their dimensions were (10.0)10.8–12.0(13.3) × (5.5)6.5–7.2(8.3) µm. However, these were very slightly longer than the Scottish collections, but other than that, they matched well. The cheilocystidia of the Hungarian collection were quite polymorphic, with a size range of 36.3–58.8 × 24.2–38.8 µm. This was slightly larger than those of the Scottish collections. They were predominantly sphaeropedunculate, but broadly clavate shapes were also present. Caulocystidia were very scanty in the collection, but their shape and size were consistent with the Scottish collections and are not discussed further. There was also no significant difference in the shape and dimensions of the elements of the pileipellis. However, those of the Hungarian collection were recorded as being slightly larger than the combined data from the Scottish collections, which prompts the following observation.

While studying the Scottish collections, we found that the size of the elements in the pileipellis may vary depending on their position on the pileus, with those in the centre being larger than those at the edge. This is demonstrated by an analysis of the measurements of the holotype specimen (which includes measurements from both the centre and margin of the pileus). The average size of the elements in the middle of the pileus was 35.0 × 22.7 µm, whereas those at the edge were 20.1 × 14.2 µm.

Bolbitius excoriatus

Our study includes the first British record of *B. excoriatus*. A single specimen was observed, appearing on dung. The basidiocarp was small, with its pileus approximately 6 mm in diameter. Microscopic characteristics matched well with Dähncke *et al.*'s (2010) original description. We obtained ITS and LSU sequences (PV021293 and PV021295, respectively). These data demonstrated that our collection clustered with the sequences of the holotype and the Swedish collection discussed below (Fig. 1). The dung type was not recorded; however, it was either cow or horse dung.

Apart from the type collection, the only other molecular data available for comparison with our specimen come from a collection made in southern Sweden in 2008 (Örstadius & Larsson 2013). Interestingly, the Swedish collectors initially expressed uncertainty in identifying their find as *B. excoriatus* due to the disparity in pileus size between their collection (2–8 mm wide) and that of the type collection (20–40 mm wide). The authors obtained DNA sequences of the type and from their own collection (KC456418 and KC456419, respectively), which confirmed conspecificity.

Our collection macromorphologically corresponds more to the Swedish collection than the type collection. In particular, this is due to the small size of the basidiocarp. This collection's microcharacters match well with the type and our collection. The only notable difference is a greater upper range for cheilocystidia size. The Swedish collection is recorded as 25–60 × 10–30 µm; the type collection as 22–40 × 12–20 µm; and our collection as 29–40 × 15–23 µm. However, we do not consider this taxonomically significant: cheilocystidia in this group are variable and do not carry as much taxonomic weight as spore shape and size (Malysheva 2018).

Another specimen was recorded and illustrated from Italy in 2017 (Ferisin & Pellizzari 2017). This collection macroscopically aligns with both the type collection, but it has larger, fleshier basidiocarps than the Swedish and Scottish collections. Microscopically, it matches the type collection, the Swedish collection, and our collection.

When describing *B. excoriatus,* Dähncke *et al*. studied an additional collection from Spain, which was 'microscopically very close' to their type collection (Dähncke *et al*. 2010). However, they were unwilling to definitively declare this collection to be the same species as their own. Instead, they labelled it *B.* aff. *excoriatus.* It had slightly larger spores and cheilocystidia.

Thus, we suggest that *B. excoriatus* may represent a species complex, similar to *B. titubans*, and include several morphologically similar taxa.

A 'competition hypothesis' for varying basidiocarp size of coprophilous fungi

Whilst studying our Scottish collections for this work, we noted the fact of significant variability in the size of basidiocarps of the studied fungi.

It has been widely noted that the basidiocarps of many coprophilous species vary in size (Arnolds 2003). One explanation for this is that size is determined by the availability of nutrients. A species producing basidiocarps that are smaller than usual is thus due to not having access to sufficient resources to grow basidiocarps to the maximum genetically determined size. In addition, some have reported that coprophilous basidiocarps may be smaller when grown indoors. However, in our study, basidiocarp size varied significantly between the four collections, with no apparent correlation between basidiocarp size and whether they were growing indoors or outdoors.

