An overview of the genus Coprotus (Pezizales, Ascomycota) with notes on the type species and description of C. epithecioides sp. nov.

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Abstract
In a mycological research performed in the Sjeverni Velebit National Park, Croatia, a new species of Coprotus was discovered, described here as C. epithecioides. Along with the microscopic examination, phylogenetic analysis of the type material, based on ITS and LSU sequences, was performed in order to evaluate its relationship with the type species, C. sexdecimsporus. The type species was sequenced in this study for the first time, providing ITS and LSU sequences from two separate collections which displayed differences in macroscopic characters and content of paraphyses. An extended description of C. sexdecimsporus based on Croatian material is also provided. A worldwide identification key to the species assigned to the genus Coprotus is presented, along with a species overview, containing a data matrix. The phylogenetic position of Coprotus in the Boubovia-Coprotus clade within Pyronemataceae s.l. is discussed. Coprotus sexdecimsporus is also reported here as new to the Croatian mycobiota.

Keywords
Coprotus epithecioides sp. nov., Coprotus sexdecimsporus, Ascomycota, identification key, phylogeny, taxonomy

Introduction
The name Coprotus Korf was first mentioned but not validly published by Korf (1954) as a seggregate of the genus Ascophanus Boud. (Boudier 1869) for species having iodine negative asci, hooked paraphyses and small guttulate spores. Kimbrough (1966)
recognized a “Coprotus group” in Ascophanus Boud. with species that have iodine negative asci staining uniformly in Congo red and ascospores with de Bary bubbles. The genus Coprotus Korf & Kimbr. was validated by Kimbrough and Korf (1967), encompassing certain species of Ascophanus and Ryparobius Boud. (Boudier 1869), with Coprotus sexdecimsporus (P. Crouan & H. Crouan) Kimbr. & Korf chosen as the type species. Eckblad (1968) implied that Leporina Velen. (Velenovsky 1947) should be the correct name instead of Coprotus, since the type specimen of Leporina multispora Velen. was found to be identical to Ryparobius sexdecimsporus (P. Crouan & H. Crouan) Sacc. This nomenclatural problem was elaborated by Kimbrough (1970), who concluded that the name Leporina should be rejected and Coprotus retained because the type material consists of mixed collections belonging to three different genera while the protologue contains “two or more entirely discordant elements”. The name Coprotus was put on a without-prejudice list of generic names of fungi for protection under the International Code of Nomenclature for algae, fungi and plants (Kirk et al. 2013).

Species of the genus Coprotus are characterised by oblate to lenticular or discoid, glabrous, translucent or whitish to yellow apothecia with coprophilous ecology. Asci are functionally operculate, non-amyloid, eight- to 256-spored, producing hyaline, smooth, eguttulate ascospores, containing gaseous inclusions referred to as de Bary bubbles when placed in anhydrous conditions. Paraphyses are filiform, mostly bent to uncinate and/or swollen at the apex, hyaline or containing pigment. The excipulum is composed primarily of globose to angular cells (Kimbrough et al. 1972).

The genus Coprotus was placed in the tribe Theleboleae (family Pezizaceae) by Kimbrough and Korf (1967). In later classifications Eckblad (1968) and Kimbrough et al. (1972) placed this genus into the family Thelebolaceae (Pezizales). Kish (1974) performed cytological and ontogenetical research on C. lacteus (Cooke & W. Phillips) Kimbr., Luck-Allen & Cain using axenic cultures, and concluded that this species shows much closer affinities with the Pyronemataceae sensu Eckblad (1968) than the Thelebolaceae. Study of the apical apparatus in C. winteri (Marchal & É.J. Marchal) Kimbr. and C. lacteus by Samuelson (1978) supported this view. Using transmission electron microscopy, Van Brummelen (1998) determined that the fine ascatal structure of the wall and operculum in C. lacteus is characteristic of members of the Pyronemataceae s.l. Contrary to the mentioned micromorphological and cytological evidences, all members of the Thelebolaceae, including Coprotus, were placed in the class Leotiomycetes (Kirk et al. 2008, Lumbsch and Huhndorf 2010).

The phylogenetic affinity of Coprotus was studied using molecular data by Hansen et al. (2013), who showed that the genus belongs to the Pezizomycetes and forms a strongly supported monophyletic group with Boubovia Svrček (Pyronemataceae). This was confirmed by Lindemann et al. (2015) and Lindemann and Alvarado (2017). Wijayawardene et al. (2017) placed the genus Coprotus in the family Ascodesmidaceae (Pezizales, Pezizomycetes), and included 29 species. Additionally, isozyme analysis performed by Suárez et al. (2006) and RAPD patterns analysed by Ramos et al. (2008) detected a high intra-specific homogeneity in three Coprotus species (C. lacteus, C. niveus and C. sexdecimsporus). Furthermore, the AFLP fingerprinting technique applied to the
same three *Coprotus* species (Ramos et al. 2015) exhibited the highest level of intraspecific variability in *C. sexdecimsporus*.

We began our own study of the genus *Coprotus* with an integrated taxonomical approach aimed at the type species, relying on vital taxonomic and phylogenetic methods. Previously only *C. ochraceus* (P. Crouan & H. Crouan) J. Moravec was included in phylogenetic analyses (Hansen et al. 2013, Lindemann et al. 2015, Lindemann and Alvarado 2017). Our inventory study of fungi in the Sjeverni Velebit National Park was aimed also on fimicolous fungi resulting with a collection of a *Coprotus* species found on a chamois dung, *Rupicapra rupicapra*, that appeared different from all other known species in the genus.

**Materials and methods**

*Ex situ* monitoring

The apothecia collected with the substrate were used for microscopic studies and DNA extraction. The remaining material (together with the original substrate) was kept in closed plastic boxes in a refrigerator under low temperature (4–8 °C) and out of doors (ca. 10–25 °C) in dark and in diffuse sunlight conditions. Over a two month period these were monitored observing a turnover of two to several generations.

**Microscopic studies**

Observations of apothecia were made using a stereomicroscope under magnifications up to 80x. Microscopic characters based on living cells and tissues (') were recorded using vital taxonomy methods (Baral 1992), while those based on dead cells and tissues (†) were obtained from fixed fresh material. All described microscopic elements were observed in tap water (H\(_2\)O); cytochemical and histochemical data were obtained using the procedure described by Kušan et al. (2015). Microscopic features were observed with transmission light microscopes (bright field, phase contrast and dark field) under magnifications up to 1000x. Drawings were made free hand to scale, and microphotographs were mostly taken with a DSLR camera mounted on the microscope’s trinocular tube. Characters of apothecial construction and hymenial elements were based on a minimum of five ascomata. Spore measurements were based on samples of 50 fully mature, normally developed, and randomly selected ascospores (from living material ejected from asci). Measurements were taken directly using an ocular micrometer and from microphotographs using PIXIMÈ-TRE software ver. 5.9 (Henriot and Cheype 2017) to an accuracy of 0.1 µm. Spore wall layers were named following Heim (1962), except perispore is used rather than exospore following Harmaja (1974). Length, width and length/width ratio (“Q” value) are given as: min. – stat. mode – max. where “min.” = minimum (lowest measured value), “stat. mode” = statistical mode, “max.” = maximum (highest measured value). Length/width ratio (without mode value) was also introduced for asci. Dried material and accompanying data for all treated collections were deposited at the Croatian National Fungarium (CNF) in Zagreb.
A dichotomous key for identification of all putative species of *Coprotus* is presented. It was compiled from data derived from the literature and from our own observations. The key, except in one case, contains data for both living and dead materials. In this way the key is comprehensive. Species(character) overview tables, containing supplementary data not used in the key, are presented as an aid for reliable identification (Tables 2-6). Ascus and ascospore measurements, originating from published sources, are enhanced by those obtained by measuring the original microphotographs and drawings. Ascus and ascospore “Q” values, taken from published references, were calculated from the original microphotographs and drawings.

Additional abbreviations:
- **KOH =** potassium hydroxide; **IKI =** Lugol’s solution; **CRB =** Brilliant Cresyl Blue; **CR =** Congo Red; **CB =** Cotton Blue; **AC =** Acetocarmine; **MLZ =** Melzer's reagent.

**DNA extraction, PCR amplification and DNA sequencing**

Total genomic DNA was extracted from samples using DNeasy Plant kit (Qiagen Inc., USA). The LSU sequences were amplified using primers LR0R and LR7 (Vilgalys and Hester 1990). The primers ITS1-F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) were used for amplification of the ITS regions (ITS1-5.8S-ITS2). All PCR amplifications consisted of 25-µL reaction volumes containing 0.2 mM of each dNTP, 0.2 µM of each primer, 1 U of Taq polymerase, 1.5 mM of MgCl and ~ 50 ng DNA. The touch-down PCR cycling profile consisted of initial 5 min at 95 °C, 10 cycles of 45 s at 95 °C, 45 s at 60 °C (decreasing 1 °C/cycle), 90 s at 72 °C, 25 cycles of 45 s at 95 °C, 45 s at 52 °C, 90 s at 72 °C, with final extension of 7 min at 72 °C. PCR products were sequenced in both directions using the same primers as for PCR by Macrogen (Macrogen Inc., Seoul, Korea). All sequences were deposited in GenBank (Table 1).

**Phylogenetic analyses**

A data matrix for alignment was constructed. Phylogenetic analyses included eight newly identified sequences from this study, along with the sequences retrieved from GenBank (Table 1), *viz.*: Amicucci et al. (2001), Hansen et al. (2001), Hansen et al. (2002), Hansen et al. (2005), James et al. (2006), Schoch et al. (2006), Spatafora et al. (2006), Tedersoo et al. (2006), Perry et al. (2007), Schoch et al. (2009), Alvarado et al. (2011), Leuchtmann and Clémençon (2012), Hansen et al. (2013), Osmundson et al. (2013), Lindemann et al. (2015), Ghosta et al. (2016), Wang et al. (2016), Lindemann and Alvarado (2017).

Newly sequenced material included one *Coprotus epithecioides* collection, two *C. sexdecimsporus* collections and one *Boubovia nicholsonii* collection (FRANCE. Nouvelle-Aquitaine, Charente-Maritime, Saint Savinien, 23 km E-SE from Rochefort, 10 m a.s.l.; on remnants and rotten branches and twigs with leaves of *Cupressus macrocarpa* lying on the heap, 22 Jan 2012, M. Hairaud and P. Tanchaud (CNF 2/9121, duplex M.H. 80112)). Sequences
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Table 1. Specimens used in this study with voucher information and GenBank accession numbers. Sequences produced by this study are indicated in bold.

