

Cuphophyllus monteверdae and *C. hygrocyboides* (Hygrophoraceae, Agaricales) in Norway and Sweden

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KEYWORDS

Cuphophyllus monteверdae, *C. hygrocyboides*, distribution, ecology, molecular systematics, taxonomy.

NØKKELOORD

Cuphophyllus monteверdae, setervokssopp *C. hygrocyboides* utbredelse, økologi, molekylær systematikk, taksonomi.

SAMMENDRAG

To lite kjente og relativt sjeldne vokssopparter, *Hygrocybe monteверdae* og *Cuphophyllus hygrocyboides* (norsk navn: setervokssopp) beskrives, med kommentarer til artenes utbredelse og habitatpreferanser i Norge og Sverige. *H. monteверdae* er en hvitaktig art som opprinnelig er beskrevet fra Kanariøyene, med skiver som svartner ved tørking. Den ligner engvokssopp *C. pratensis* i formen, men er hvitaktig. *C. hygrocyboides* ligner også på engvokssopp både i form og farge, men kan skilles morfologisk. *C. hygrocyboides* er funnet i kalkrike semi-naturlige enger,

særlig naturbeitemarker, og også i kalkrik fjellvegetasjon. Den er ikke funnet under mellomboreal sone, selv om den er funnet ned til havnivå i Nord-Norge. *H. monteверdae* synes å være en lavlandsart, som er funnet i semi-naturlige enger, alvar-vegetasjon, og åpen beitet skog på kalkrik grunn.

Fylogenetiske analyser viser at *H. monteверdae* tilhører slekta *Cuphophyllus*, og den nye kombinasjonen i *Cuphophyllus* foreslås her.

ABSTRACT

Two poorly known and relatively rare waxcaps *Hygrocybe monteверdae* and *Cuphophyllus hygrocyboides* are described, with notes regarding their distribution and ecological preferences in Norway and Sweden. *H. monteверdae* is a whitish species originally described from the Canary Islands, characterized by the darkening lamella upon drying. It resembles a slender *C. pratensis* in habitus but is whitish. *C. hygrocyboides* also resembles *C. pratensis* in both colour and habitus but can be separated based on morphology. *C. hygrocyboides* is found in calcareous semi-natural grasslands, especially pastures, and also in the low alpine zone and higher alpine vegetation. It is not found below the mid-boreal zone even if it has been found at sea level in the northern part of Norway. *H. monteверdae* seems to be a strict lowland species found in semi-natural grasslands, alvar vegetation, and open grazed forests on calcareous ground. Phylogenetic analysis

shows that *H. monteверdae* belongs in *Cuphophyllum*, and the new combination to *Cuphophyllum* is here proposed.

INTRODUCTION

Cuphophyllum (Donk) Bon is a genus belonging to Hygrophoraceae Lotzy, with species distributed both in the northern and southern hemispheres. Lodge et al. (2014) showed that *Cuphophyllum* occupied a relatively isolated phylogenetic position in the family. Several species in the genus have a broad distribution and 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 and these are especially found among species with a northern boreal to arctic-alpine distribution range, e. g. *C. atlanticus* (Jordal & Larsson 2021) and *C. hygrocyboides* (Voitk et al. 2020).

The species in *Cuphophyllum* are characterised 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 characteristics for separating *Cuphophyllum* from other white-spored agaric genera. Species of *Cuphophyllum* are 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).

Hygrocybe monteверdae Bañares & Arnolds was described from La Palma, Canary Islands, where it was growing on soil among leaves of *Laurus azorica*, *Persea indica*, *Ilex can-*

ariensis and *Dryopteris oligodonta* in humid "monte-verde" forest (Bañares & Arnolds 2002). In this study, we show that the generated ITS sequence data of the holotype of *H. monteверdae* is identical with ITS sequence data of collections from Norway and Sweden often labelled as *Cuphophyllum pratensis* var. *pallidus* (Berk. & Broome) Bon.

Cuphophyllum hygrocyboides (Kühner) Bon was originally described as *Camarophyllum hygrocyboides* by Kühner (1977) from environments of Pralognan-la-Vanoise in France, growing among *Salix herbacea* and *S. reticulata* in the alpine zone. In association to the work on the volume on Hygrophoraceae of Flora Agaricina Neerlandica it was combined to *Hygrocybe* by Arnolds (1987). In the study by Voitk et al. (2020) sequence data of the holotype of *H. hygrocyboides* (Kühner) Arnolds was included in the phylogenetic analyses and confirmed that the species belong in *Cuphophyllum*. Here we present further data of the species both from Norway and Sweden.

