# Cuphophyllus atlanticus (Hygrophoraceae, Agaricales) — a new sister species to the North American C. canescens

John Bjarne Jordal<sup>1</sup>, Ellen Larsson<sup>2</sup>

<sup>1</sup> Miljøfaglig Utredning, Gunnars veg 10, NO-6630 Tingvoll, Norway <sup>2</sup> University of Gothenburg, Department of Biological and Environmental Sciences and Gothenburg Global Biodiversity Centre, P.O. Box 461, SE-40530 Göteborg, Sweden

Corresponding author: Ellen.Larsson@bioenv.gu.se

#### Norsk tittel:

Cuphophyllus atlanticus (Hygrophoraceae, Agaricales) - en ny søsterart til den nordamerikanske C. canescens

John Bjarne Jordal, Ellen Larsson. Cuphophyllus atlanticus (Hygrophoraceae, Agaricales) — a new sister species to the North American C. canescens. Agarica 2021, vol. 42:39-48

### **KEYWORDS**

Cuphophyllus canescens, molecular systematics, new species, taxonomy

### NØKKELORD

tinnvokssopp, molekylær systematikk, ny art, taksonomi

### SAMMENDRAG

Cuphophyllus canescens er en art som opprinnelig ble beskrevet fra Nord-Carolina, USA. Det vitenskapelige navnet er også blitt brukt om europeisk materiale rapportert fra Norge, Sverige og Storbritannia. I forbindelse med studier av materiale av tinnvokssopp fra Norge avdekket molekylære undersøkelser at vår art har ITS-sekvens som er forskjellig fra isotypen av C. canescens og derfor bør beskrives som en ny art. Cuphophyllus atlanticus er foreslått som navn for den nye arten, som viser seg å ha en interkontinental utbredelse.

Utbredelsen av Cuphophyllus canescens synes å være begrenset til Nord-Amerika.

### ABSTRACT

Cuphophyllus canescens is a species originally described from North Carolina, USA. The name has been applied to specimens collected in Europe, and the species has been reported from Norway, Sweden and Great Britain. In connection with an inventory and study of C. canescens in Norway, the molecular investigations revealed that the Scandinavian specimens differ in ITS sequence data from the isotype of C. canescens and therefore should be described as a new species. Cuphophyllus atlanticus is proposed as a new name for this species, which is shown to have an intercontinental distribution range while Cuphophyllus canescens seems to be restricted to North America.

### INTRODUCTION

Cuphophyllus (Donk) Bon is a genus of Hygrophoraceae Lotzy, with species globally distributed in the northern and southern hemispheres. In the systematic review of Hygrophoraceae, Lodge et al. (2014) it was found that Cuphophyllus occupied a relatively isolated phylogenetic position in the family. Several species in the genus are shown to have a broad distribution range and to occur from the nemoral to the arctic-alpine zones in Europe (Boertmann 2010). Most European species differ from the ones occurring in North America, but there are exceptions. These are

especially found among species having a northern boreal to arctic-alpine distribution range, for example *C. hygrocyboides* (Kühner) Bon (Voitk et al. 2020).

The species in Cuphophyllus are characterized by having clitocyboid basidiomata with thick decurrent lamellae and a white spore print. In micro-morphology they have an interwoven or rarely almost subregular lamellar trama, with or without a regular or subregular central strand; smooth, hyaline, inamyloid basidiospores; very long basidia relative to spore length (usually 7-8, rarely 5-6 times the spore length), and a basal clamp on the basidia (Lodge et al. 2014). An interwoven lamellar trama, together with large basidia to spore length ratio are the most reliable characters for separating Cuphophyllus from other white-spored agaric genera. Species of Cuphophyllus are now regarded to have a biotrophic mode of nutrition, but the nature of the fungus-plant association is largely unknown (e. g. Halbwachs et al. 2018).

Cuphophyllus canescens (A.H. Sm. and Hesler) Bon was originally described from the Great Smoky Mountains National Park, North Carolina, USA by Smith and Hesler (1942). It has been described as a rare species in Europe, occurring in semi-natural grasslands of Norway, Sweden and Great Britain (Boertmann 2010). In connection with a study and inventory of C. canescens in Norway (Jordal 2019a), investigations with molecular methods were also undertaken and revealed that the ITS sequence data of the Norwegian specimens differ from the isotype of C. canescens. Cuphophyllus atlanticus is therefore proposed here as a new name for this species, which is so far identified from Norway, Sweden, South Europe and also from USA and Canada.