| Species                                | Voucher / strain number | ITS            | LSU            |
|----------------------------------------|-------------------------|----------------|----------------|
| *Aleuria aurantia*                     | OSC 100018              | DQ491495       | AY544654       |
| *Anthracobia macrocystis*              | OSC 100026              | –              | AY544660       |
| *Ascolobus crenulatus*                 | KH.02.005(C)            | DQ491504       | AY544678       |
| *Ascomyces nigricans*                  | CBS 389.68              | –              | DQ168335       |
| *Boubovia luteola*                     | R.K. 94/05              | KX592793       | KX592805       |
| *Boubovia nicholsonii*                 | CNF 2/9121              | MG593545       | MG593546       |
| *Boubovia ovalispora* (as *Pulvinula ovalispora* in NCBI) | BTO 95206 (C)           | –              | DQ220394       |
| *Boubovia* sp.                         | M.H. 80813              | KP309839       | KP309876       |
| *Bysonecctria deformis*                | N.V. 2009.04.09         | KP309843       | KP309866       |
| *Coprotus epithecioides*               | CNF 2/10450             | MG593539       | MG593540       |
| *Coprotus ochraceus*                   | JHP-06.121 (C)          | –              | KC012673       |
| *Coprotus sexdecimsporus* (1)          | CNF 2/8942              | MG593541       | MG593542       |
| *Coprotus sexdecimsporus* (2)          | CNF 2/4928              | MG593543       | MG593544       |
| *Cephalocephala irregularis*           | ITS from YG-C22; LSU from CBS 218.62 | KX683420       | KC012668       |
| *Cheilymenia stercorea*                | OSC 100034              | DQ491500       | AY544661       |
| *Eleutherascus lectardii*              | CBS 626.71              | –              | DQ470966       |
| *Geopora cooperi*                      | ITS from 16977; LSU from BAP 517 (FH) | JF908023       | KC012678       |
| *Geopryxis carbonaria*                 | PRM149720               | KU9323495      | KU932547       |
| *Geopryxis delactans*                  | KH.04.56a (FH)          | KU932505       | KU932555       |
| *Glaziella aurantiaca*                 | PR 6576 (FH)            | –              | KC012681       |
| *Heydenia alpina*                      | isolate 0732            | HQ688653       | HQ596526       |
| *Humaria hemisphaerica*                | ITS from KH.03.100 (FH); LSU from KH.03.31 (FH) | DQ200832       | KC012683       |
| *Hydnocystis piligera*                 | AH39303                 | JN048886       | JN048881       |
| *Lasiobolus spirale*                   | CBS 782.70              | –              | FJ176873       |
| *Lasiobolus ciliatus*                  | KS-94.005 (C)           | –              | DQ167411       |
| *L. cunculi*                           | C.F-54526 (C)           | –              | DQ168338       |
| *Miladina lecithina*                   | KH.03.156 (FH)          | –              | DQ220371       |
| *Paurocotylis pila*                    | Trappe 12583 (OSC)      | KU932506       | DQ168337       |
| *Peziza vesiculosa*                    | TL-6398 (C)             | AF491623       | AF378367       |
| *Pseudaleuria quinaultiana*            | OSC 45766               | EU69387        | EU69429        |
| *Pseudoboubovia benkertii*             | N.V. 2006.12.04         | KP309854       | KP309874       |
| *Pseudombrophila daniana* (as *Kotlabaea daniana* in NCBI) | isolate 6483 (B, Collection Benkert) | KX592794       | KX592806       |
| *Pseudombrophila theiouca*             | C.F-70057 (C)           | –              | DQ062989       |
| *Pulvinula constellatio*               | N/A for ITS; KH.03.64 (FH) for LSU | AF289074       | DQ062987       |
| *Pulvinula convexella*                 | KH.01.020 (C)           | –              | DQ062986       |
| *Pulvinula niveola*                    | M.A.R. 290809 27        | KX592796       | KX592808       |
| *Pyronema domesticum*                  | OSC 100503 (strain CBS 666.88) | DQ491517       | DQ247805       |
| *Scutellinia scutellata*               | OSC 100015              | DQ491492       | DQ247806       |
| *Sowerbyella imperialis*               | KH.09.222               | KJ619953       | KJ619950       |
| *Stephensia bombycina*                 | Trappe 3268 (OSC, FH)   | KU932484       | DQ220435       |
| *Tarzetta catus*                       | KS-94-10A (C)           | DQ200833       | DQ062984       |
alignments were obtained using CLUSTAL W in BIOEDIT 7.0.5.3 (Hall 1999). A con-
catenated alignment of ITS + LSU was generated. The final alignment contained 1590 bp. The maximum likelihood analyses were performed using MEGA 6 (Tamura et al. 2013) with GTR + G + I model and 1000 bootstrap replicates to assess branch support. *Ascobolus crenulatus* was used as the outgroup. Besides the combined (ITS + LSU) analyses, the LSU dataset, with additional species (Table 1), was also generated. The LSU alignment consisted of 894 characters. The evolutionary history was inferred by using the maximum likelihood method based on the general time reversible model, with discrete gamma distribution and some sites evolutionary invariable (GTR + G + I). *Peziza vesiculosula* and *Ascobolus crenulatus* were used as outgroups. Branch support was assessed using 1000 bootstrap replicates. All analyses were performed in MEGA 6 software ver. 6.0 (Tamura et al. 2013).

**Results**

**Phylogenetic analyses**

The ITS + LSU alignment consisted of 1590 characters including gaps, of which 763 were conserved, 777 were variable, and 230 were parsimony informative. The LSU alignment consisted of 894 characters including gaps, of which 32 were conserved, 319 were variable, and 224 were parsimony informative. The type species *Coprotus sexdecimsporus* was sequenced for the first time to ascertain the real phylogenetic position of the genus *Coprotus*. The two phylogenies (based on LSU, and concatenate analysis of LSU and ITS) firmly nested the *Coprotus* species in the order Pezizales, as a member of the *Boubovia-Coprotus* lineage inside the Pyronemataceae s.l., in a species group next to the *Geopyxis-Tarzetta* and *Ascodesmis-Pulvinula* clades (but without high support in our contracted analyses, Figs 1, 2). In both phylogenetic trees, species in the genera *Boubovia* and *Coprotus* were clustered together, with high support values. *Coprotus ochraceus* showed a distant relationship to the type species *C. sexdecimsporus* as a phylogenetically earlier diverging lineage. Our newly described species appeared closely related to the type species. The two collections of *C. sexdecimsporus* sequenced displayed 100% sequence identity (ITS and LSU).

**Taxonomy**

*Coprotus* Korf & Kimbr., American Journal of Botany 54(1): 21, 1967.

[≡ *Coprotus* Korf, Rapports et communications VIII Congrès International de Botanique I 1954 (sect. 18/20): 80, 1954, nomen nudum]

**Type species.** *Coprotus sexdecimsporus* (P. Crouan & H. Crouan) Kimbr. & Korf.  
As presently circumscribed, the genus *Coprotus* is clearly characterised by the following combination of characters: obligate coprophilous ecology, eugymnohymenial
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Figure 1. Maximum likelihood phylogenetic tree based on a concatenated ITS and LSU dataset. Sequences recovered during this study are shown in bold type. Bootstrap values greater than 50% are indicated at the nodes. *Ascobolus crenulatus* was used as the outgroup. The bar length indicates the number of nucleotide substitutions per site.

apotheical development, apothecia with reduced marginal tissue without setose hairs; inamyloid asci uniformly stainable in CR, with functional operculum; prolate, smooth (under transmission light microscope), eguttulate ascospores in all developmental stages sporoplasm of which have strong affinities to form de Bary bubble in any anhydrous conditions (especially in media such Cotton Blue). Mature spores ejected from living asci possess temporary thick and gelatinous sheath. Anamorph not known.
Figure 2. Maximum likelihood phylogenetic tree inferred from the LSU dataset. Sequences recovered during this study are shown in bold type. Bootstrap values greater than 50% are indicated at the nodes. The tree was rooted to *Peziza vesiculosa* and *Ascobolus crenulatus*. The bar length indicates the number of nucleotide substitutions per site.
**Coprotus sexdecimsporus** (P. Crouan & H. Crouan) Kimbr. & Korf, *American Journal of Botany* 54(1): 22, 1967.

Fig. 3

≡ *Ascobolus sexdecimsporus* P. Crouan & H. Crouan, *Annales des Sciences Naturelles Botanique* ser. 4., 10: 195, 1858.

≡ *Ascophanus sexdecimsporus* (P. Crouan & H. Crouan) Boud., *Annales des Sciences Naturelles Botanique* ser. 5., 10: 247, 1869.

≡ *Ryparobius sexdecimsporus* (P. Crouan & H. Crouan) Sacc., *Sylloge Fungorum* 8: 541, 1889.

**Description.** *Apothecia* not confluent, circular from the top view, at first globular, then flattened-turbinate and finally lenticular from the side view, sessile, evenly hyaline to creamy white or translucent pale greyish-rosy (if subjected to strong insolation), glabrous, 0.1–0.5 mm in diameter, solitary to gregarious. Hymenium granulose due to the protrusion of living mature asci, concolorous with excipular surface, matte. Margin rounded in vertical median section, entire, smooth, not raised above hymenial plane. Outer surface smooth, concolorous with the hymenium. Subicular hyphae indistinguishable. *Hymenium* 95–140 µm thick. *Asci* clavate with truncate apex, 84–143 × 21.4–29.6 µm, 89–104 × 16.4–23.3 µm, Q = 4.1–5.6, significantly shorter and more clavate at the marginal rim, when mature protruding above hymenium up to 26 µm, *pars sporifera* 47.3–63.3 µm, 16-spored, hyaline, base attenuated, bifurcate, arising from perforated croziers, only fully mature asci with flat lentiform operculum clearly delimited prior the spore discharge, 6.6–8 µm in diam. and 0.6 µm thick, lateral wall 3-layered, 0.7–0.8 µm thick, after spore discharge operculum as a rule clearly visible; in IKI inamylloid; in CR outermost wall vividly rutile-red throughout the ascal length, median layer pale rutile-yellow, innermost layer greyish; in CB cyanophobic. *Ascospores* 10.7–11.7–13.8 × 6.8–7.9–8.5 µm, Q = 1.4–1.7–1.7, ellipsoid to narrowly ellipsoid and most often radially symmetrical, with rounded-obtuse poles, rarely slightly bilaterally symmetrical with one side somewhat less convex but never flattened, 1-celled, hyaline; in living asci bi- to triseriate; when freshly ejected remain in a single group for a while due to the delicate sticky sheath enveloping individual spores; surface smooth; wall 3-layered, 0.6–0.7 µm thick, epispore dull, epispore brightly refractive, endospore layer with pale greyish-isabelline refractivity; in IKI no notable differential stainings; egguttulate, uninucleate, nucleus ±centrally to unipolarly positioned, 2.7–3 µm wide, in CRB nucleus and sheath more contrasted, perispore dull deep bluish-violet/deep cyan, epispore CRB-, endospore purplish lilac/medium violet; after applying KOH spore sheath dissolves instantly, all structures discoloured, perispore not loosening, endospore layer purplish-rosaceous; in CR perispore dull, not stained as epispore, but endospore lilac reddish; in AC completely devoid of staining; in CB de Bary bubbles present only in mature spores, perispore not loosening, weakly cyanophilic. *Paraphyses* cylindric, apically obtuse to subclavate, always slightly bent to uncinate, densely septate, rarely simple but often richly branched in the upper part; apically producing abundant medium to strongly refractive golden-yellow to cinnamon-yellow granular exudate, in IKI copper orange, in
Figure 3. *Coprotus sexdecimporus*. a Fresh apothecia on *Equus asinus* dung b Cross section with immature asci, paraphyses and marginal cells c, d Asci protruding above hymenium e Ascus with ascogenous cells f Paraphyses g Freshly ejected ascospore with a sheath h Mature ascospores i 16-spored freshly ejected packet of ascospores j Marginal cells from side view k Ectal excipulum cells in top view l Fresh apothecia on *Lepus europaeus* dung m Freshly ejected ascospores held together with a sheath n Ascus with ascogenous cells o Paraphyses with granular pigment and copious exudate p Excipular and marginal tissue. b, c, e–g, i, m–p *tap water* d, h *IKI* j, k *CB* a–i from CNF 2/8394 j–p from CNF 2/8942. Scale bars: a, l 1 mm, b–k, m–o 10 µm, p 20 µm; del. N. Matočec, phot. N. Matočec & I. Kušan.
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CRB dark grey blue, after applying KOH rubis red-grey; apical cells *6.9–16.4 × 2–3.4 µm, †1.4–2.8 µm wide, wall thin and hyaline, cells in the upper half contain minute medium to strongly refractive hyaline globules *0.2–1 µm wide or in pigmented apothecia with beer-yellow to beer-orange scattered dotted granules which are in IKI greyish green, in CRB deep purplish-lilac to deep violet; in CB wall cyanophobic, cytoplasm weakly cyanophilic. *Subhymenium* only slightly differentiated from medullary excipulum, †12–19 µm thick, composed of hyaline *textura globulosa-angularis*, cells †3.8–7.5 µm wide. *Medullary excipulum* hyaline, in the middle flank †12–22 µm thick, composed of *textura porrecta*, cells running parallel to the surface, †1.4–4.8 µm wide. *Margin* subhyaline, fairly reduced to a thin cellular zone †9.6–11.3 µm thick at ½ of hymenium height, composed of small celled *textura angularis* 1–2 cell thick, cells clavate or elongated angular, 2.4–8.8 µm wide, marginal rim composed of prismatic terminal cells which do not protrude above hymenium; in CB cell walls strongly cyanophilic. *Ectal excipulum* hyaline, in the middle flank †48–56 µm thick, composed of *textura globulosa*, cells †7.2–16 µm wide, walls yellowish; in IKI some cells with visible moderate accumulations of glycogene; in CB cell walls slightly cyanophilic; in AC cell walls and cytoplasm deeply lilac. Overall excipulum devoid of crystalline matter, without colouring in KOH, in IKI completely inamyloid. Anamorph not found.