Dung is a nutrient-rich substrate (Richardson 2001, Sarrocco 2016) characterised by intense competition between fungi and bacteria, as well as among different species of fungi (Doveri 2004, Sarrocco 2016, Kuyper *et al*. 2021). Competition is a key component of the succession of coprophilous fungi, and it has been used to help explain the 'nutritional theory' of succession (Doveri 2004, Krug *et al*. 2005, Sarrocco 2016, Kuyper *et al*. 2021). 'Exploitation competition' (Kuyper *et al*. 2021) or 'capture' (Sarrocco 2016) is where one species outcompetes another by germinating and expanding its mycelial body to colonise and degrade part of the dung. 'Interference competition' (Kuyper *et al*. 2021) or 'combat' (Sarrocco 2016) is where a species either defends substrate colonised by itself or seizes substrate colonised by another. This can be achieved either at a distance, by the secretion of secondary metabolites, or by hyphal contact (Kuyper *et al*. 2021).

Direct hyphal interference was demonstrated for *Coprinellus heptemerus* (M. Lange & A.H. Sm.) Vilgalys, Hopple & Jacq. Johnson (2001: 234) against *Pilobolus crystallinus* (F.H. Wiggers) Tode (1784: 46) and *Ascobolus crenulatus* P. Karst. (1868: 763) resulting in lysis and subsequent mortality of the mycelium of the sensitive species (Ikediugwu & Webster 1970a). A corresponding investigation examined a broader range of coprophilous fungi species and their capacity to cause (and sensitivity to) hyphal interference (Ikediugwu & Webster 1970b). The study demonstrated that hyphal interference is common among coprophilous Basidiomycota, suggesting that this form of antagonism could play a crucial role in the disappearance of fungi that fruit early in the succession of dung (Ikediugwu & Webster 1970b). Furthermore, in concluding his presidential address to the British Mycological Society, Webster (1970) noted that 'the phenomenon of hyphal interference may be of profound significance'.

Interspecific competition between fungi on dung has historically been described as resulting from various forms of interaction, including competition for nutrients, hyphal interference, such as mycoparasitism, and the production of antibiotics.

We suggest that ecological niche theory can help explain the variation in basidiocarp size among coprophilous fungi. The ecological niche has been defined in various ways, but in essence, it refers to a species' position within

an ecosystem, both in terms of the resources it requires and its role in the environment (Kearney *et al*. 2010, Moore 2013, Polechová & Storch 2019). Within this framework, species can be understood to have a fundamental niche and a realised niche (Hutchinson 1957). The fundamental niche is the total range of favourable conditions in which a species could potentially survive and reproduce (Polechová & Storch 2019). The realised niche is a subset of the fundamental niche. It is the actual range of conditions in which a species can survive and reproduce, taking into account interactions such as predation, antagonism, and competition from other species (Moore 2013, Polechová & Storch 2019, Kearney *et al*. 2010). The specific energy budget of a species is restricted by the characteristics of its niche (Kearney *et al*. 2010). Correspondingly, investment in a morphological reproductive trait, such as fruit body size, is constrained by a limited energy budget (Halbwachs *et al*. 2018).

We suggest this applies to coprophilous fungi as follows. The fundamental niche of obligately coprophilous fungi (those species that are only found on dung, as opposed to facultatively coprophilous species) is theoretically the entire continuous piece of dung. The realised niche is the proportion of the dung that a given fungus actually has access to.

Our suggestion is that the variation in the realised niche of coprophilous fungi is primarily caused by the antagonism and competition of fungi, bacteria, and invertebrates, and a small basidiocarp size is attributed to the mycelial body being confined to a small space within the dung.

Therefore, the presence of a small basidiocarp for a species that typically produces larger basidiocarps may indicate the presence of certain other species in the dung. It may be that particular species have outcompeted the species in question, leaving it with a small amount of dung to draw energy from. This hypothesis is more likely to come into effect for fresher dung, which may contain a greater amount of potential nutrients. For dung that is more degraded and has reduced nutritional potential, the outcome may be the same: a reduction in basidiocarp size. However, here, the cause of the reduced size is not the fungus being outcompeted, but rather the fact that there is simply less relevant nutrition in the substrate. In other words, the fungus may have colonised a substantial proportion of the substrate, but there is not enough nutrition to support larger basidiocarps. These hypotheses are not mutually exclusive.