# MATERIAL AND METHODS Morphological methods

Fresh basidiomata were photographed in situ and the habitat was noted and described. Information from other collectors like photos and habitat data has been compiled (Jordal 2019a). Detailed observations of macromorphological characters were made on fresh and photographed material together with field notes. Micro-morphological characters were observed and measured from dried material dehvdrated in 3% KOH and ammoniacal Congo red solution at 1000× magnifications using a Zeiss Axioskop 2 microscope and ZEN imaging software (Zeiss). A minimum of 20 spores were measured from each basidioma, abnormally large or small spores were not considered. Spore measurements exclude apical appendage. Basidial measurements exclude sterigmata, and the sterigmata were measured separately. The measurements in the description below are based on five sequenced collections with mature and well developed basidiomata (GB-0076131, OF241128, OF288790, OF288304, OF287870).

# **Molecular methods**

Nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) sequence data of 14 specimens of *C. atlanticus* were newly generated for this study.

DNA was extracted using DNeasy Plant Mini Kit (Qiagen, Hilden), and for the PCR reactions Illustra PuReTaq Ready to go PCR beads (GE Healthcare, Buckinghamshire) were used with 0.5  $\mu$ M of each primer and 1- $3\mu$ L of DNA solution. PCR clean-up was made with QIAquick PCR purification kit (Qiagen, Hilden). Primers used to amplify the ITS region were ITS1F (Gardes and Bruns 1993) and LR21 (Hopple and Vilgalys 1999). Sequences were generated by Macrogen Europe (Amsterdam, The Netherlands) using primers ITS1, ITS4 (White et al. 1990). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan). The sequences have been deposited in GenBank (MW332281 – MW332294), see also material studied below.

The ITS data set was compiled based on the results from the ITS analysis of Cuphophyllus and data presented in Voikt et al. (2020). ITS sequence data of two collections of the Cuphophyllus hygrocyboides complex were used for rooting of trees. The ITS of the target species in this study was blasted in GenBank (Clark et al. 2016) and the UNITE database (Kõljalg et al. 2013) to seek additional available sequence data of similar and closely related taxa. Seven additional sequences deposited as Cuphophyllus sp., C. canescens and C. basidiosus (Peck) Lodge & Matheny were found and added to the data set, among them the ITS1 of the isotype of C. canescens (HO185699).

Alignment of the data set was performed using the L-INS-i strategy implemented in MAFFT 7.017 (Katoh and Standley 2013). The alignment was adjusted using ALIVIEW 1.17.1 (Larsson 2014). For inference of phylogenetic relationships of the dataset, heuristic searches for the most parsimonious trees were performed using PAUP\* under the maximum parsimony (MP) criterion (Swofford 2003). All transformations were considered unordered and equally weighted and gaps were treated as missing data. Heuristic searches with 1000 random-addition sequence replicates and TBR branch swapping were performed. Relative robustness of clades was assessed by the bootstrap (BT) method using 1000 heuristic search replicates with 10 random taxon addition sequence replicates and TBR branch swapping, saving 100 trees in each replicate.

# RESULTS

The aligned ITS dataset consisted of 37 sequences and 873 characters. After exclusion of ambiguous data, mainly from the beginning and the end of the data set, 838 characters remained for the analysis. Of these, 269 were

constant, 21 were variable but parsimony uninformative, and 548 were parsimony informative. The MP analysis yielded 6 equally most parsimonious trees (length = 939 steps, CI = 0.8427, and RI = 0.9597). One of these trees is presented in Fig. 1. Bootstrap analysis recovered nine supported terminal clades, corresponding to C. flavipes (Britzelm.) Bon (100%), C. pseudopallidus (Hesler and A.H. Sm.) Lodge, Boertm. & E. Larss. (84%), C. cinerellus (Kühner) Bon (99%), C. esteriae Voitk, I. Saar and E. Larss. (97%), C. colemannianus (A. Bloxam) Bon (100%), C. lacmus (Schumach.) Bon (93%), C. atlanticus (94%), C. canescens (91%) and C. basidiosus (100%). A BT value greater that 70% is considered strong.