MATERIAL AND METHODS

Fresh basidiomata were photographed *in situ* and the habitat was noted and described. Detailed observations of macro-morphological characteristics were made on fresh and photographed material together with field notes. Micro-morphological characteristics were observed and measured from dried material dehydrated 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 nuc rDNA ITS1-5.8S-ITS2 (ITS barcode) and partial LSU sequence data of 24 specimens of *Cuphophyllus*, including the holotype of *H. monteверdae* were newly generated for this study. Permission to extract DNA of the holotype was granted by the staff at Herbarium TFC. Methods used for DNA extraction, PCR and sequencing of the ITS region follow Jordal and Larsson (2021). Primers used to amplify the 5' end of the LSU were LR0R and LR7, and primers used for sequencing of the region were Ctb6, LR5 and LR3R (Hopple and Vilgalys 1999). Sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Ann Arbor, Michigan). The sequences have been deposited in GenBank (ON117573-ON117594).

The ITS-LSU data set of *Cuphophyllus* for this study was compiled based on the results from previous studies of *Cuphophyllus* (Crous et al. 2021, Jordal and Larsson 2021, Lodge et al. 2014, Voitk et al. 2020). Beside the newly generated data, ITS and LSU data of 15 species in *Cuphophyllus* was included. *Hygrophorus* was selected as representatives of Hygrophoraceae and two sequences of *Lepista* were used as outgroup in the analyses. 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. One additional ITS sequences of *C. monteверdae* originating from United Kingdom was found and added to the data set.

Alignment of the data set was performed using the L-INS-i strategy implemented in MAFFT 7.017 (Kato 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 and LSU dataset consisted of 45 sequences and 2386 characters. After exclusion of ambiguous data, mainly from the beginning and the end of the data set, and from the ITS region, 2161 characters remained for the analysis. Of these, 1523 were constant, 127 were variable but parsimony uninformative, and 511 were parsimony informative. The MP analysis yielded 1825 equally most parsimonious trees (length = 1736 steps, CI = 0.5847, and RI = 0.7843). One of these trees is presented in Fig. 1. The Bootstrap analysis recovered *Hygrophorus* (100%) and *Cuphophyllus* (78%) as distinct clades within Hygrophoraceae. A BT value greater than 70% is considered strong. The sequenced collections of *Hygrocybe monteверdae*, including the ITS of the holotype, form a clade (100%) within *Cuphophyllus* and support the transfer of *H. monteверdae* to *Cuphophyllus*. It comes out as a sister clade to *C. virgineus*, *C. borealis* and *C. russocoreaceus* (97%) suggesting a close relationship with the whitish species in that group. The sequence data of *C. hygrocyboides* form a clade (99%) within *Cuphophyllus* with low intraspecific variation. Both species are well defined and delimited based on molecular methods Fig 1.

TAXONOMY

Cuphophyllus monteверdae (Bañares & Arnolds) E. Larss. **comb. nov.** – Fig 2. A-D. MycoBank MB843691

Basionym: *Hygrocybe monteверdae* Bañares & Arnolds, Persoonia 18 (1): 137. 2002.

Description based on Norwegian and Swedish collections:

Pileus 10-40(-50) mm in diameter, plano-convex with slightly incurved margin, with age becoming more plane, sometimes slightly depressed and with a lobed or irregular incurved margin, dry to weakly greasy (never slimy), matt, whitish or pale beige, at centre cream to pale ochraceous, upon drying pale ochraceous brown. Not translucently striate or hygrophanous. *Lamellae* decurrent, distant to subdistant, lamellae that reach the stipe = 30 – 40(50), interspaced with lamellulae, a few furcate, intervening, whitish, as fresh with a peach-cream tone, upon drying dark ochraceous brown, Fig 2. D. *Stipe* 30–90 × 3–10 mm, slender, cylindrical and thickest at the apex, slightly tapering and bending towards the base, whitish to pale greyish, context concolourous, upon drying pale ochraceous brown, Fig 2. D. Smell indistinct or weakly unpleasant, taste mild.