**Distribution and ecology.** The species has a cosmopolitan distribution and can be found on dung of various wild and domestic animals, mainly herbivores (especially ruminant animals and rodents). In the temperate zone it is distributed in the habitats from maritime to alpine zones.

**Specimens examined.** CROATIA. Zadar County, Island of Dugi Otok, Velo jezero area, 5 km W from Sali, 43°56.46’N; 15°06.00’E, 5 m a.s.l., on dung of *Equus asinus*, 1 Jun 1998, N. Matočec (CNF 2/3806); Split-Dalmatia County, Island of Vela Palagruža, 70 m E-NE from the lighthouse, 42°23.58’N; 16°15.38’, 60 m a.s.l., on dung of *Equus asinus*, 29 Mar 1999, N. Matočec (CNF 2/4200); Dubrovnik-Neretva County, Koprendol area, 7.5 km N-NE from Metković, 42°59.30’N; 17°37.44’, 130 m a.s.l., on dung of *Ovis aries*, 5 Mar 2001, N. Matočec (CNF 2/4928); Dubrovnik-Neretva County, Peninsula Prevlaka (Oštra), 4.8 km N-NW from Vitaljina, 42°24.22’N; 18°30.53’, 25 m a.s.l., on dung of *Equus asinus*, 31 Dec 2009, I. Kušan and N. Matočec (CNF 2/8394); Lika-Senj County, Sjeverni Velebit National Park, northern part of the Mt. Velebit, 280 m SW from the Vučjak peak (1644 m), 44°48.83’N; 14°58.46’, 1550 m a.s.l.; on dung of *Lepus europaeus*, 11 Jun 2011, N. Matočec and I. Kušan (CNF 2/8942).

**Notes.** De Sloover (2002) summarises the data on the distribution of pigments in microscopic elements in the *Coprotus* species described up to that time. His overview suggests that paraphyses are not the only cause of the overall apothecial pigmentation. However, our detailed study on living material of *C. sexdecimsporus* over a period of two months clearly showed that cytoplasmic pigments in the paraphyses develop with exposure to light. These observations used apothecia on original substrate and were carried out under controlled conditions. The pigments developed under sunlight or artificial light with a sufficient amount of the ultraviolet wave-length. On the other hand, pigmentation was completely absent if apothecia were grown continually under dark or low-light conditions. There is considerable variability in ascospore dimensions given in the literature. Although it seems that ascospore length may vary regardless of any presently visible cause,
the ascospore diameter seems to be smaller in material from the Southern Europe / Mediterranea region. Accordingly, material from Italy (Doveri 2004) and Tunisia (Häffner 1996), almost completely overlap with our studied material from the East Adriatic region. These are in the range of ascospore widths from 6.9–8.5 µm. Specimens from the European Atlantic (Crouan’s material restudied by Le Gal, 1960), Norway (Aas, 1983) and both Americas (Kimbrough et al. 1972, Dokmetzian et al. 2005) have spores with greater spore widths, ranging from 7.5–10 µm. These differences might point to some ecological-geographical causes. The type material is missing according to Kimbrough et al. (1972).

**Coprotus epithecioides** Matočec & I. Kušan, sp. nov.
Mycobank: MB823596
Figs 4, 5

**Type.** CROATIA. Lika-Senj County, Šjeverni Velebit National Park, northern part of the Mt. Velebit, Hajdučki kukovi area, 150 m W from Golubić peak (1650 m), 44°46.05’N; 15°00.88’E, 1580 m a.s.l.; on dung of chamois (*Rupicapra rupicapra*), 11 Oct 2017, I. Kušan (holotype CNF 2/10450, GenBank sequences ITS MG593539, LSU MG593540).

**Etymology.** The specific epithet refers to epithecium-like ascal protective formation composed of swollen apical paraphyses cells.

**Description.** Apothecia not confluent regularly circular to irregular from the top view, at first oblate, then turbinate, finally pulvinate from the side view, sessile, subhyaline to creamy grey or pale yellowish, glabrous, ’170–420 µm in diameter, solitary or gregarious. Hymenium only very finely scurfy, ascal protrusions not clearly visible. Margin rounded in vertical median section, entire and smooth, expanded with downwards positioned rim, never raised above hymenial plane. Outer surface smooth, concolorous with the hymenium. Subicular hyphae indistinguishable. Hymenium ’75–98 µm thick. Asci shortly cylindrical with slightly truncate apex, ’60–74.8 × 13.4–15.5 µm, ’51.5–62 × 11.8–14 µm (Q = 3.8–5.2), when mature protruding above hymenium up to 7.5 µm, *pars sporifera ’28–34 µm, 8-spored, hyaline; base attenuated, bifurcate, arising from perforated croziers; only optimally oriented fully mature asci with flat lentiform operculum clearly delimited prior the spore discharge, ’6.3–6.6 µm in diam. and ’0.5 µm thick, lateral wall 3-layered, ’0.6 µm thick, after spore discharge operculum as a rule clearly visible; in IKI inamyloid; in CR outermost wall vividly rutille-red throughout the ascal length, median layer pale rutile-yellow, innermost layer greyish; in CB asci cyanophobic. Ascospores ’7.9–8.8–9.6 × 4.8–5.2–5.6 µm, ’8–9.1–9.5 × 4.2–5–5.2 µm, ’Q = 1.5–1.6–1.9, ’Q = 1.6–1.9–2.0, bilaterally symmetrical with one side flattened, subphaseoliform to phaseoliform, poles rounded, 1-celled; uni- to biseriate in living asci, freshly ejected remain in a group for a while due to the delicate subglobose sticky sheath enveloping individual spores; hyaline, smooth; wall 3-layered, 0.4 µm thick, perispore dull, epispore brightly refractive, endospore subhyaline, barely optically differentiated; eguttulate, uninucleate, nucleus always ±polarly positioned, 2.2–2.5 µm wide; in IKI perispore and epispore not stained, endospore purplish, nucleus slightly contrasted; in CRB without differential stainings, the edges of spore sheath sharply contrasted, after applying KOH spore sheath instantly dissolves, perispore not
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**Figure 4.** *Coprotus epithecioides* (CNF 2/10450, holotype). 

a. Fresh apothecia on *Rupicapra rupicapra* dung  
b. Cross section through the whole apothecia  
c. Cross section in dark field  
d. Asci  
e. Freshly ejected ascospores glued together with a sheath and individual ascospores  
f. Freshly ejected ascospores in phase contrast  
g. Epithecioid paraphyses  
h. Clavate paraphyses with pigment content  
i. Epithecioid hymenial cover  
j. Excipular flank  
k. Marginal tissue. All elements observed in tap water and in living state, except two asci on d marked with a cross ('); Scale bars: a 0.5 mm, b, c 50 µm, d–k 10 µm, phot. N. Matočec & I. Kušan.

loosening, endospore layer purplish-rosaceous; in CB with one eccentrically positioned de Bary bubble in mature spores, perispore not loosening, moderately cyanophilic. *Paraphyses* ±densely septate, with thin, hyaline walls, cylindric in the lower part, often branched in the upper part, rarely simple, apically ±bent clavate or capitate, not producing copious
Figure 5. Coprotus epithecioides (CNF 2/10450, holotype). a Asci with ascospores containing de Bary bubbles, red markings show opercular delimitation b Paraphyses c Ectal excipulum from top view d Excipular flank f Paraphyses g Ascospores. a–c ’CB d ’MLZ e ’CRB f ’IKI. Scale bars: a–f 10 µm, phot. N. Matočec & I. Kušan.

exudate; of two types: (a) epithecioid, reaching higher level, with apical short and capitate cell, 6.8–10 × 5–9.9 µm, 6.2–11.2 × 4–8 µm, with 1–2 subapical cells often also swollen (moniliform), forming ±continuous layer above living immature asci, and (b) of usual type with elongated clavate apical cells, 8.2–14.8 × 2.3–4.4 µm, 5.5–11 × 2–3.3 µm; both types may contain yellow-orange pigment, often of crystalloid, fibrillar structure; pigment in IKI cinnamon-grey, in CRB purplish-lilac, often barely visible since mainly included in large globose, deeply stained blue-violet vacuole; in CB wall cyanophobic, cytoplasm pale greyish-blue. Margin reduced, composed of textura globulosa-angulāris, cells not elongated, 3.8–6 µm wide, cylindric-elongated cells absent; weakly cyanophilic in CB. Subhymenium hyaline, not differentiated from medullary excipulum. Medullary excipulum hyaline, in the central part 32–56 µm thick, in the middle flank 10–14 µm thick, composed of textura epidermoidea, cells thin-walled, 2.3–4.8 µm wide, in CB cyanophobic. Ectal excipulum hyaline, in the middle flank 17–22 µm thick, composed of textura globulosa-angulāris, cells 9.8–16.5 × 7.8–14.7 µm, 4.5–12 × 2.3–9.5 µm, walls thickened, refractive, yellowish, 0.5–0.7 µm thick, in CB cell walls slightly cyanophilic. Overall excipulum without crystalline matter, dextrinoid reaction in MLZ and colouring in KOH; in IKI inamyloid and devoid of glycogene accumulations. Anamorph not found.

Distribution and ecology. The species is known so far only from Mt. Velebit, Croatia. The only collection originates from chamois dung in the alpine karstic habitat.
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**Other specimens examined.** None.

**Notes.** *Coprotus epithecioides* has several characters making it distinct from other species in the genus. The paraphyses are of two types, along with the usual filiform-clavate ones, there are also an abundance of those with very short, swollen apical cells, that mutually form an epithecioid protective layer over immature asci, a character not recorded so far in the genus *Coprotus*. Additionally, in the epithecioid type, 1–2 subapical cells are often also swollen. This gives the paraphyses a moniliform appearance. When present, paraphysal pigments are most often orange to reddish-orange and crystalloid, i.e. of fibrillar shape, resembling the carotenoid pigmentation of *Scutellinia* species. Spores are highly bilaterally symmetric compared to *C. glaucellus*, *C. subcylindrosporus*, *C. argenteus* and *C. sexdecimsporus* (which has only inconspicuously and partly bilaterally symmetric spores) and the spores are significantly shorter than those of *C. subcylindrosporus*, *C. argenteus* and *C. sexdecimsporus*. *Coprotus glaucellus* differs by the presence of only apically uninflated to subclavate paraphyses which do not form an epithecioid protective cover over immature asci. Also it has notably elongated cells at the marginal edge. As elaborated above, paraphysal cytoplasmic pigments normally also develop in this species if the fungus is strongly exposed to sunlight or artificial light with ultraviolet wave-lengths. The pigmentation is completely absent if the apothecia is grown continually under dark or low-light conditions (see notes under *C. sexdecimsporus*).

**Worldwide identification key to the putative species of the genus *Coprotus***

1 Apothecial margin and/or upper flank beset with very long, paraphysis-like terminal cells, over 60 µm long, raising above hymenial plane ..........................2
- Apothecial margin not raised above hymenial plane, composed of ±isodiametric or somewhat elongated cells up to 25 µm long.................................4

2 Apothecial margin composed of large globose cells accompanied by greatly elongated cylindric-obtuse terminal cells on upper flank, up to 200 µm long; asci narrowly cylindric (Q ~10–11), 150–185 µm long; ascospores ellipsoid (Q = 1.5–1.9), 12.5–15.5 µm long; paraphyses broad cylindric, 6–9 µ wide..........

................................................................. *C. arduennensis* J.R. De Sloover
- Apothecial margin devoid of globose cells, beset only with apically widened elongated terminal cells resembling paraphyses; asci cylindric to cylindric-ventricose (Q = 8.4–9.8), 70–100 µm long; ascospores narrowly to elongated ellipsoid (Q = 1.8–2.2), not exceeding 13.5 µm in length; paraphyses filiform, below 4 µ wide.......................................................3

3 Terminal cells on margin greater than 100 µm long; ascospores elongated ellipsoid (Q = 2.0–2.2), 8.5–10 × 4–5 µm; apothecia comparatively large, over 1 mm diam................................. *C. marginatus* Kimbr., Luck-Allen & Cain
- Terminal cells on margin 60–95 µm long; ascospores narrowly ellipsoid (Q = 1.8–2), 10–13.5 × 6–7 µm; apothecia 290–650 µm diam.................................