The C. canescens group formed a wellsupported clade with 100% BT value, Fig 1. Within the clade the ITS 1 sequence of the isotype of C. canescens come together with two other sequences originating from North America. Of the three sequences representing C. basidiosus originating from North America are two identical and form a supported clade and one rather divergent from the others that merge on a single branch, suggesting that there may be more taxa involved here. However, sequence data of the type is not available. The 17 sequences in the C. atlanticus clade are homogenous. The sequences originate from Norway, Sweden, South Europe and North America, suggesting a broad an intercontinental distribution range.

### TAXONOMY

*Cuphophyllus atlanticus* J.B. Jordal & E. Larss. sp. nov. – Figs. 2-3.

MycoBank: MB838472

*Etymology*: the epithet refers to the occurrence of the species on both the European and the North American side of the Atlantic Ocean, and its main European distribution in the northwestern, atlantic parts.

# J.B. Jordal, E. Larsson



Figure 1. Phylogram showing the phylogenetic position of *Cuphophyllus atlanticus* based on ITS sequence data, placed as a supported clade together with *C. basidiosus* and *C. canescens* as sister species. Bootstrap values are indicated on branches. Sequences originating from type specimens are marked.

*Holotype*: NORWAY. Vestland (former Hordaland) county, Austevoll municipality, island of Møgster (northern part), in semi-natural grassland grazed by sheep, 6 Oct 2008,  $60.0700^{\circ}$ N,  $5.0902^{\circ}$ E ( $\pm$  7 m), leg. Asbjørn Knutsen, John Bjarne Jordal, OF287870 (holotype O, isotype GB), ITS sequence GenBank No. MW332288.



Figure 2. *In situ* photo of the basidiomata of the holotype of *C. atlanticus* in Norway, county of Vestland (Hordaland), Austevoll municipality, Møgster (OF287870). Photo J.B. Jordal.

Diagnosis: Macroscopically similar to C. canescens but differ in pileus colour, where that of C. atlanticus as young and fresh is grey, often with a weak bluish tint (grey-blue or tin-coloured) and with paler greyish white areas, without any brown, while C. canescens is described as «benzo brown» to «drab grey». Also, the stipe of *C. atlanticus* is pale greyish to almost white without any longitudinally streakes, while the stipe of C. canescens is described as near «pallid purplish gray» somewhat longitudinally streaked and white at base. The spores in *C. atlanticus* are slightly larger and subglobose to broadly ellipsoid  $(5.4-5.9 \times 4.4-4.8 \ \mu\text{m}, \text{ average } 5.6 \times 4.5 \ \mu\text{m},$ Q = 1.2-1.3) than those given in the original diagnosis of C. canescens (4-5 µm and globose). The two differ in ITS1 sequence

data, by 7 substitutions and one 4bp, two 2bp and 6 single bp insertion/deletion events.

*Pileus* 15-40(45) mm in diameter, obtuse to convex sometimes with a broad and blunt umbo and margin long remaining incurved, later becoming more plane, sometimes slightly depressed and with a lobed or irregular incurved margin, dry or weakly greasy (never slimy), matt, greyish, tin-coloured with a bluish tint and with paler greyish white areas, with age pale greyish. Not translucently striate or hygrophanous. *Lamellae* adnate to decurrent, sometimes deeply decurrent, distant to subdistant, lamellae that reach the stipe = 30 - 40(50), interspaced with lamellulae, a few furcate, intervening, pale grey, to grey with a weak bluish tint, with age pale



Figure 3. Micromorphological characters of the holotype of *C. atlanticus* (OF287870). A – Hymenium with basidia. B – Basidiospores among hyphae and basidia. C – Hymenophoral trama. D – Pileipellis. E – Stipetipellis. F – Subpileus trama. Scale bars  $10\mu m$ . Photo E. Larsson.

greyish. *Stipe*  $25-65 \times 3-7$  mm, cylindrical and thickest at the apex, often twisted, tapering and often bending towards the base, with age hollow, dry, matt with a whitish felty covering, pale greyish to almost white towards apex

and mostly whitish below. Context concolourous. The smell is weak and indistinct, taste not observed.



Figure 4. Habitat view from the type locality of *C. atlanticus* in Austevoll, Møgster. The species was found in the middle of the picture, in old semi-natural grassland that has been grazed, mostly by sheep, for centuries. Photo J.B. Jordal.