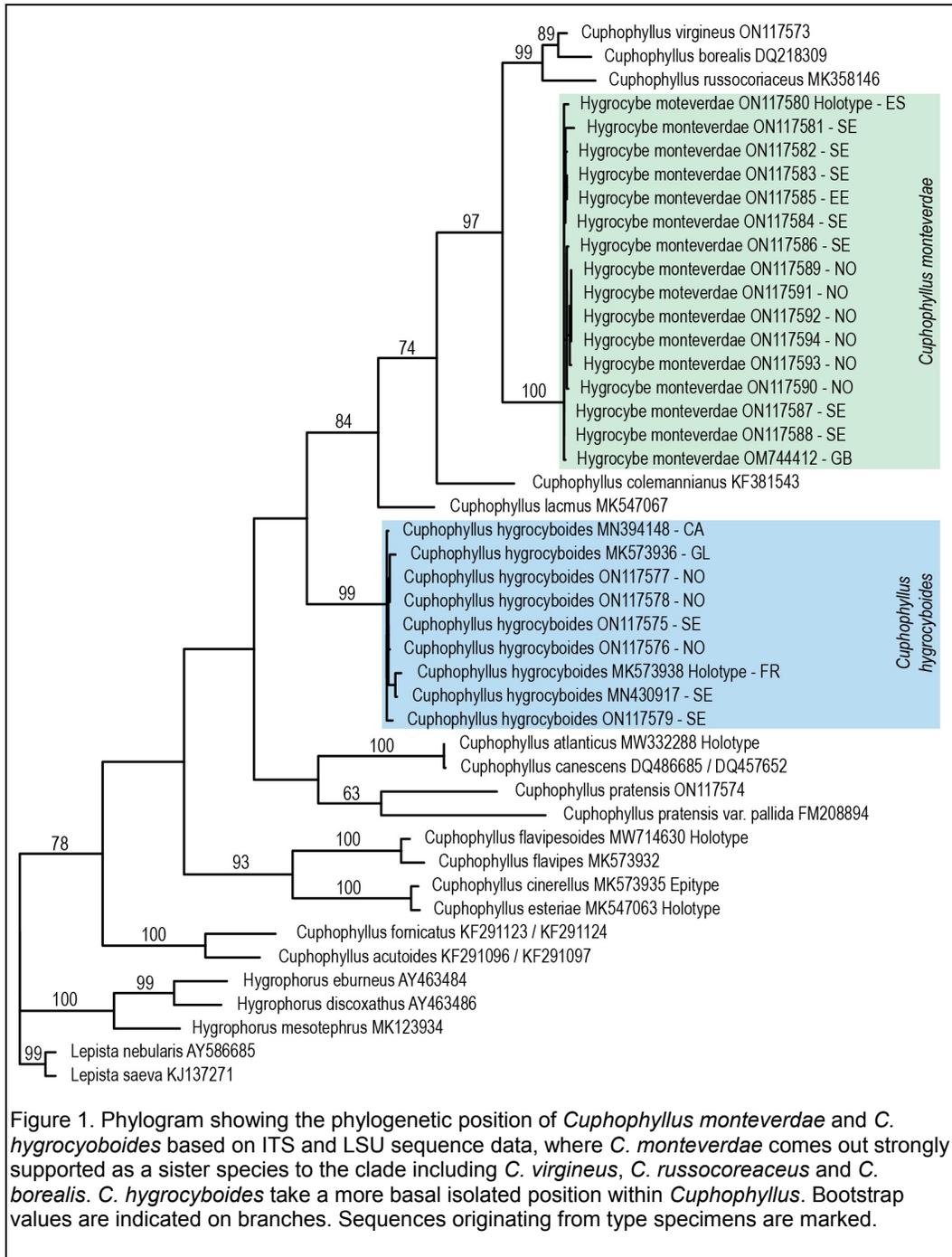
Spores [54] (6.6–)7.5–8.6(–9.8) × (4.3–)4.9–5.3(–5.9) μm, average 8.3 × 5.1 μm, Q = 1.5–1.7, variable, ellipsoid, ovoid to lacrymoid, with a distinct often bend apiculus, hyaline, white in deposit, non-amyloid. *Basidia* 40–50 × 6–8 μm, slender clavate, four-spored, two-spored observed, sterigmata 6–8 μm. *Lamellar trama* irregular interwoven, made up of cylindrical hyphae 4–8 μm wide and 30–80 μm long. *Pileipellis* is a dry cutis with radially interwoven hyphae 4–7 μm wide, 20–50 μm long, with repent to erect hyphae, and finely granular yellowish intracellular pigments observed. *Clamp* connections present in all tissue.