................................................................. *C. dhofarensis* Gené, El Shafie & Guarro
Apothecia discoid or saucer shaped with complex excipular structure: medullary excipulum thick and sharply differentiated from the ectal layer, composed of *textura intricata*, ectal excipulum of *textura globulosa-angularis*; asci narrowly cylindric (Q > 10) ................................................................. 5

Apothecia principally subglobose, turbinate to pulvinate with excipular layers weakly or not differentiated, composed mostly of *textura globulosa-angularis*, with inner and marginal cells of gradually smaller diameter; asci stout (Q < 10)........ 6

Ectal excipular layer covered with cortical layer of elongated cylindrical cells; asci 60–90 × 6–9 µm (Q = 10–11.5); ascospores elongated ellipsoid, 7–8.5 × 3.5–4.5 µm; paraphyses filiform, apically bent.......... *C. baeosporus* Jeng & J.C. Krug

Ectal excipular layer composed only of large-celled *textura globulosa-angularis*; asci 163–200 × 10–16 µm (Q = 14); ascospores narrowly ellipsoid, 13.7–18 × 7.5–9 µm; paraphyses apically clavate, straight.......................................................... *C. ochraceus* ss. Thind et al. (Thind et al. 1978)

Apothecial margin composed of *textura globulosa-angularis* as in the excipular flanks, though cells gradually smaller ........................................ 7

Apothecial margin composed of elongated, prismatic cells, 6–25 × 2–10 µm, and excipular flanks of *textura globulosa-angularis*............................................. 11

Asci cylindric (Q = 8.2–9.7), 85–150 × 9.0–17.5 µm; paraphyses filiform, 1.5–3 µm wide; apothecia markedly constricted below to a ±substipitate base.......... 8

Asci broad clavate or short cylindric (Q = 2.2–5.2), 38–75 × 13.5–30 µm; paraphyses cylindric-obtuse, 3–4 µm wide or markedly swollen apically, 3–10 µm wide; apothecia entirely sessile and broadly attached to the substrate .... 9

Asci 125–150 × 12.5–17.5 µm, 8-spored; ascospores narrowly ellipsoid (Q = 1.7–1.9), 14–16 × 7.5–10 µm; paraphyses uncinate to helicoid............................ ................................. *C. uncinatus* Yei Z. Wang

Asci 85–130 × 9–13 µm, 4-spored; ascospores broadly ellipsoid (Q = 1.1–1.3), 8.7–10.1 × 6.9–7.8 µm; paraphyses ±straight .................................... *C. tetrasporus* Häffner, nom. inval.

Asci short cylindric (Q = 3.8–5.2), 60–75 × 13.5–15.5 µm; living mature ascospores bilaterally symmetric, subphaseoliform to phaseoliform, 7.9–9.6 × 4.8–5.6 µm; paraphyses of two types: (a) epithecioid, apically short-celled, capitate, 6.8–10 × 5–9.9 µm, often also bi- to tri-monomiliform celled, forming protective layer over immature asci, and (b) narrowly clavate 2.3–4.4 µm wide.................... *C. epidtechioides* Matočec & I. Kušan

Asci broad clavate (Q = 2.2–3.4), 38–60 × 14–30 µm; living mature ascospores ±radially symmetric, ellipsoid or oblong, 9–14.4 × 5–9.5 µm; paraphyses of a single type, apically cylindric obtuse to clavate and long-celled, 3–8 µm wide, not forming protective layer over immature asci...................... 10

Ascospores ellipsoid to narrowly-ellipsoid (Q = 1.4–1.8), 9.5–14.5 × 6–9.5 µm; paraphyses apically bent, clavate, 4–8 µm wide........................................ *C. granuliformis* (P. Crouan & H. Crouan) Kimbr.

Ascospores narrowly oblong (Q = 1.7–2), 9–14 × 5–6 µm; paraphyses cylindric-obtuse and ±straight, apically 3–4 µm wide.... *C. trichosuri* A.E. Bell & Kimbr.
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Number of spores in each ascus is a ±multiple of 8 in powers of two (i.e. 16, 32, 64 or -256) .......................................................... 12

– Asci 8-spored ............................................................................. 12
– Asci 16-spored ......................................................................... 13
– Asci with 32, 64 or -256 spores .................................................. 14

Asci clavate, 90–140 × 20–30 μm; ascospores 11–16 × 7–10 μm ..........

C. *sexdecimsporus* (P. Crouan & H. Crouan) Kimbr. & Korf

– Asci cylindric, 70–90× 10–18 μm; ascospores 7.5–10 × 4–6.5 μm ..

.......................................................... C. *duplus* Kimbr., Luck-Allen & Cain

Asci 32-spored .............................................................................. 15
– Asci 64 or -256 spores ................................................................. 16

Asci broad clavate (Q ca. 3.5), 100–175 × 48–75 μm; ascospores narrowly ellipsoid (Q = 1.6–1.8), 13.5–17 × 7–8 μm; paraphyses filiform, apically bent and branched, up to 2 μm wide ....... C. *rhyparobioides* (Heimerl) Kimbr.

– Asci clavate (Q = 4.8–6.0), 75–112 × 19–30 μm; ascospores elongated ellipsoid (Q = 1.9–2.2) 10–12.5 × 5–7.5 μm; paraphyses apically clavate and unbranched, 5–6 μm wide .......... C. *albidus* (Boud.) Kimbr.

Asci 64-spored, 140–165 × 30–60, †80–130 × 28–40 μm; paraphyses filiform, usually simple, 2–2.5 μm wide .......................................................... C. *niveus* (Fuckel) Kimbr., Luck-Allen & Cain

– Asci -256-spored, 160–210 × 45–55 μm; paraphyses filiform, apically branched, 1–2 μm wide .......... C. *winteri* (Marchal & É.J. Marchal) Kimbr.

Apothecial margin beset with partially protruding prismatic terminal cells exceeding 15 μm and reaching 25 μm in length ........................................ 18

– Apothecial margin smooth, composed of elongated cells up to 15 μm in length, not protruding from the surface ............................................... 19

Apothecial greyish-brown; ascospores broadly ellipsoid (Q = 1.2–1.4) with obtuse ends, 12–16 × 9–11.5 μm; paraphyses filiform, 2–2.5 μm wide ........

.......................................................... C. *sarangpurensis* K.S. Thind & S.C. Kaushal

– Apothecia white to yellowish; ascospores ellipsoid to narrowly ellipsoid (Q = 1.4–1.9) with tapered ends, 10–14 × 5–9 μm; paraphyses apically clavate, 3–4 μm wide .......... C. *disculus* Kimbr., Luck-Allen & Cain

Paraphyses always contain abundant globular to granular yellow or orange to reddish pigment; apothecia always vividly yellow, orange or reddish-orange .. 20

– Paraphyses lacking yellow, orange or reddish pigment, may contain refractive but hyaline globules or cytoplasm completely non-refractive and hyaline; apothecia hyaline, whitish to creamy-greyish, often becoming yellowish .......... 29

Ascospores ±bilaterally symmetric, loaf-shaped (Q = 1.7–2.3), 14–17.3 × 6.5–8.9 μm; paraphyses markedly swollen apically, 3–8 μm wide ..........

.......................................................... C. *subcylindrosporus* J. Moravec

– Ascospores ±radially symmetric, ellipsoid, narrowly ellipsoid or oblong; paraphyses filiform, apically not inflated to cylindric-clavate, not exceeding 5 μm in width ........................................ 21
Apothecia often reaching 1 mm in diam. or more; ectal excipulum of large celled *textura globulosa-angularis* with basal cells 20–45 µm diam.; asci 100–190 µm in length .................. *C. ochraceus* (P. Crouan & H. Crouan) J. Moravec  

– Apothecia seldom exceeding 0.5 mm diam. (at most 0.8); ectal excipulum composed of smaller cells, 5–24 µm diam.; asci 45–120 µm long ............ 22

Ascospores oblong (*Q* = 1.5–1.8), with broadly rounded ends, very large, 17–25 × 11–14 µm .......... *C. vicinus* (Boud.) Kimbr., Luck-Allen & Cain  

– Ascospores not exceeding 18.5 µm in length and 11.5 µm in diam, either broadly oblong (*Q* = 1.4–1.6) or ellipsoid to narrowly ellipsoid.......................... 23

Ascospores 11.5–18.5 µm long; paraphyses apically straight to bent and markedly swollen, 3–5.5 µm wide.......................... 24

– Ascospores 8–12 µm long; paraphyses apically uncinate and filiform, 1.5–3.5 µm wide.......................... 27

Asci cylindric (*Q* = 6.1–9.5), 75–140 × 12–17 µm; ascospores 12–15 × 6–9 µm; paraphyses frequently branched above ............................................. *C. aurora* (P. Crouan & H. Crouan) K.S. Thind & Waraitch  

– Asci short cylindric or broad clavate to clavate (*Q* = 2.5–4.7), 45–95 × 17–30 µm; ascospores exceeding 9 µm in width; paraphyses simple or branched near the base............................................. 25

Asci clavate (*Q* = 4–4.7), 80–90 × 17–20 µm; ascospores broadly oblong (*Q* = 1.4–1.6), 11.5–16 × 8.5–10 µm ........... *Ascophanus* aurantiacus Velen.  

– Asci broad clavate or short cylindric (*Q* = 2.5–3.9), 20–30 µm wide; ascospores ellipsoid to narrowly ellipsoid (*Q* = 1.4–1.8), always exceeding 16 µm in length.......................... 26

Asci often with only 6–7 fully matured spores, broad clavate, 60–115 × 22–30 µm; ascospores with obtuse ends, 16–18.5 × 10–11.5 µm...................... *C. bilobus* (Velen.) J. Moravec  

– Asci regularly 8-spored, short cylindric, 45–60 × 20–28 µm; ascospores with tapered ends, 12.5–18 × 7.5–12 µm ............................................. *C. breviascus* (Velen.) Kimbr., Luck-Allen & Cain  

Asci broad clavate (*Q* = 3.8–4.1), 45–65 × 11–15 µm ....................... *C. breviascus* ss. Dokmetzian et al. (Dokmetzian et al. 2005)  

– Asci cylindric (*Q* = 6.2–10.0), 60–105 × 10–17 µm ..................... 28

Ascospores with obtuse ends, 8–11 × 4.5–7 µm; paraphyses apically 2–3.5 µm wide..................... *C. luteus* Kimbr.  

– Ascospores with tapered ends, 10.5–12 × 6.5–7.5 µm; paraphyses apically 1.5–2 µm wide.......................... *C. aff. luteus* (cf. Doveri 2004)  

Asci longer than 90 µm or ascospores exceed 13.5 µm in length and always broader than 7.5 µm; paraphyses apically notably swollen, clavate .......... 30

– Asci shorter than 90 µm; ascospores shorter than 13.5 µm and narrower than 7 µm; paraphyses filiform or cylindric-obtuse, apically not inflated..... 32
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30 Asci broad clavate (Q = 2–3.8), 55–90 × 14.5–24 µm; ascospores ±bilaterally symmetric, hemiellipsoid i.e. with regular ellipsoid outline in dorsoventral view and inequilateral ±loaf-shaped outline in lateral view, 10.5–16 × 8.5–10.5 µm; paraphyses ±straight, not containing refractive content; apothecia turbinate, minute, up to 0.2 mm diam.; ectal excipulum composed of small globose to angular cells up to 10 µm diam. .... *C. argenteus* (Curr.) Waraith

– Asci clavate or short cylindric to cylindric-ventricose (Q = 3.9–6), 80–125 µm long; ascospores ±radially symmetric, ellipsoid to narrowly ellipsoid; paraphyses predominantly apically bent, usually with hyaline to subhyaline refractive content; apothecia discoid to lenticular, always exceeding 0.2 mm diam. at maturity; ectal excipulum contains globose to angular cells 4–17 µm diam., cyanophilic and dextrinoid. ............................................................ 31

31 Asci clavate; ascospores 11–13.2 × 7.3–10 µm ........................................

........................................................................... *C. dextrinoides* Kimbr., Luck-Allen & Cain

– Asci short cylindric to cylindric-ventricose; ascospores 14–18 × 7.5–11.5 µm.......................... *C. leucopocillum* Kimbr., Luck-Allen & Cain

32 Asci broad clavate (Q = 2.2–2.3), 50–60 × 20–26 µm; ascospores narrowly oblong (Q = 1.7–2), 9–14 × 5–6 µm; paraphyses cylindric-obtuse and ±straight; apothecia minute, 125–175 µm diam., known from dung of *Trichosurus vulpecula* .................................................. *C. trichosuri* A.E. Bell & Kimbr.