Spores [161] (4.7–)5.4–5.9(–6.8) × (3.3–)4.4 -4.8(–5.4)  $\mu$ m, average 5.6 × 4.5  $\mu$ m, Q = 1.2–1.3, globose to subglobose, hyaline, white in deposit, non-amyloid.

*Basidia* 40–55  $\times$  5–7  $\mu$ m, four-spored, two-spored observed, sterigmata 6–8  $\mu$ m.

*Lamellar trama* interwoven, made up of cylindrical hyphae 3–7  $\mu$ m wide and 30–60  $\mu$ m long. *Pileipellis* a cutis with radially interwoven hyphae 3.5–6  $\mu$ m wide, 30–50  $\mu$ m long, upper layer with few repent to erect hyphae. Subcutical hyphae interwoven 4–7  $\mu$ m wide. *Stipetipellis* with parallel and finely interwoven hyphae 3.5–5.5  $\mu$ m wide and 30–70  $\mu$ m long. Incrusted, finely granular pigmented hyphae observed. *Clamp* connections frequent in all tissues.

*Habitat*: The species is associated with seminatural grasslands, among mosses, herbs and grasses, with the soil ranging from rather acid to moderately calcareous (Fig 4.) Most localities are situated in the boreonemoral (hemiboreal) to southern boreal vegetation zones.

*Distribution*: The species is shown to have an intercontinental distribution range and is confirmed from Norway, Sweden, USA (NC), Canada and with one sequence originating from soil sample from an alpine meadow area in the European Alps or Carpathian Mountains.

AGARICA vol. 42

# Specimens studied:

NORWAY. Vestland (Hordaland): Austevoll, Møgster northern part, semi-natural grassland (grazed by sheep), 6 Oct 2008, A. Knutsen, J. B. Jordal, OF287870 (ITS GenBank MW332288) Holotype. Bømlo, Brandasund, old grassy road (semi-natural grassland, grazed by livestock), 22 Sept 2012, Per Fadnes, OF245811 (ITS GenBank MW332284). Bømlo, Spyssøya: Myra, semi-natural grassland (grazed by sheep), 2 Oct 2009, A. Knutsen, J. B. Jordal, OF291300 (ITS GenBank MW332281). Tverrborgvika, Bømlo, semi-natural grassland (grazed by sheep), 29 Sept 2013, A. Vatten, P. Fadnes, J. B. Jordal, OF247485 (ITS GenBank MW332286). Alver (Lindås), Lygra, Bløddalen nord, small spot of seminatural grassland surrounded by Calluna heath (grazed by sheep), 26 Sept 2018, J. B. Jordal, JB18-041 OF257333 (ITS GenBank MW332283). Masfjorden, Hopsdalen, seminatural grassland (pasture), 2 Oct 2008, G. Gaarder. OF288790 (ITS GenBank MW332292). Masfjorden, Vågset, seminatural grassland (pasture), 2 Oct 2008, G. OF288698 Gaarder, (ITS GenBank MW332293). Alver (Radøy), Bøøyna, seminatural grassland (grazed by sheep), 18 Sept 2013, G. Gaarder, OF245904 (ITS GenBank MW332285). Vestland (Sogn og Fjordane): Solund, Gåsvær: Fiskholmen, semi-natural grassland/coastal Calluna heath (grazed by sheep), 12 Oct 2006, B. H. Larsen, OF288304 (ITS GenBank MW332294). Møre og Romsdal: Aure, Husfest, semi-natural grassland (grazed by sheep), 22 Sept 1995, J. B. Jordal, OF241128 (ITS GenBank MW332290). Herøv (Møre og Romsdal), Skorpa, semi-natural grassland (grazed by goat), 27 Sept 1994, G. Gaarder, J. B. Jordal, OF241127 (ITS GenBank MW332289). Fjord (Norddal), Valldal, Heimsetra, semi-natural grassland on summer farm (grazed by cows), 3 Sept 2009, J. B. Jordal, OF291137 (ITS GenBank MW332287). Fjord (Stordal), Dyrkorn, Indresæter, Josætra,

semi-natural grassland, 10 Sept 2002, J. B. Jordal, OF178756 (ITS GenBank MW332291). SWEDEN. Värmland: Svanskog, Mosserud, Yttre Hedane, semi-natural grassland (hayfield), 17. Aug 2002, L. Gustavsson, GB-0076131 (ITS GenBank MW332282).