Ecology: The species is originally described from humid deciduous forest “monte verdae” on the Canary Islands growing among leaves. In Norway it is mainly associated with semi-natural grasslands, growing among mosses, herbs and grasses with the soil at least moderately calcareous. Most localities are situated in the boreonemoral (hemiboreal) to southern boreal vegetation zones near the coast, often on calcareous marine deposits-shell beds. In Sweden most collections originate from the calcareous islands of Öland and Gotland where it was found growing among grass and mosses in grazed open coniferous forest, grazed and manured meadows and alvar vegetations. From the mainland of Sweden, it has been found in the southern parts and on the west coast on grazed and semi-natural grasslands with long continuity and more calcareous soils.

Distribution: The species seems to have a wide distribution in the northern parts of Europe, beside Spain (Canary Islands) it is confirmed from Estonia, Norway, Sweden and United Kingdom.

Specimens studied:

ESTONIA. Saare Co., Lümanda Comm., Viidumäe Nature Reserve, in coniferous forest, 23 Sep 2010, V. Liiv, TU118043 (ITS GenBank ON117586); Saare Co., Kärla Comm., Sauvere, mixed forest, 16 Sep 2007, V. Liiv TU106101 (ITS GenBank ON117585). NORWAY. Møre og Romsdal, Herøy, Mulevika, semi-natural grassland grazed by sheep, on (calcareous) marine deposits, 23 Sep 2019, J.B. Jordal, JBJ19-058, (O) (ITS-LSU GenBank ON117589); MR, Smøla, Jøstøløy, semi-natural grassland grazed by sheep, on (calcareous) marine deposits, 9 Oct 2018, J.B. Jordal, JB18-068, (O) (ITS-LSU GenBank ON117591); Møre og Romsdal, Tingvoll, Solvang, in semi-natural grassland (grazed by cattle), 3 Oct 2011, G. Gaarder 6430, OF-242806 (ITS-LSU GenBank



ON117594); Trøndelag, Ørland, Valsøya: Brandhaugen, semi-natural grassland grazed by cattle, on (calcareous) marine deposits, 3 Oct 2019, J.B. Jordal and K. Mandal, JBJ19-080 (O) (ITS-LSU GenBank ON117590); Ørland, Tarva, Karlsøya, semi-natural grassland grazed by cattle and sheep, on (calcareous) marine deposits, 22 Sep 2020, J.B. Jordal JBJ20-18 (O); Snillfjord, Åstan, in semi-natural grassland (grazed by cattle), 14 Oct 2011, G. Gaarder 6452, OF-242828, (ITS-LSU GenBank ON117592); SPAIN. Islas Canarias, La Palma, Puente nuevo a Cuevas Calientes, 800 m.s.m. Laurisilva húmeda, 1 Feb 1991, Á. Bañares TFC Mic.6456 holotypus, (ITS GenBank ON117580); Ibidem,

10 Dec 1998, Á. Bañares TFC Mic.8295. SWEDEN. Bohuslän, Lysekil, Bro, Näverkärrs NR, open grassland, 29 Sep 1984, L. and A. Stridvall LAS84/175, GB0063836; Gotland, Sproge, Braidfloor, grazed grassland meadow, 28 Sep 2011, P. Marstad, T. Kristiansen, GB0201279 (ITS GenBank ON117584); Gotland, Vall, Rolex, grazed part of open coniferous forest, 6 Oct 2021, C. Ingvert, E. Larsson 169B-21 (GB-0207632) (ITS-LSU GenBank ON117588); Gotland, Hejnum, Suderby väst, grassland, 8 Oct 2021, E. Svensson, E. Larsson 193-21 (GB-0207633) (ITS GenBank ON117581); Småland, Nybro, Hälleberga, Högelycke naturbetesmark, 29 Sep 2014, Carlsson RGC14-