In conclusion, it is clear that further undescribed species of coprophilous *Bolbitius* exist worldwide. Our study was the result of a careful study of the coprophilous fungi of a relatively small area. There are many more discoveries to be made, particularly as molecular analysis becomes more accessible.

TABLE 1. A list of species, specimen and GenBank accession numbers of sequences used in this study. The newly generated sequences are in bold

Species name	Sample No.	ITS	nrLSU	Country	References
Bolbitius callistus	JKZ15	ON503052	—	USA	Matheny *et al*. 2022
Bolbitius callistus	PBM 2638	EU477860	—	USA	Hughes & Matheny 2008
Bolbitius callistus	LE F 331684	MW763060	—	Russia	Malysheva & Kalinina 2021
Bolbitius callistus	LE F 331685	MW763061	—	Russia	Malysheva & Kalinina 2021
Bolbitius sp.	MycoMap 6985	MK564538	—	USA	Russell 2024
Bolbitius pallidus	LE<RUS>:303557	KR425535	KR425565	Russia	Malysheva *et al*. 2015
Bolbitius pallidus	LE<RUS>:234343*	KR425536	KR425566	Russia	Malysheva *et al*. 2015
Bolbitius aleuriatus	—	AY219917	—	—	Mehl & Davis 2003
Bolbitius cf. aleuriatus	HAY-F-004664	OR778347	—	USA	Ostuni *et al*. 2023
Bolbitius sp.	HAY-F-000288	OR387405	—	USA	Singer *et al*. 2023
Bolbitius cf. aleuriatus	MO367253	MK990232	MN005948	USA	Rockefeller 2022
Bolbitius excoriatus	WU16355*	KC456418	KC456418	Spain	Larsson & Rstadius 2013
Bolbitius excoriatus	LO23-10	KC456419	KC456419	Sweden	Larsson & Rstadius 2013
Bolbitius excoriatus	**BX6**	**PV021293**	**PV021295**	**Scotland**	**Present study**
Bolbitius corrugatus	**BX5**	**PV021290**	**PV021296**	**Scotland**	**Present study**
Bolbitius corrugatus	**BX7***	**PV364117**	**PV364118**	**Scotland**	**Present study**
Bolbitius corrugatus	**BX4**	**PV021289**	**PV021294**	**Scotland**	**Present study**
Bolbitius corrugatus	**BX2**	**PV021291**	—	**Scotland**	**Present study**
Bolbitius titubans	NL-1994	JX968252	JX968369	Hungary	Toth *et al*. 2012
Bolbitius corrugatus	**BX1**	**PV021292**	—	**Scotland**	**Present study**

.....continued on the next page

TABLE 1. (Continued)