– Asci clavate, short cylindric to cylindric-ventricose (Q = 4–8), 7–20 µm diam.; ascospores broadly to narrowly ellipsoid or loaf-shaped (bilaterally symmetric) (Q = 1.1–1.8), 6–10 × 5–7 µm; paraphyses filiform and straight to uncinate; apothecia 0.2–1 mm diam., known from dung of placental mammals, ruminants and rodents............................................................ 33

33 Ascospores broadly ellipsoid (Q = 1.1–1.3), 8–8.5 × 5.5–6 µm; paraphyses ±straight; ectal excipulum composed of small globose to angular cells up to 6.5 µm diam. ........................................... *C. sphaerosporus* J.L. Gibson & Kimbr.

– Ascospores ellipsoid to narrowly ellipsoid or loaf-shaped (Q = 1.4–1.8); paraphyses always uncinate; ectal excipulum contains cyanophilic globose to angular cells 4–15 µm diam. .................................34

34 Asci clavate (Q = 4.0–4.8), 40–70 × 7–14 µm; ascospores ±bilaterally symmetric, hemiellipsoid (i.e. ellipsoid to significantly more flattened on one side) with obtuse ends, 6–10 × 3.5–5.8 µm; paraphyses above 2.9–4.3 µm wide; apothecial margin with elongated cells up to 10 µm long .........................

........................................................................... *C. glaucellus* (Rehm) Kimbr.

– Asci short cylindric to cylindric-ventricose (Q = 4–8), 65–95 × 12–20 µm; ascospores radially symmetric, ellipsoid to narrowly ellipsoid with tapered ends, 7.5–13 × 5–7 µm; paraphyses above 1.5–3 µm wide; apothecial margin with elongated cells 8–17.5 µm long...........................................

........................................................................... *C. lacteus* (Cooke & W. Phillips) Kimbr., Luck-Allen & Cain
Table 2. *Coprotus* species overview - macroscopy and ecology.

| Species                  | Apothecial shape | Apothecial diam. / mm | Pigmentation variation                      | Substrate / dung of:                      |
|--------------------------|------------------|-----------------------|---------------------------------------------|-------------------------------------------|
| *C. albidus* (1, 29)     | glob-lent        | 0.2–0.7               | always hyaline to creamy-grey               | *Bos, Lepus, Felis, Canis*               |
| *C. arduennensis* (2)    | cup-disc         | 0.5–1.5               | light orange                                | *Sus scrofa*                              |
| *C. argenteus* (3, 4)    | obpyr-disc       | -0.1–0.2              | always hyaline to white                     | ruminants                                |
| *C. aurora* (1, 5, 6, 7, 8, 9, 28, 29) | glob-disc       | 0.2–0.7               | always yellow to orange                     | ruminants, rodents                       |
| "*Ascophanus* aurantiacus* (10, 11) | lent            | 0.3–0.6               | always orange                               | *Bos*                                    |
| *C. baeosporus* (12)     | cup-disc         | 0.2–0.65              | white to yellowish                          | *Cervus*                                 |
| *C. bilobus* (10, 11, 13) | turb-lent      | 0.1–0.6               | always yellow, orange to rosy               | *Bos*                                    |
| *C. breviascus* (1, 10, 11) | disc-lent     | 0.2–0.6               | always yellow to orange                     | ruminants                                |
| *C. breviascus* ss. Dokmetzian et al. (14) | disc-lent     | 0.2–0.6               | always yellowish-orange                     | *Equus*                                  |
| *C. dextrinoideus* (1, 15, 29) | cup-disc    | 0.1–0.5               | whitish, becoming yellowish                 | ruminants, *Leptus*                      |
| *C. dbofarensis* (16)    | glob-cup         | 0.3–0.7               | orange to brownish-orange                   | *Capra*                                  |
| *C. disculus* (1, 8, 9, 17, 18, 29) | disc-lent     | 0.3–1                 | hyaline to white, becoming yellowish        | ruminants, rodents, *Sus*                |
| *C. duplus* (1)          | cup-disc         | 0.3–0.8               | white to yellowish                          | ruminants, rodents, *Birds*              |
| *C. epithecioides* (this paper) | lent          | 0.2–0.4               | white to yellow                             | *Rupicapra rupicapra*                    |
| *C. glaucellus* (1, 7, 8, 13, 29) | disc-lent     | 0.2–1                 | white to yellow                            | ruminants, rodents                       |
| *C. granuliformis* (1, 7, 8, 18, 19, 29) | glob-lent     | 0.2–0.6               | white to yellowish                          | ruminants                                |
| *C. lacteus* (1, 7, 8, 9, 14, 17, 18, 20, 21, 22, 29) | glob-lent     | 0.2–0.6               | white to yellowish-ochre                     | ruminants, rodents                       |
| *C. leucopocillum* (1, 8, 9, 18, 29) | cup-lent      | 0.2–0.5               | white to yellowish                          | ruminants, rodents                       |
| *C. luteus* (1, 9, 18, 29) | disc-lent     | 0.2–0.8               | always yellow to orange                     | ruminants                                |
| *C. aff. luteus* (8)     | disc-lent        | 0.2–0.3               | yellow                                      | ruminants                                |
| *C. marginatus* (1)      | disc-lent        | 1–1.6                 | white to yellowish                          | ruminants, rodents                       |
| *C. niveus* (1, 9, 14)   | cup-disc         | 0.2–0.5               | white to yellowish                          | various dung types                       |
| *C. ochraceus* (1, 5, 6, 8, 9, 14, 26) | glob-disc     | 0.5–1.8               | always yellow to orange or ochraceous       | ruminants                                |
| *C. ochraceus* ss. Thind et al. (7, 17, 18) | disc-lent     | 0.5–1                 | yellow                                      | mix of dung & *Quercus* / *Cedrus* foliage |
| *C. rhyparobioides* (1, 14) | glob-disc  | 0.1–0.4               | always hyaline to white                     | ruminants, *Leptus*                      |
| *C. sarangpurensis* (17) | disc            | ≤0.5                  | always greyish-brown                        | *Bos*                                    |
| *C. sexdecimsporus* (1, 6, 8, 14, 18, 19, 26, 27, this paper) | disc-lent     | 0.5–0.8               | white to yellowish                          | ruminants, rodents, *Sus*               |
| *C. spherosporus* (23)   | glob-disc        | 0.2–0.7               | always hyaline to white                     | *Equus*                                  |
An overview of the genus *Coprotus* (Pezizales, Ascomycota). . .

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### Table 3. *Coprotus* species overview - apothecial structure.

| Species                  | Medullary excipulum | Ectoexcipular cell diam. / µm | Marginal structure          | Marginal cell dim. / µm |
|--------------------------|---------------------|-------------------------------|-----------------------------|-------------------------|
| *C. albidus* (1, 29)     | red txt intr        | 5–12                          | elongated cells             | 2.4–4.3 diam.           |
| *C. arduennensis* (2)    | (–)                 | 10–45                         | globose + paraphysiform     | < 200                   |
| *C. argenteus* (3, 4)    | (–)                 | ≤ 10                          | elongated cells             | n/a                     |
| *C. aurora* (1, 5, 6, 7, 8, 9, 28, 29) | red txt intr | 7–24                          | elongated cells             | 8–12x5–6                |
| "Ascothusaurus"aurantiacus (10, 11) | (–)                 | ≤ 16                          | elongated cells             | n/a                     |
| *C. baeosporus* (12)     | dev txt intr        | 3–9+cort                      | elongated cells             | n/a                     |
| *C. bilobus* (10, 11, 13) | (–)                 | 6–20                          | elongated cells             | 12–18x5–11              |
| *C. breviascus* (1, 10, 11) | (–)                 | ≤ 15                          | elongated cells             | n/a                     |
| *C. breviascus* ss. Dokmetzian et al. (14) | (–)                 | n/a                           | elongated cells             | n/a                     |
| *C. dextrinoideus* (1, 15, 29) | (–)                 | 3–16.8                        | elongated cells             | 8–15x3–7                |
| *C. dhofarensis* (16)    | dev glob-ang        | 15–26                         | raised, paraphysiform       | 60–95x6.5–14            |
| *C. disculus* (1, 8, 9, 17, 18, 29) | (–)                 | 5–20                          | elongated cells             | 10–24x2.5–10            |
| *C. duplus* (1)          | (–)                 | 10–12                         | elongated cells             | 10–12x4–6              |
| *C. epithecioideus* (this paper) | red txt intr | 5–12                          | ±isodiametric cells         | 3.8–6 diam.            |
| *C. glaucellus* (1, 7, 8, 13, 29) | red txt intr | 4–14                          | elongated cells             | < 10 long              |
| *C. granuliformis* (1, 7, 8, 18, 19, 29) | (–)                 | 5.5–22                        | ±isodiametric cells         | 5.3–13.2 diam.         |
| Species                        | Shape                                | Q     | Dimensions / µm | Number of spores |
|-------------------------------|--------------------------------------|-------|-----------------|------------------|
| *C. lacteus* (1, 7, 8, 9, 14, 17, 18, 20, 21, 22, 29) | (-)                                  | 4–15  | elongated cells  | 8–17.5×4–10      |
| *C. leucopodium* (1, 8, 9, 18, 29)   | (-)                                  | 4–17  | elongated cells  | 12–15×3–8.4      |
| *C. luteus* (1, 9, 18, 29)       | (-)                                  | 10–20 | elongated cells  | 8–12×4–5         |
| *C. aff. luteus* (8)            | (-)                                  | 5–10  | elongated cells  | n/a              |
| *C. marginatus* (1)            | (-)                                  | 12–15 | raised, paraphysiform | > 100 long |
| *C. niveus* (1, 9, 14)         | (-)                                  | 5–7   | elongated cells  | 12–15×6–7        |
| *C. ochraceus* (1, 5, 6, 8, 9, 14, 26) | (-)                              | 25–52 | elongated cells  | 12–14×6–8        |
| *C. ochraceus* ss. Thind et al. (7, 17, 18) | dev txt intr | ≤ 56×45 | ±isodiametric cells | n/a              |
| *C. rhyparobioides* (1, 14)    | (-)                                  | n/a   | elongated cells  | n/a              |
| *C. sarangpurensis* (17)       | dev txt intr-epi                    | ≤ 25×20| elongated cells  | < 25×8           |
| *C. sexdecimsporus* (1, 6, 8, 14, 18, 19, 26, 27, this paper) | red                              | 7–12  | elongated cells  | 5–13.2×2.5–6     |
| *C. sphaerosporus* (23)        | (-)                                  | 5–6.5 | elongated cells  | 6–8.5×2–3.5      |
| *C. subcylindrosporus* (8, 10, 13) | (-)                              | 8–30  | elongated cells  | n/a              |
| *C. tetrasporus* (27)          | (-)                                  | 7–14  | ±isodiametric cells | n/a              |
| *C. trichosuri* (24)           | (-)                                  | n/a   | n/a              | n/a              |
| *C. uncinatus* (25)            | (-)                                  | 5–20  | ±isodiametric cells | n/a              |
| *C. vicinus* (1, 6)            | (-)                                  | ≤ 14  | elongated cells  | 8–11×6–8         |
| *C. winteri* (1)               | (-)                                  | n/a   | elongated cells  | 10–12×4–5        |

# (-) almost lacking / not clearly differentiated from ectal eacippulum, red - reduced, txt intr - textura intricata, dev - well developed, glob-ang - textura globulosa-angularis, txt intr-epi - textura intricata-epidermoidea.

Table 4. Coprotus species overview - ascus characters.
An overview of the genus *Coprotus* (Pezizales, Ascomycota)...