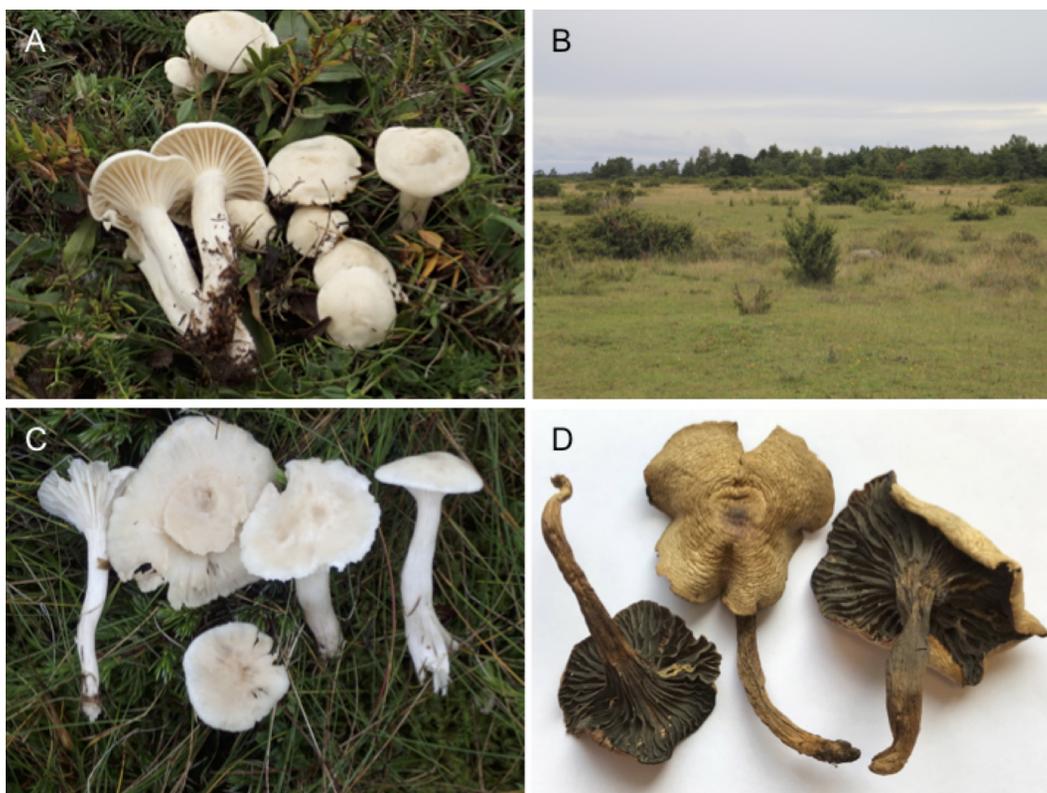


Figure 2. *Cuphophyllus monteverdae*. A: *In situ* young basidiomata Sweden, Öland, Bärby (GB-0207634). B: Habitat on alvar vegetation grazed by sheep on Öland, Bärby alvar. C: *In situ* mature basidiomata, Norway, Møre og Romsdal, Smøla (Jøstølen) (JB18-068). D: Dried basidiomata (GB-0201279). Photo by the autores.

118, GB-0234343 (ITS-LSU GenBank ON117583); Sörmland, Hölö, Tullgarns slott, grazed oak meadow, 1 Oct 2010, E. Lilliesköld GB-0201280 (ITS-LSU GenBank ON117587); Öland, Resmo, Bärby alvar, grazed alvar vegetation, 29 Sep 2021, E. Larsson 143-21 (GB-0207634) (ITS GenBank ON117582).

Comments on distribution, ecology and threats

Cuphophyllus monteverdae is a species that we rather recently have been aware of and recognize, so the actual distribution and occurrence is still a bit unclear. One aim with this paper is to recognize the species and make people aware of it and hopefully report it during coming field seasons. The darkening lamellae upon drying and the non-translucent pileus are good discriminating characters that differ it from white forms of *C. pratensis* and species in the *C. virgineus* group. It seems mainly to be associated to semi-natural grasslands, grazed and manured meadows and alvar vegetations on calcareous soils. On the calcareous islands Gotland, (Sweden) and Saaremaa (Estonia) it is also found in grazed herb rich *Picea* forests. *Cuphophyllus monteverdae* is included as DD (data deficient) in the red list of Sweden (SLU Artdatabanken 2022b) and in the Norwegian red list as VU (vulnerable) (Artdatabanken 2021). Habitats where it is found is at risk of declining, as old treatments of land use have changed. Nature conservation action by moving meadows and apply grazing by sheep and cows is needed to keep many of these localities open and suitable for the species as well as other grassland fungi.