### DISCUSSION

Based on the original description of C. canescens (Smith and Hesler 1942) and the somewhat emended description in Hesler and Smith (1963) it is easy to understand that the name in Northern Europe (Boertmann 2010) has been applied to the species we now describe as C. atlanticus. They are indeed very similar. We have shown that both C. canescens s.str. and C. atlanticus occur in North America, and both species even in North Carolina. Therefore, we cannot be sure what species are included in the emended description of C. canescens in Hesler and Smith (1963), and we rely on the original description by Smith and Hesler (1942), which is based on the type. For instance, the spore form and measurements differ in the two publications. The type is said to have globose spores 4-5 µm in Smith and Hesler (1942); while later the spores of C. canescens are described as, at times globose, more often subovoid, 4-5.5(6)x 4-4.5 um (Hesler and Smith 1963). This is based on more collections where no further sequence data are available, and a mixture of species cannot be excluded.

In the phylogenetic analysis *C. basidiosus* comes out as a sister species to *C. atlanticus* and *C. canescens* in a strongly supported clade, Fig. 1. The species is also similar in morphology but differ and can be distinguished by the greyish-brown colour of pileus and stipe, and striations on the pileus. The species is not so far known from Europe.

Due to the red-listing the species *C. canescens* has been given attention and inventories have been undertaken, especially in Norway. This has improved our knowledge of occur-

rence and habitat preferences (Jordal 2019a).

In Norway, all finds have been done in open, semi-natural grasslands mainly without trees or bushes, with the soil ranging from rather acid to moderately calcareous. One find was on a grassy road surrounded by old cultural landscape. Most localities were within the hemiboreal to southern boreal vegetation zones (Moen 1999), except one (OF291137) that was found in the mid boreal zone near a summer farm. Along the coast-inland gradient, it occurred mostly in the strongly oceanic vegetation section (along the outer coast), but also sometimes in the markedly oceanic, and once in the weakly oceanic section. In Sweden the records available also suggest that it is associated to nutrient poor open semi-natural grassland, both on grazed and mown localities (SLU ArtDatabanken 2020). Most records are from the coast or inland of south Sweden and associated with the old cultural landscape.

The species C. canescens s. l. seems to be rare in North America and GBIF (2020) lists only about 20 records from eastern USA and eastern Canada. The habitat information is scarce, but waxcaps are generally found in forests or forest margins, preferably under trees that don't form ectomycorrhiza (Lodge et al. 2014, Halbwachs et al. 2018). Grasslands could be an underestimated waxcap habitat in North America due to limited attention (Griffith et al. 2013). On the label of the type of C. canescens it is said to be collected under Fagus and Hemlock in the Great Smoky Mts. National Park, North Carolina, suggesting a forest habitat. Due to the lack of information, it is hard to decide if habitat is a key factor for discrimination of the two species.

*Cuphophyllus atlanticus* is on the red list and evaluated as endangered (EN) in both Sweden (SLU ArtDatabanken 2020) and Norway (Artsdatabanken 2015) because its habitat of nutrient poor semi-natural grassland, is rapidly decreasing. *Cuphophyllus atlanticus* is in Europe an indicator of mycologically rich but nutrient-poor, semi-natural grasslands, and a member of the waxcap grassland assemblage. As a whole, most waxcap grasslands are among the habitat types that are listed as VU, EN or CR in the EU Red List of habitats (Janssen et al. 2016).

We conclude that *C. atlanticus* is the name to be applied to the red-listed and strongly threatened species in Norway and Sweden. *Cuphophyllus canescens* has been evaluated as vulnerable (VU) on the global red list (Jordal 2019b), and as endangered (EN) regionally in Europe (Jordal 2019c). The assessment for Europe should from now be applied to *C. atlanticus*, and the global assessment should be applied to *C. canescens s. l.*, including both *C. atlanticus* and *C. canescens s. s.* until a new assessment is done.

#### ACKNOWLEDGEMENTS

We thank the curator of Herbarium O for arranging loans, Per Fadnes and Geir Gaarder for generously sharing photos of their collections, and The Swedish Taxonomy Initiative, SLU Artdatabanken, Uppsala (EL).