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### Table 5. *Coprotus* species overview - ascospore characters.

| Species                         | Symmetry | Shape                                  | Poles         | Dimensions / µm     | Q   |
|---------------------------------|----------|----------------------------------------|---------------|---------------------|-----|
| *C. albidus* (1, 29)            | radial   | elongated-ellipsoid                    | tapered       | 10–12.5×5–7.5       | 1.9–2.2 |
| *C. arduennensis* (2)           | radial   | ellipsoid                              | tapered       | 12.5–15.5×6.5–7.5   | 1.5–1.9 |
| *C. argenteus* (3, 4)           | bilateral| hemiellipsoid                          | obtuse        | 10.5–16×8.5–10.5    | 1.4–1.8 |
| *C. aurora* (1, 5, 6, 7, 8, 9, 28, 29) | radial | ellipsoid - narrowly-ellipsoid         | subobtuse     | 12–15×6–9           | 1.4–1.6 |
| “*Ascophanus*” aurantiacus (10, 11) | radial | broadly-oblong                        | obtuse        | 11.5–16×8.5–10      | 1.4–1.6 |
| *C. baesoporus* (12)            | radial   | elongated-ellipsoid                    | subobtuse     | 7–8.5×3.5–4.5       | 1.9–2.2 |
| *C. bilobus* (10, 11, 13)       | radial   | ellipsoid - narrowly-ellipsoid        | obtuse        | 16–18.5×10–11.5     | 1.4–1.8 |
| *C. breviascus* (1, 10, 11)     | radial   | ellipsoid - narrowly-ellipsoid        | tapered       | 12.5–18×7.5–12      | 1.4–1.8 |
| *C. breviascus* ss. Dokmetzian et al. (14) | radial | narrowly-ellipsoid                    | tapered       | 9.8–11.1×6.5–7.2    | 1.7–1.8 |
| *C. dextrinoideus* (1, 15, 29)  | radial   | ellipsoid                             | subobtuse     | 11–13×2.7–3–10      | 1.4–1.8 |
| *C. dhofarensis* (16)           | radial   | narrowly-ellipsoid                    | tapered       | 10–13×5×6–7         | 1.8–2 ||
Species | Symmetry | Shape | Poles | Dimensions / µm | Q |
--- | --- | --- | --- | --- | --- |
*C. disculus* (1, 8, 9, 17, 18, 29) | radial | ellipsoid - narrowly-ellipsoid | tapered | 10–14×5–9 | 1.4–1.9 |
*C. duplus* (1) | radial | ellipsoid | tapered | 7.5–10×4–6.5 | 1.5–1.8 |
*C. epitheciioides* (this paper) | bilateral | subphaseoliform - phaseoliform | obtuse | 7.9–9.6×4.8–5.6 | 1.5–1.9 |
*C. glutecellus* (1, 7, 8, 13, 29) | bilateral | hemiellipsoid | obtuse | 6–10×3.5–5.8 | 1.4–1.8 |
*C. granuliformis* (1, 7, 8, 18, 19, 29) | radial | ellipsoid - narrowly-ellipsoid | obtuse | 9.5–14.5×6–9.5 | 1.4–1.8 |
*C. glaucellus* (1, 7, 8, 13, 29) | bilateral | subphaseoliform - phaseoliform | obtuse | 7.9–9.6×4.8–5.6 | 1.5–1.9 |
*C. luteus* (1, 9, 18, 29) | radial | ellipsoid - narrowly-ellipsoid | tapered | 7.5–13×5–7 | 1.4–1.8 |
*C. leucopocillum* (1, 8, 9, 18, 29) | radial | ellipsoid - narrowly-ellipsoid | tapered | 14–18×7.5–11.5 | 1.4–1.8 |
*C. luteus* (1, 9, 18, 29) | radial | ellipsoid - narrowly-ellipsoid | tapered | 8–11×4.5–7 | 1.4–1.9 |
*C. aff. luteus* (8) | radial | ellipsoid - narrowly-ellipsoid | tapered | 10.5–12×6.5–7 | 1.5–1.8 |
*C. marginatus* (1) | radial | elongated-ellipsoid | obtuse | 8.5–10×4–5 | 2–2.2 |
*C. niveus* (1, 9, 18, 29) | radial | ellipsoid - narrowly-ellipsoid | tapered | 14–18×5–9 | 1.4–1.8 |
*C. ochraceus* (1, 5, 6, 8, 9, 14, 26) | radial | ellipsoid - narrowly-ellipsoid | tapered | 13.7–18×7.5–9 | 1.8–2 |
*C. ochraceus* ss. Thind et al. (7, 17, 18) | radial | narrowly-ellipsoid | obtuse | 13.5–17×7–8 | 1.6–1.8 |
*C. sarangpurensis* (17) | radial | broadly-ellipsoid | obtuse | 12–16×9–11.5 | 1.2–1.4 |
*C. sexdecimsporus* (1, 6, 8, 14, 18, 19, 26, 27, this paper) | radial to slightly bilateral | ellipsoid - narrowly-ellipsoid | obtuse | 11–16×7–10 | 1.3–1.8 |
*C. sphaerosporus* (23) | radial | broadly-ellipsoid | obtuse | 8–8.5×5.5–6 | 1.1–1.3 |
*C. subcylindrosporus* (8, 10, 13) | bilateral | loaf-shaped | obtuse | 14–17.3×6.5–8.9 | 1.7–2.3 |
*C. tetrasperus* (27) | radial | broadly-ellipsoid | obtuse | 8.7–10.1×6.9–7.8 | 1.1–1.3 |
*C. trichonuri* (24) | radial | narrowly-oblong | obtuse | 9–14×5–6 | 1–1.7 |
*C. uncinnatus* (25) | radial | narrowly-ellipsoid | tapered | 14–16×7.5–10 | 1.7–1.9 |
*C. vicinus* (1, 6) | radial | oblong | obtuse | 17–25×11–14 | 1.5–1.8 |
*C. winteri* (1) | radial | narrowly-ellipsoid | obtuse | 10–11×5–6 | n/a |

# Radially symmetric spores - after Kušan et al. (2014); bilaterally symmetric homopolar spores: hemiellipsoid with one side significantly to nearly flattened - Q = 1.4–1.8, loaf-shaped with one side significantly to nearly flattened - Q = 1.81–2.30; subphaseoliform with one side entirely flattened to slightly concave - Q = 1.31–1.70, phaseoliform with one side entirely flattened to slightly concave - Q = 1.71–2.00.

**Table 6.** *Coprotus* species overview - paraphysis characters.
| Species                                      | Apices       | Width / µm | Branching | Bending     | Refractive globules | Pigments         |
|----------------------------------------------|--------------|------------|-----------|-------------|--------------------|------------------|
| *Ascophanus* auraniacus (10, 11)             | cylindric-clavate | 3–5        | below     | bent        | orange             | n/a              |
| *C. baeosporus* (12)                        | filiform     | n/a        | branched  | bent        | yellowish          | yellowish        |
| *C. bilobus* (10, 11, 13)                   | cylindric-clavate | 2.5–5.5    | branched  | straight-bent| orange             | granules         |
| *C. breviscas* (1, 10, 11)                  | cylindric-clavate | 3–4        | simple    | straight-bent| yellowish          | n/a              |
| *C. breviscas* ss. Dokmetzian et al. (14)    | filiform     | 1.5–2      | n/a       | uncinate    | yellowish          | granules         |
| *C. dextrinoideus* (1, 15, 29)               | cylindric-clavate | 1.5–4.3    | branched  | straight-bent| hyaline-subhyaline | none             |
| *C. dhubarensis* (16)                       | filiform     | 2–3        | simple    | straight    | hyaline            | none             |
| *C. disculus* (1, 8, 9, 17, 18, 29)         | cylindric-clavate | 3–4        | below     | straight-bent| none               | none             |
| *C. duplus* (1)                             | filiform     | 2.2–2.5    | below     | uncinate    | hyaline            | none             |
| *C. epithecioides* (this paper)              | epithecioid+  | 5–9.9'     | branched  | bent        | ± carotenoid       |                  |
| *C. glaucellus* (1, 7, 8, 13, 29)           | filiform     | 2.9–4.3    | branched  | uncinate    | none to yellow     | none to yellow   |
| *C. granuliformis* (1, 7, 8, 18, 19, 29)    | clavate      | 4–8        | below     | bent        | none to diffuse    | none to yellow   |
| *C. lacteus* (1, 7, 8, 9, 14, 17, 18, 20, 21, 22) | filiform     | 1.5–3      | below     | uncinate    | hyaline to yellow  | globs            |
| *C. leucopocillum* (1, 8, 9, 18, 29)        | cylindric-clavate | 2–5        | below     | bent        | none or hyaline    | none             |
| *C. luteus* (1, 9, 18, 29)                  | filiform     | 2–3.5      | below     | bent        | yellow to orange   | globs            |
| *C. aff. luteus* (8)                        | filiform     | 1.5–2      | mostly    | uncinate    | yellow             | yellow globes    |
| *C. marginatus* (1)                         | filiform     | 2–3        | below     | bent        | none               | none             |
| *C. niveus* (1, 9, 14)                      | filiform     | 2–2.5      | below     | straight-bent| none               | none             |
| *C. ochraceus* (1, 5, 6, 8, 9, 14, 26)      | cylindric-clavate | 3–5        | below     | straight-bent| yellow             | granules         |
| *C. ochraceus* ss. Thind et al. (7, 17, 18)  | cylindric-clavate | 3.5–5      | simple    | straight    | yellow             | yellow content   |
| *C. rhyparobioides* (1, 14)                 | filiform     | 1.8–2      | mostly    | bent        | none               | none             |
| *C. sarangpurensis* (17)                    | filiform     | 2–2.5      | below     | straight    | n/a                | n/a              |
| *C. sexdecimsporus* (1, 6, 8, 14, 18, 19, 26, 27, this paper) | filiform | 1.7–3.5 | branched | bent to uncinate | hyaline or pigmented | none |
| *C. sphaerosporus* (23)                     | filiform     | n/a        | below     | straight    | hyaline            | none             |
| *C. subcylindrosporus* (8, 10, 13)          | clavate      | 3–8        | below     | straight-bent| yellow             | yellow content   |
| *C. tetrasperus* (27)                       | filiform     | 1.5–2      | branched  | straight    | hyaline            | n/a              |
| *C. trichosuri* (24)                        | cylindric-obtuse | 3–4       | branched  | straight    | none               | none             |
| *C.uncinatus* (25)                          | filiform     | 2–3        | branched  | uncinate-helicoid | n/a                | n/a              |
| *C. vicinus* (1, 6)                         | cylindric-clavate | 4–5        | below     | straight    | yellow             | yellow globes    |
| *C. winteri* (1)                            | filiform     | 1–2        | mostly    | uncinate    | none               | none             |
Discussion

Together with the newly described species, 29 species are currently accepted in the genus *Coprotus*. One species is published invalidly (Häffner 1996), while four misapplied species concepts were recognized in our study and considered as separate taxonomic entities: *Ascophanus aurantiacus* Velen. (Velenovský 1934, Svrček 1976), which is erroneously synonymised by Kimbrough et al. (1972) with *Coprotus aurora* (P. Crouan & H. Crouan) K.S. Thind & Waraich (Thind and Waraich 1970); *Coprotus breviascus* (Velen.) Kimbr., Luck-Allen & Cain ss. Dokmetzian et al. (2005); *C. aff. luteus* Kimbr. (Doveri 2004) and *C. ochraceus* (P. Crouan & H. Crouan) J. Moravec ss. Thind et al. (1978). Furthermore, Kimbrough et al. (1972) synonymised *Ascophanus bilobus* Velen. (≡ *Coprotus bilobus* (Velen) J. Moravec) with *Coprotus ochraceus*, an entity we consider a separate species.

In this, our first contribution to the knowledge of the genus *Coprotus*, we aimed to ascertain the exact phylogenetic position of the genus, bearing in mind that the type species *C. sexdecimsporus* had not previously been sequenced. We also undertook to determine the variability in colour noted in this species. To do this a typical non-pigmented sample of *C. sexdecimsporus* and a pigmented 16-spored *Coprotus* collection were analysed using molecular and vital taxonomic methods. The non-pigmented *C. sexdecimsporus* and the pigmented form proved to be the same species with 100% bp identity, showing that the apothecia of *C. sexdecimsporus* may be pigmented or not. The same behaviour regarding pigmentation was also recorded in the newly described *C. epithecioides* by performing the same light-test procedure through prolonged monitoring of apothecia on original substrate. The apothecia of both *C. sexdecimsporus* and *C. epithecioides*, fully grown in dark first, were devoid of any notable pigmentation in the paraphyses, while new generations of apothecia started to develop pigment granules soon after exposure to sunlight or artificial light rich in UV radiation. This would indicate that future testing along these lines on other species in the genus would be fruitful and informative in further developing the identification key. All *Coprotus* keys published so far, that containing significant numbers of species (Kimbrough et al. 1972, Aas 1983, Prokhorov 1998, Doveri 2004, Melo et al. 2015) use paraphysal and apothecial pigmentation that we show are unstable/unreliable.