Cuphophyllus hygrocyboides (Kühner) Bon, Doc Mycol 14(56):12. 1985. – Fig. 3A-D.

≡ *Camarophyllus hygrocyboides* Kühner (basionym), Bull Soc Mycol Fr 93(1):144. 1977.

≡ *Hygrocybe hygrocyboides* (Kühner) Arnolds, Persoonia 13:386. 1987.

The species is thoroughly described by Borgen & Boertmann (2008), who studied material from Greenland, Sweden, France, Switzerland and Italy, including the type collection. Also, by Voitek et al. (2020) that in addition included material from Canada, British Columbia. Descriptions are also provided by Kühner (1977), Candusso (1997) and Boertmann (2010).

Below we provide some additional comments base on the Norwegian and Swedish collections: The pileus of *C. hygrocyboides* is normally brightly to dark orange-brown to apricot, also with bright, golden yellow colours, while *C. pratensis* has more dull orange to brown colours without yellow or golden tinges. The pileus surface in *C. pratensis* is normally rather dry, while in *C. hygrocyboides* it is usually weakly lubricous in fresh specimens and may appear shiny in fresh specimens, like in Fig. 3A. The stipe is warm brownish or orange-brown, while in *C. pratensis* it is whitish, cream or pale buff yellow. In addition, the basidiomata of *C. hygrocyboides* are on average smaller than those in *C. pratensis*.

The photo from the alpine area in Sweden (Fig. 3C) shows a rather compact fungus with a short stipe, resembling the photo in Boertmann (2010) from alpine habitat in France. The photo from boreal grasslands in Norway, Vågå (Fig. 3A) shows a mushroom with a longer and slender stipe than in the alpine specimens, and it is more slender than it usually is in *C. pratensis*. The spores of *C. hygrocyboides* are ellipsoid to ovoid and

longer (7,5-10 μm) compared to the spores of *C. pratensis* (5,5-7,5 μm) that are more broadly ellipsoid to subglobose. The Q value is on the average 1,5-1,8 in the former and 1,2-1,5 in the latter. Differences are also found in the pileipellis that is more of a gelatinised cutis in *C. hygrocyboides* and a dry cutis in *C. pratensis* (own observations and Borgen & Boertmann 2008).

Ecology: The species was described by Kühner (1977) from the alpine zone in France growing among mosses and dwarf *Salix*. In Sweden three of the four known localities are in alpine areas associated with base rich/calcareous vegetation, in Pite, Torne and

Åsele lappmark, and one from semi-natural-grasslands. In Norway all collections are from semi-natural grasslands, among mosses, herbs and grasses, on calcareous soil, localities situated from the mid-boreal to low alpine vegetation zones.

Distribution: Sequenced material is confirmed from Canada, France, Greenland, Sweden, and here we also add Norway.

Specimens studied:

DENMARK. Greenland, Narsarsuaq, Kiattut Qaqqaat, dry grassland slope with *Alchemilla alpina*, 31 Aug 2002, T. Borgen C-F-121571



Figure 3. *Cuphophyllus hygrocyboides*. A: *In situ* basidiomata Norway, Innlandet, Vågå, Tjønnflate, calcareous semi-natural grassland in mid boreal zone. B: Habitat in Norway, Nordland, Bodø, Urdsetodden, a calcareous semi-natural grassland on marine sediments at sea level, in the mid boreal zone. C: *In situ* basidiomata Sweden, Åsele lappmark, Vilhelmina, Murfjället (GB-0207635) D: Habitat from Sweden, Pite lappmark, Arjeplog, Åkharis, calcareous low alpine vegetation zone with mosses, herbs, dwarf and *Salix* shrubs, grazed by reindeer. Photo by the autores.