Species name	Sample No.	ITS	nrLSU	Country	References
Bolbitius sp.	MO527422	PP047665	—	USA	Clements 2024
Bolbitius sp.	iNat98431915	OP549060	—	USA	Russell 2022
Bolbitius sp.	MES-2341	MH930330	—	Chile	Mujic & Smith 2018
Bolbitius muscicola	PDD:87721	JQ694118	—	New Zealand	Cooper *et al*. 2020
Bolbitius muscicola	OTA:72199	OQ064991	—	New Zealand	Beaumont *et al.* 2022
Bolbitius bisporus	3029	JF907770	—	Italy	Garbelotto *et al*. 2020
Bolbitius bisporus	LE<RUS>:303558*	KR425534	KR425564	Russia	Malysheva *et al*. 2015
Bolbitius reticulatus	WU30001	JX968249	JX968366	Hungary	Toth *et al*. 2013
Bolbitius reticulatus	LE<RUS>:227536	KR425531	KR425561	Russia	Malysheva *et al*. 2015
Bolbitius reticulatus	LE<RUS>:253961	KR425529	KR425559	Sweden	Malysheva *et al*. 2015
Bolbitius reticulatus	LE<RUS>:303560	KR425533	KR425563	Russia	Malysheva *et al*. 2015
Bolbitius reticulatus	LE<RUS>:234342	KR425532	KR425562	Russia	Malysheva *et al*. 2015
Bolbitius reticulatus	LE<RUS>:215469	KR425528	KR425558	Russia	Malysheva *et al*. 2015
Bolbitius subvolvatus	WU28379	JX968248	JX968365	Hungary	Toth *et al*. 2013
Bolbitius lacteus	LE<RUS>:303559	KR425523	KR425553	Russia	Malysheva *et al*. 2015
Bolbitius cf. vitellinus	SOC1248	FJ235157	—	USA	Frank 2008
Bolbitius titubans	LE<RUS>:258041	KR425514	KR425544	Russia	Malysheva *et al*. 2015
Bolbitius vitellinus	AFTOL-ID 730	DQ200920	AY691807	USA	Matheny *et al*.
Bolbitius titubans	LE<RUS>:235346	KR425509	KR425539	Russia	Malysheva *et al*. 2015
Bolbitius titubans	LE<RUS>:303562	KR425513	KR425543	Russia	Malysheva *et al*. 2015
Bolbitius titubans	LE<RUS>:11335	KR425515	KR425545	Russia	Malysheva *et al*. 2015
Bolbitius elegans	WU23943	JX968250	JX968367	Hungary	Toth *et al*. 2013
Bobitius titubans	LE<RUS>:202345	KR425512	KR425542	Russia	Malysheva *et al*. 2015
Bolbitius titubans	LE<RUS>:303576	KR425520	KR425550	Russia	Malysheva *et al*. 2015
Bolbitius titubans	LE<RUS>:287256	KR425518	KR425548	Russia	Malysheva *et al*. 2015
Bolbitius lacteus	MSC 378485	AY194520	AY293585	USA	Hallen 2003
Bolbitius titubans	LE<RUS>:289428	KR425519	KR425549	Russia	Malysheva *et al*. 2015
Bolbitius vitellinus	MSC 378484	AY194519	AY293583	USA	Hallen 2003
Bolbitius titubans	LE<RUS>:303575	KR425516	KR425546	Russia	Malysheva *et al*. 2015
Bolbitius varicolor	MSC 378488	AY194535	AY293586	USA	Hallen 2003
Bolbitius variicolor	2303	JF907768	—	Italy	Osmundson *et al*. 2012
Bolbitius variicolor	F-2166	PQ652553	PQ652553	Sweden	Fritzson & Bravander 2024
Bolbitius titubans	LE<RUS>:214359	KR425521	KR425551	Russia	Malysheva *et al*. 2015
Bolbitius titubans	LE<RUS>:303556	KR425522	KR425552	Russia	Malysheva *et al*. 2015
Bolbitius coprophilus	LE<RUS>:11317	KR425527	KR425557	Russia	Malysheva *et al*. 2015
Bolbitius coprophilus	LE<RUS>:18599	KR425526	KR425556	Russia	Malysheva *et al*. 2015
Bolbitius coprophilus	LE<RUS>:18905	KR425525	KR425555	Russia	Malysheva *et al*. 2015
Bolbitius demangei	4030	JF907771	KX246930	Italy	Osmundson *et al* 2013
Bolbitius coprophilus	LE<RUS>:287244	KR425524	KR425554	Russia	Malysheva *et al*. 2015
Conocybe apala	NL-1012	JX968209	JX968326	Hungary	Toth *et al*. 2013

* is shown for type material; — means the data is unavailable.

Acknowledgements

We thank Roy Watling and Mike Richardson for reviewing the text and providing helpful comments. We thank Gus Routledge for advising on the ecological classification of the Scottish locality. We thank Terri Clements for providing information about the American collection referred to in this study. We thank the staff at the herbaria of the Royal

Botanic Garden Edinburgh and the Royal Botanic Gardens, Kew, for their assistance in depositing and cataloguing the material from this study.

ADH would like to thank Simon Kennedy for providing him with a compound microscope and stereomicroscope early in his journey into mycology. In doing so, he enabled this study and others to follow. ADH would also like to thank Humphrey Drummond for providing him with a microscope camera, which further helped his studies. Part of the work performed by EM was supported by the project No. 124013100829-3 of the V.L. Komarov Botanical Institute of the Russian Academy of Sciences. DS and LGN were supported by the National Academy of Scientist Education and by the National Research Development and Innovation Office (grant no. OTKA 142188).

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