Phylogenetic analyses of both forms of the type species confirmed the position of the genus *Coprotus* in the order Pezizales, inside a large species group of the Pyronemataceae s.l., placing the *Coprotus-Boubovia* lineage next to the *Ascodesmis* species group but without high support in our contracted analyses (cf. also Hansen et al. 2013, Lindemann et al. 2015, Lindemann and Alvarado 2017). In our study *C. epithecioides* clustered in the *Coprotus* core group (sister to the type species). Our analysis confirmed that both eight-spored and multispored (in our case 16-spored) species belong in the genus *Coprotus* (cf. Hansen et al. 2013).

Previously only *C. ochraceus* was included in phylogenetic analyses (cf. Hansen et al. 2013, Lindemann et al. 2015, Lindemann and Alvarado 2017). In our analyses, this species clearly falls outside both the *Coprotus* core group and the group containing putative members of the genus *Boubovia* (Figs 1, 2). The isolated position of *C. ochraceus*
is furthermore supported by the detailed re-examination of Crouan’s material by Le Gal (1960), who managed to observe several to many granules inside the sporoplasm that could not represent de Bary bubbles, a feature that is absent in all other known Coprotus species. However, paraphyletic relationship of analysed members of Boubovia should be clarified in future studies with more species and more DNA regions included. A number of Coprotus species (but not C. ochraceus) that we have studied so far in detail, including the type species C. sexdecimsporus and the new species C. epitheciodes, did not possess any refractive granular / guttulate content in the sporoplasm at any developmental stage (see also Kimbrough 1966, Kimbrough and Korf 1967). All known species of Coprotus are obligatory fimicolous (cf. Doveri 2011). Those species in the closely related genus Boubovia, that were included in our phylogenetic analyses, placed next to each other (Figs 1, 2), are principally found on other types of substrate (dump soil, pebbles, litter and decayed organic material), and their ascospores possess internal guttules, at least during the early stages of development (Svrček 1977, Yao and Spooner 1996). The present study implies the necessity for further phylogenetic studies of more Coprotus collections and species (reliably identified), as well as more DNA regions. Until more research is done, we restrict the genus to strictly fimicolous species, the spores of which are smooth under the light microscope, and are devoid of any internal refractive granular content at any developmental stage. Also, freshly ejected ascospores of all the species analysed by us possessed thick and sticky temporary sheaths in the living state, a rarely reported, but important character, also detected by Le Gal (1960). An example of the importance of such a character in generic characterisation is the encapsulating, rather firm spore sheath present in the genus Paratricharina Van Vooren, U. Lindemann, M. Vega, Ribes, Illescas & Matočec (VanVooren et al. 2015) but absent from almost all pezizalean genera.

Since the need for the standardisation of defining taxonomic characters (especially spore shapes) is already elaborated in Kušan et al. (2014), we tested the shape of the asci as a useful taxonomic character too. The asci of the genus Coprotus vary considerably in both shape (from broad clavate to narrow cylindric) and size (38–210 × 6–55 µm) (Table 4). However, individual species in this genus mostly possess asci with comparatively little variation in size and shape. This prompted us to introduce a standardisation of ascus shape types and length/width ratio (“Q” value) for describing asci, in order to enhance differentiation between Coprotus species. Ascus shape types were grouped in the current study into three series, defined by the position of its broadest point and “Q” value: clavate, cylindric and fusiform (see explanation under the Table 4).

Baral (1992) observed that considerable alterations in quantitative taxonomic characters between dead and living cells exist in Ascomycota, due to the turgor loss causing cell shrinkage (especially in hymenial elements). This phenomenon, resulting in significantly lower measurements in dead cells, was recorded during the current study in ascal length and width (frequently with altered length/width ratio), and paraphysal width in all Coprotus collections studied in the living state. Therefore, great care should be taken when measuring the asci and paraphyses in order not to mix up the measurements of living and dead cells. On the other hand, ascospores in Coprotus showed little
quantitative alteration. This can be explained by rigid spore walls and the capability of the sporoplasm to reversibly reduce its volume (caused by loss of cytoplasmic water) by forming gaseous de Bary bubble without significant cell shrinkage. This behaviour is not only characteristic to the genus *Coprotus*, but also to other phylogenetically closely related genera such as *Boubovia* (cf. Kristiansen and Schumacher 1993) and *Lasiobolus* Sacc. (cf. Kimbrough and Korf 1967). The ascospores of a number of more distantly related fungi usually possess pliant and thin walls, that easily irreversibly collapse unilaterally, together with the sporoplasm (e.g. *Peziza*, *Iodophanus* or *Morchella*), or both the wall and the sporoplasm irreversibly shrink, decreasing the ascospore's size evenly in all parts (numerous species of *Helotiales*), as shown diagrammatically in Baral (1992).

We recommend that future studies of newly collected material of *Coprotus* include careful observations of microscopic characters in the living state, especially in cases of rare and potentially new species, for the following reasons: (1) Living mature asci, besides representing a valuable standard for measurement and shape definition, may with proper orientation display useful characteristics related to the dehiscence apparatus as it appears immediately before spore ejection. This is also the case if living material is directly fixed with CB (Fig. 5a) or CR; (2) Freshly ejected ascospores are normally at a uniform ontogenetic, mature stage, structurally complete and presumably viable, thus in this condition they represent a valuable standard for measurement, vital staining and description of structural features. Spores shape is unaltered because they are fully hydrated. This allows the differentiation of bilateral symmetry from those spores that may appear to have bilateral symmetry because of collapse due to the loss of turgor. We repeatedly recorded this alteration not only in this genus but throughout different pezi-zalean taxa; (3) A spontaneous (natural) spore discharge from living mature asci enables the monitoring of the presence and properties of the ascospore sheath. This structural detail can be of great help in taxonomical studies of every single species putatively assigned to the genus *Coprotus*, as well as to related taxa. It is already known that the presence or absence of such structures represents important taxonomic information in a number of ascomycetous taxa; (4) Both the paraphysal internal pigmentation and the exudate may disappear in older dried material. Observation of shrunken paraphysis tips on dead material minimises the difference among a number of species. All the above-mentioned characters, are only visible in the living state. However, they can be easily recorded (e.g. microphotography) for future use from every fresh and viable collection.

**Acknowledgements**

We wish to thank Dr Francesco Doveri, Dr Uwe Lindemann and Mr Michel Hairaud for providing missing literature. Mr Michel Hairaud and Mr Patrice Tanchaud are appreciated for sharing their collection of *Boubovia nicholsonii* and Ms Lana Baričević for her help during some fieldwork sessions and laboratory analyses. We are thankful to Mr Lee Knight for English language editing. This work was partially financially supported by the Public Institution Sjeverni Velebit National Park.
References

Aas O (1983) The genus *Coprotus* (Pezizales) in Norway. Nordic Journal of Botany 3(2): 253–259. https://doi.org/10.1111/j.1756-1051.1983.tb01075.x

Alvarado P, Moreno G, Manjón JL, Gelpi C, Kaounas V, Konstantinidis G, Barseghyan GS, Venturella G (2011) First molecular data on *Delastria rosea*, *Fischerula macrospora* and *Hydnocystis piligera*. Boletín de la Sociedad Micológica de Madrid 35: 31–37.

Amicucci A, Zambonelli A, Guidi C, Stocchi V (2001) Morphological and molecular characterisation of *Pulvinula constellatio* ectomycorrhizae. FEMS Microbiology Letters 194(2): 121–125. https://doi.org/10.1111/j.1756-6968.2001.tb09456.x

Baral HO (1992) Vital versus herbarium taxonomy: morphological differences between living and dead cells of Ascomycetes, and their taxonomic implications. Mycotaxon 44(2): 333–390.

Bell A, Kimbrough JW (1973) *Coprotus trichosurus* sp. nov. from New Zealand. Transactions of the British Mycological Society 61(1):190–193. https://doi.org/10.1016/S0007-1536(73)80103-2

Boudier É (1869) Mémoire sur les Ascobolés. Annales des Sciences Naturelles Botanique ser. 5., 10: 191–268.

Chang J-H, Wang Y-Z (2009) Notes on coprophilous discomycetes from Taiwan. V. Collection and Research 22: 127–130.

Cooke MC (1877) New British fungi. Grevillea 5(35): 118–122.

Crouan PL, Crouan HM (1858) Note sur neuf *Ascobolus* nouveaux. Annales des sciences naturelles botanique ser. 4., 10: 193–199.

Crouan PL, Crouan HM (1867) Florule du Finistère. Contenant les descriptions de 360 espèces nouvelles de sporogames, de nombreuses observations et une synonymie des plantes cellulaires et vasculaires qui croissant spontanément dans ce département. Friedrich Klincksieck and J.B. et A. Lefournier, 1–262, 31 Pl. + 1 Suppl. Pl.

Currey F (1864) Notes on British Fungi. The Transactions of the Linnean Society of London 24(3): 491–496. https://doi.org/10.1111/j.1096-3642.1863.tb00174.x

De Sloover JR (2002) *Coprotus arduennensis*, a new species of coprophilous discomycetes (Pezizales, Ascomycota). Persoonia 17(4): 649–656.

Doveri F (2004) Fungi Fimicoli Italici. A.M.B. Fondazione Centro Studi Micologici, 1–1104.

Doveri F (2011) Addition to Fungi Fimicoli Italici: An update on the occurrence of coprophilous Basidiomycetes and Ascomycetes in Italy with new records and descriptions. Mycosphere 2(4): 331–427. http://www.mycosphere.org/pdf/MC2_4_No4.pdf

Doveri F (2012) Coprophilous discomycetes from the Tuscan archipelago (Italy). Description of two rare species and a new *Trichobolus*. Mycosphere 3(4): 503–522. https://doi.org/10.5943/mycosphere/3/4/13

Dokmetzian DA, Ramos AM, Cinto IE, Suárez ME, Ranalli ME (2005) Six species of the genus *Coprotus* (Pyronemataceae) from Argentina studied in culture. Hickenia 3(57): 243–252.

Eckblad F-E (1968) The genera of the operculate discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. Nytt Magasin for Botanikk 15(1–2): 1–191.

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for Basidiomycetes: application to identification of mycorrhizae and rusts. Molecular Ecology 2: 113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x
Gene J, ElShafie AE, Guarro J (1993) Two new coprophilous Pezizales from the Sultanate of Oman. Mycotaxon 46: 275–284.

Ghosta Y, Poursafar A, Qarachal JF (2016) Study on coprophilous fungi: new records for Iran mycobiota. Rostaniiha 17(2): 115–126. https://doi.org/10.22092/BOTANY.2017.109405

Gibson JL, Kimbrough JW (1980) A new spherical spored species of Coprotus (Pezizales). Mycotaxon 11(1): 376–380.

Häffner J (1996) Pilzaufsammlungen vom Rand der Sahara. Rheinland-Pfälzisches Pilzjournal 5+6(2+1): 134–176.

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

Hansen K, Læssøe T, Pfister DH (2001) Phylogenetics of the Pezizaceae, with an emphasis on Peziza. Mycologia 93(5): 958–990. https://doi.org/10.2307/3761760

Hansen K, Læssøe T, Pfister DH (2002) Phylogenetic diversity in the core group of Peziza inferred from ITS sequences and morphology. Mycological Research 106(8): 879–902. https://doi.org/10.1017/S0953756202006287

Hansen K, Perry BA, Dranginis AW, Pfister DH (2013) A phylogeny of the highly diverse cup-fungus family Pyronemataceae (Pezizomycetes, Ascomycota) clarifies relationships and evolution of selected life history traits. Molecular Phylogenetics and Evolution 67(2): 311–335. https://doi.org/10.1016/j.ympev.2013.01.014

Hansen K, Perry BA, Pfister DH (2005) Phylogenetic origins of two cleistothecial fungi, Orbicula parietina and Lasiobolidium orbiculoides, within the operculate discomycetes. Mycologia 97(5): 1023–1033. https://doi.org/10.1080/15572536.2006.11832752

Harmaja H (1974) Observations on the presence of a cyanophilic perispore in the spores of the Pezizales. Karstenia 14: 123–125. https://doi.org/10.29203/ka.1974.100

Heim R (1962) L’organisation architecturale des spores de Ganodermes. Revue de Mycologie (Paris) 27: 199–211.