(ITS-LSU GenBank MK573936). FRANCE. Savoie, Parc. Nat. de la Vanoise Région de Pralognan, Super Génepy, 14 Sep 1969, Kühner 69-319, G-00052005 holotypus (ITS GenBank MK573938). NORWAY. Oppland: Vågå, Tjønflate, calcareous pasture, 25 Aug 2012, J.B. Jordal, JB12-A3479 (O) (ITS-LSU GenBank ON117576); Oppland: Vågå, Nordigard Storrøvik, calcareous pasture near farm, 25 Aug 2012, J.B. Jordal, JB12-A3554 (O) (ITS-LSU GenBank ON117577); Nordland: Bodø, Urdsetodden in Misværøfjorden, calcareous pasture at sea shore, 10 Sep 2012, J.B. Jordal, JB12-A3754 (O) (ITS-LSU GenBank ON117578); Sør-Trøndelag: Oppdal, Kjerkbakksetra in Loslia, calcareous subalpine pasture grazed by sheep near summer farm, 30 Aug 2016, J.B. Jordal JB16-1030 (O);); *ibid.* 26 Aug 2020, J.B. Jordal (30 fruitbodies). SWEDEN. Pite lappmark, Arjeplog, Ákharis, among mosses and herbs in the alpine zone, 14 Aug 2018, J.B. Jordal & E. Larsson 141-18 (GB-0207636) (ITS GenBank ON117579); Torne lappmark, Jukkasjärvi, Abisko, Latnja, among herbs and mosses in alpine meadow vegetation on calcareous ground, 22 Aug 2013, E. Larsson 177-13, GB-0156992 (ITS-LSU GenBank MK573937); Lule lappmark, Jokkmokk, Állojaur, manage lawn outside Bokenskolan, 7 Sep 2004, M. Karström 2004-08 (ITS GenBank MK573937); Åsele lappmark, Vilhelmina, Murfjället, alpine meadow among mosses and herbs as *Thalictrum* and *Bistorta*, 20 Aug 2019, J.B. Jordal & E. Larsson 40-19 (GB-0207635).

Comments on distribution, ecology and threats

The distribution known so far in Europe indicate a mid/northern boreal to alpine/subarctic species (vegetation zones refer to Moen 1999). The Norwegian localities are lying from 2 - 926 m a.s.l., the Swedish from 280 - 950 m a.s.l. The locality in Greenland is 150 m a.s.l. (ancient dry grassland slope, subarctic and

subcontinental climate, Borgen & Boertmann 2008). In Central Europe the sites are described as follows: French Alps (Vanoise, type locality) 2400 m and Swiss Alps (Grisons) 2400 m (“avec *Salix herbacea* ou *Salix reticulata*”, Kühner 1977), French Pyrénées 2300-2350 m (“*Arabidion caeruleae*”, Corriol 2008), Italian Alps 2102 m (alpine pasture with *Alnus viridis*, Candusso 1997), corresponding more or less to the Fennoscandian low alpine zone. Further, the known localities are lying in weakly oceanic to rather continental regions. All known localities, including the sea shore in Bodø, Northern Norway, seem to have a stable/long-lasting snow cover during the winter. This could eventually explain why the species is not reported from well-studied countries like Denmark, the Netherlands and UK. The habitats reported from Europe include both meadows/semi-natural grasslands and alpine vegetation like snowbeds and rich heath with herbs and grasses. Where information is available, the soil is mostly calcareous/basophilous. This includes all localities in Norway and Sweden, also the localities reported by Kühner (1977) including the type locality (*Salix reticulata* is a species of calcareous soil), and by Corriol 2008 the locality in the French Pyrénées (“*Arabidion caeruleae*” is a basophilous subtype of *Salix herbacea* snowbeds. There are reasons to believe that the species is a rare. In Sweden four localities are known, three of them in the alpine zone and one from a managed lawn in the northern boreal zone. In Norway also four localities are known, all in semi-natural grasslands in mid-to northern boreal zone.

Cuphophyllus hygroclyboides is included as VU (vulnerable) in the red list of Sweden (SLU Artdatabanken 2022a), as EN (strongly threatened) in the red list of Norway (Artsdatabanken 2021), and as VU (vulnerable) in a regional red list of the Midi-Pyrénées (Corriol 2014). In Fennoscandia we do not

know how large part of the population that is living in semi-natural grasslands compared to alpine habitats. Semi-natural grasslands in boreal regions have been strongly declining over the last 100 years, and are still declining. Therefore, it seems reasonable to assume that at least the populations in mid- and northern boreal grasslands are declining and at threat. Measures to maintain boreal semi-natural grasslands will therefore be important both to *C. hygrocyboides* and other grassland fungi. Alpine meadows, heaths and snowbeds may be threatened by climatic change, causing the snow to melt earlier and many snow-beds to dry out and change to other vegetation types. We see already how the tree-line is climbing upwards, even if areas with large population of grazing reindeers are less affected, there is an increased cover of bushes with *Salix* spp., *Betula nana* and *Betula pubescens*, where it some decades ago were open alpine heath and meadow areas.

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