#### REFERENCES

- Artsdatabanken 2015. Rødliste for arter [2015 Red List of Norwegian Species online database]. https://www.artsdatabanken.no/Rodliste. Assessed December 10, 2020.
- Boertmann D, 2010. The genus *Hygrocybe*. 2nd revised edition. Fungi of Northern Europe Vol. 1. Copenhagen, Denmark: Svampetryk. 200 pp.
- Clark K, Karsch-Mizrachi I, Lipman DJ, Ostell J, Sayers E, 2016. Nucleic Acids Research 44 (database issue): D67–D72.
- Gardes M, Bruns TD, 1993. ITS primers with enhanced specificity for basidiomycetes d application to the identification of mycorrhizas and rusts. Molecular Ecology 2: 113-118.
- GBIF 2020. Global Biodiversity Information Facility (GBIF) data portal. Collection of online herbarium specimens. http://data.gbif.org. Assessed December 10, 2020.

- Griffith GW, Gamarra JP, Holden EM, et al., 2013. The international conservation importance of welsh 'waxcap' grasslands. Mycosphere 4: 969-984.
- Halbwachs H, Easton GL, Bol R, Hobbie EA, Garnett MH, Peršoh D, Dixon L, Ostle N, Karasch P, Griffith GW, 2018. Isotopic evidence of biotrophy and unusual nitrogen nutrition in soil-dwelling Hygrophoraceae. Environmental Microbiology 20(10): 3573-3588.
- Hesler LR, Smith AH, 1963. North American species of *Hygrophorus*. Knoxville, Tennessee: University of Tennessee Press. 416 p.
- Hopple jr JS, Vilgalys R, 1999. Phylogenetic relationships in the mushroom genus *Coprinus* and dark-spored allies based on sequence data from the nuclear gene coding for the large ribosomal subunit RNA: divergent domains, outgroups, and monophyly. Molecular Phylogenetics and Evolution 13: 1-19.
- Janssen JAM, Rodwell JS, García Criado M, et al., 2016. European Red List of Habitats. Part 2. Terrestrial and freshwater habitats. European Union, Luxembourg.
- Jordal JB, 2019a. Tinnvokssopp *Cuphophyllus canescens* som eventuell prioritert art. Forslag til økologiske funksjonsområder på artens lokaliteter. Miljøfaglig Utredning rapport 2019-19. 47 p. [English title: *Cuphophyllus canescens* as a possible priority species. Proposal for ecological functional areas in its habitats.]
- Jordal JB, 2019b. *Cuphophyllus canescens*. The IUCN Red List of Threatened Species 2019: e.T147321031A147934053. [global assessment] http://dx.doi.org/10.2305/ IUCN. UK.2019-2.RLTS.T147321031A147934053.en
- Jordal JB, 2019c. *Cuphophyllus canescens*. The IUCN Red List of Threatened Species 2019: e.T147321031A148330671. [assessment for Europe] https://www.iucnredlist.org/species / 147321031/148330671
- Katoh K, Standley DM, 2013. MAFFT: multiple sequence alignment software version 7: improvements in perfor- mance and usability. Molecular Biology and Evolution 30: 772-780.

- Kõljalg U, Nilsson RH, Abarenkov K, ett al., 2013. Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22: 5271-5277.
- Larsson A, 2014. AliView: a fast and lightweight alignment viewer and editor for large data sets. Bioinformatics 22: 3276-3278.
- Lodge DJ, Padamsee M, Matheny PB, et al., 2014. Molecular phylogeny, morphology, pigment chemistry and ecology in Hygrophoraceae (Agaricales). Fungal Diversity 64(1): 1-99.
- Moen A, 1999. National Atlas of Norway: Vegetation. Norwegian Mapping Authority, Hønefoss.
- Smith AH, Hesler LR, 1942. Studies in North American species of *Hygrophorus* II. Lloydia 5: 1-94.
- SLU ArtDatabanken 2020. Tennvaxskivling *Cuphophyllus canescens*. https://artfakta.se/ artbestamning/taxon/cuphophylluscanescens-794. Assessed December 10, 2020.
- Swofford DL, 2003. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and other methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Voitk A, Saar I, D. Lodge J, Boertmann D, Berch SM, Larsson E, 2020. New species and reports of *Cuphophyllus* from northern North America compared with related Eurasian species. Mycologia 112(2): 438-452, DOI: 10.1080/00275514.2019.1703476
- White TJ, Bruns T, Lee L, Taylor JW, 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sininski JJ, White TJ, eds. PCR protocols: a guide to methods and applications. New York: Academic Press. p. 315-322.