Henriot A, Cheyve J-L (2017) Piximètre: La mesure de dimensions sur images. Version 5.9 R1530. http://ach.log.free.fr/Piximetre.

James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung GH, Johnson D, O’Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schüßler A, Longcore JE, O’Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkman-Kohlmeyer B, Spotts RA, Serdani M, Crous PW, Hughes KW, Matsaura K, Langer E, Langer G, Unterreiner WA, Lücking R, Biedel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R (2006) Reconstructing the early evolution of Fungi using a six-gene phylogeny. Nature 443: 818–822. https://doi.org/10.1038/nature05110

Jeng RS, Krug JC (1977) New records and new species of coprophilous Pezizales from Argentina and Venezuela. Canadian Journal of Botany 55(24): 2987–3000. https://doi.org/10.1139/b77-336

Kimbrough JW (1966) Studies in the Pseudoascoboleae. Canadian Journal of Botany 44(5): 685–704. https://doi.org/10.1139/b66-082
An overview of the genus *Coprotus* (Pezizales, Ascomycota)...

Kimbrough JW (1970) Segregates of *Ascophanus*, *Coprotus* vs. *Leporina* (Thelebolaceae, Pezizales). Taxon 19(5): 779–781. https://doi.org/10.2307/1219291

Kimbrough JW, Korf RP (1967) A synopsis of the genera and species of the tribe Theleboleae (= Pseudoascoboleae). American Journal of Botany 54(1): 9–23. http://www.jstor.org/stable/2440883

Kimbrough JW, Luck-Allen ER, Cain RF (1972) North American species of *Coprotus* (Thelebolaceae: Pezizales). Canadian Journal of Botany 50(5): 957–971. https://doi.org/10.1139/b72-116

Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) Ainsworth and Bisby's Dictionary of the Fungi, 10th ed. CAB International, Wallingford.

Kirk PM, Stalpers JA, Braun U, Crous PW, Hansen K, Hawksworth DL, Hyde KD, Lücking R, Lumbsch TH, Rossman AY, Seifert KA, Stadler M (2013) A without-prejudice list of generic names of fungi for protection under the International Code of Nomenclature for algae, fungi, and plants. IMA Fungus 4(2): 381–443. https://doi.org/10.5598/imafungus.2013.04.02.17

Kish LP (1974) Culture and cytological development of *Coprotus lacteus* (Pezizales). Mycologia 66(3): 422–435. https://doi.org/10.2307/3758486

Korf RP (1954) A revision of the classification of ooperculate Discomycetes (Pezizales). Rapports et communications / Huitième Congrès International de Botanique, Paris 1954. Parvenus avant le congrès aux sections 18, 19 et 20: 80.

Kristiansen R, Schumacher T (1993) Nye ooperculate begersopper i Norges flora. Blyttia 51(3–4): 131–140.

Kušan I, Matočec N, Antonić O, Hairaud M (2014) Biogeographical variability and re-description of an imperfectly known species *Hamatocanthoscypha rotundispora* (Helotiales, Hyaloscyphaceae). Phytotaxa 170(1): 1–12. http://dx.doi.org/10.11646/phytotaxa.170.1.1

Kušan I, Matočec N, Mešić A, Tkalčec Z (2015) *Tricharina tophiseda* – a new species from Croatia with a revision of *T. japonica* (Pyronemataceae, Pezizales). Phytotaxa 221(1): 35–47. http://dx.doi.org/10.11646/phytotaxa.221.1.3

Le Gal M (1960) Les Discomycètes de l’herbier Crouan. Deuxième série. Annales des sciences naturelles, Botanique, 12 sér., 1: 441–467.

Leuchtmann A, Clémençon H (2012) The taxonomic position of the genus *Heydenia* (Pyronemataceae, Pezizales) based on molecular and morphological data. Mycological Progress 11(3): 699–710. https://doi.org/10.1007/s11557-011-0779-5

Lindemann U, Alvarado P (2017) Revision der Gattung Kotlabaea, Teil 2: *K. aurantiaca*, *K. carestiae*, *K. danuviana* und *K. trondii* nebst taxonomischen Bemerkungen zu *Boubovia vermiphila*, *Cheilymenia stercoraria* und zur Gattung *Pseudombrophila*. Zeitschrift für Mykologie 83(1): 103–126.

Lindemann U, Vega M, Alvarado P (2015) Revision der Gattung Kotlabaea: *K. deformis*, *K. delectans* und *K. benkertii*. Zeitschrift für Mykologie 81(2): 373–402.

Lumbsch HT, Huhndorf SM (2010) Myconet Volume 14. Part One. Outline of Ascomycota – 2009. Part Two. Notes on Ascomycete Systematics. Nos. 4751–5113. Fieldiana Life Earth Science 1: 1–64. https://doi.org/10.3158/1557.1

Melo RFR, Miller AN, Maia LC (2015) *Coprotus* (Thelebolaceae, Thelebolales) in herbivore dung from Brasil. Nova Hedwigia 101(1–2): 35–48. https://doi.org/10.1127/nova_hedwigia/2014/0232
Moravec J (1971) Diskomycety čeledi Thelebolaceae (Brumm.) Eckbl. z okresu Mladá Boleslav v Čechách. Česká Mykologie 25(3): 150–160.

Osmundson TW, Robert VA, Schoch CL, Baker LJ, Smith A, Robich G, Mizzan L, Garbelotto MM (2013) Filling gaps in biodiversity knowledge for macrofungi: contributions and assessment of an herbarium collection DNA barcode sequencing project. PLoS ONE 8(4): e62419. https://doi.org/10.1371/journal.pone.0062419

Perry BA, Hansen K, Pfister DH (2007) A phylogenetic overview of the family Pyronemataceae (Ascomycota, Pezizales). Mycological Research 111(5): 549–591. https://doi.org/10.1016/j.mycres.2007.03.014

Prokhorov VP (1998) The genera Coprotus, Ascozonus, Thelebolus and Trichobolus (Pezizales): the keys to identification of species. Mikologiya i Fitopatologiya 32(2): 40–43.

Ramos AM, Dokmetzian DA, Ranalli ME, Ferreyra LI (2008) RAPD patterns in three Argentine Coprotus species: a test case. Mycotaxon 103: 9–19.

Ramos AM, Tadic LF, Policelli N, Ferreyra LI, Cinto IE (2015) AFLP characterization of three argentine Coprotus species. Mycotaxon 130(1): 265–273. http://dx.doi.org/10.5248/130.265

Rehm H (1896) Ascomyceten: Hysteriaceen und Discomyceten. In: Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz, 2. 1(3): 1–1272.

Saccardo PA (1889) Sylloge Fungorum omnium hucusque cognitorum. 8: 1–1143.

Samuelson DA (1978) Asci of the Pezizales III: The apical apparatus of eugymnohymenial reprentatives. American Jouranl of Botany 65(7): 748–758. http://www.jstor.org/stable/2442150

Schoch CL, Kohlmeyer J, Volkmann-Kohlmeyer B, Tsui CKM, Spatafora JW (2006) The halotolerant fungus Glomerobolus gelineus is a member of the Ostropales. Mycological Research 110(3): 257–263. https://doi.org/10.1016/j.mycres.2005.10.001

Schoch CL, Sung G-H, López-Giráldez F, Townsend JP, Miadlikowska J, Hofstetter V, Robbertse B, Matheny PB, Kauff F, Wang Z, Gueidan C, Andrie RM, Trippe K, Ciufetti LM, Wynns A, Fraker E, Hodkinson BP, Bonito G, Groenewald JZ, Arzanlou M, de Hoog GS, Crous PW, Hewitt D, Pfister DH, Peterson K, Gryzenhout M, Wingfield MJ, Aptroot A, Suh S-O, Blackwell M, Hillis DM, Griffith GW, Castlebury LA, Rossman AY, Lumbsch HT, Lücking R, Büdel B, Rauhut A, Diederich P, Ertz D, Geiser DM, Hosaka K, Inderbitzin P, Kohlmeyer J, Volkman-Kohlmeyer B, Mostert L, O’Donnell K, Sipman H, Rogers JD, Shoemaker RA, Sugiyama J, Summerbell RC, Untereiner W, Johnston PR, Stenroos S, Zuccaro A, Dyer P, Crittenden PD, Cole MS, Hansen K, Trappe JM, Yahr R, Lutzoni F, Spatafora JW (2009) The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. Systematic Biology 58(2): 224–239. https://doi.org/10.1093/sysbio/syp020

Spatafora JW, Sung GH, Johnson D, Hesse C, O’Rourke B, Serdani M, Spotts R, Lutzoni F, Hofstetter V, Miadlikowska J, Reeb V, Gueidan C, Fraker E, Lumbsch T, Lücking R, Schmitt I, Hosaka K, Aptroot A, Roux C, Miller AN, Geiser DM, Hafellner J, Westmark G, Arnold AE, Büdel B, Rauhut A, Hewitt D, Untereiner WA, Cole MS, Scheidegger C, Schultz M, Sipman H, Schoch CL (2006) A five-gene phylogeny of Pezizomycotina. Mycologia 98(6): 1018–1028. https://doi.org/10.1080/15572536.2006.11832630

Suárez ME, Ranalli ME, Dokmetzian DA, Ramos AM (2006) Characterization of three species of the genus Coprotus (Ascomycota) by isozyme analysis. Mycotaxon 97: 257–273.
An overview of the genus *Coprotus* (Pezizales, Ascomycota)...

Svrček M (1976) A taxonomic revision of Velenovský’s types of operculate discomycetes (Pezizales) preserved in National Museum, Prague. Sborník Národního muzea v Praze 32 B (2–4): 115–194.

Svrček M (1977) New combinations and new taxa in operculate Discomycetes (Pezizales). Česká Mykologie 31(2): 69–71.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. Molecular Biology and Evolution 30(12): 2725–2729. https://doi.org/10.1093/molbev/mst197

Tedesco L, Hansen K, Perry BA, Kjøller R (2006) Molecular and morphological diversity of pezizalean ectomycorrhiza. New Phytologist 170(3): 581–596. https://doi.org/10.1111/j.1469-8137.2006.01678.x

Third KS, Kaushal SC, Kaushal R (1978) The genus *Coprotus* in India. Journal of the Indian Botanical Society 57: 63–67.

Third KS, Waraitch KS (1970) The Pezizales of India – X. Research Bulletin (N.S.) of the Panjab University 21(1–2): 145–155.

van Brummelen J (1998) Reconsideration of relationships within the Thelebolaceae based on ascus ultrastructure. Persoonia 16(4): 425–469.

Van Vooren N, Lindemann U, Vega M, Ribes MÁ, Illescas T, Matočec N, Kušan I (2015) *Lachnea poinaultii* (Pezizales), rediscovered after more than one hundred years. Ascomycete.org 7(3): 105–116.

Velenovský J (1934) Monographia Discomycetum Bohemiae. Praha, 1–436, 31 Pl.

Velenovský J (1947) Novitates mycologicae novissimae. Opera botanica Čechica 4: 1–158.

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. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Wang X-H, Huhtinen S, Hansen K (2016) Multilocus phylogenetic and coalescent-based methods reveal dilemma in generic limits, cryptic species, and a prevalent intercontinental disjunct distribution in *Geopyxis* (Pyronemataceae s. l., Pezizomycetes). Mycologia 108(6): 1189–1215. http://dx.doi.org/10.3852/16-100

Wang Y-Z (1994) Two new coprophilous discomycetes (Pezizales) from Taiwan. Mycotaxon 52(1): 83–89.

Waraitch KS (1977) A contribution to the knowledge of coprophilous Pezizales of India. Sydowia 29(1-6): 1–9.

White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Wijayawardene NN, Hyde KD, Rajeshkumar KC, Hawksworth DL, Madrid H, Kirk PM, Braun U, Singh RV, Crous PW, Kukwa M et al. (2017) Notes for genera: Ascomycota. Fungal Diversity 86(1): 1–594. https://doi.org/10.1007/s13225-017-0386-0

Yao Y-J, Spooner BM (1996) Delimitation of *Boubovia* and *Pulvinula*. Mycological Research 100(2): 193–194. https://doi.org/10.1016/S0953-7562(96)80120-1