

The secrets of *Cryptomyces maximus* (Rhytismataceae). Ecology and distribution in the Nordic countries (Norden), and a morphological and ontogenetic update

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GRANMO, A., RÄMÄ, T. & MATHIASSEN, G. 2012: The secrets of *Cryptomyces maximus* (Rhytismataceae). Ecology and distribution in the Nordic countries (Norden), and a morphological and ontogenetic update. – *Karstenia* 52:59–72. HELSINKI. ISSN 0453-3402.

The anatomy and ontogeny of the rare *Cryptomyces maximus* have previously been insufficiently known and poorly communicated. It is here described and illustrated in detail based on recently collected material from Norway in different states of development. The connection between the sexual and anamorph stage is verified by molecular data. The parasitism and its role as a pathogen is treated and discussed, as well as its common types of habitat based on our observations in North Norway. Its distribution in Norden is mapped. Finds of this colourful and large ascomycete in this area are curiously few and occasional, and many of those date a century or so back in time. The species also appears to be rare on a global scale. We think the reason for the scattered records both in time and space has been lack of knowledge of its ecology and how it appears in nature.

Key words: *Cryptomyces maximus*, distribution, ecology, morphology, Nordic countries, Norden, ontogeny, Rhytismataceae

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Introduction

For several years we have been looking for *Cryptomyces maximus* (Fr.: Fr.) Rehm in Norway without success. When we observed it for the first time in the field in 2008, after more than 80 years of anonymity in this country, it was hard to understand why nobody else had discovered such a brilliant and large species during all this time. As additional sites were discovered later on, we came to the conclusion that this was due to lack of a) ecological knowledge, and b) good illustrations or photos in modern literature, or

on the web until 2008 (Harries 2008). We were strengthened in these assumptions when we found that none of the Nordic countries except for Sweden, had any recent record of the species. The small number of occurrences and lack of records during past decades in most of Norden struck us. Before the recent record from Sweden in 2009, the previous record from that country was in 1930. In Denmark and Finland it has not been found since 1912 and 1913, respectively. The only record from Iceland is from 1971. This should indicate that we were dealing with a quite rare fungus.

The very first to illustrate and describe the outward appearance of *Cryptomyces maximus* was James Sowerby, as *Sphaeria aurea* Sowerby, based on specimens collected near Cambridge in England during 1801 (Sowerby 1803: Pl. 356, and text). His drawing clearly shows the essentials of the species, both the astonishing colours, its growth habit, and the white interior contrasting the black surface.

Though there exist some outlines of the morphology of *Cryptomyces maximus*, only a few give details of its development or internal stroma morphology. And as for the latter, the descriptions may be hard to understand, or are inaccurate and rather ambiguous. The best depictions have been those of Tulasne & C. Tulasne (1865) and Arx & Müller (1954). We will herein provide a detailed description with figures of stroma anatomy and ontogeny, and treat the ecology and distribution of the species in Norden. Thus we hope to contribute to a better understanding of this cryptic fungus, and encourage a further search for it.

Material and methods

Material for this study was afforded us from the herbaria C, H, LD, O, S, TROM, and UPS. Information from other public Nordic herbaria told us there were no further vouchers, or only duplicates of material from those mentioned. In addition to the Nordic material we have studied a few vouchers from Central Europe. Names and delimitation of the Nordic biogeographical provinces are according to Knudsen & Vesterholt (2008).

DNA was extracted from fresh herbarium samples using a cetyltrimethyl ammonium bromide (CTAB) extraction protocol (Murray & Thompson 1980) with some modifications described in detail in Mysterud et al. (2007). PCR amplification was targeted to amplify the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, using the primer pair ITS5/ITS4 (White et al. 1990) and Illustra PuReTaq Ready-To-Go PCR beads (GE Healthcare, Buckinghamshire, UK). The PCR was performed on a PTC-0200 DNA engine (MJ Research, Waltham, Massachusetts, USA), and PCR products were cleaned using 10x diluted ExoSAP-IT (Affymetrix, Santa Clara, CA, USA). Sequencing reactions were performed on a Applied Biosystems 3730 DNA analyzer in BigDye Terminator sequencing buffer using PCR primers as sequencing primers and BigDye Cycle Sequencing kit v3.1 (Applied Biosystems, Foster City, California, USA).

Sequenced forward and reverse amplicons were assembled automatically using Geneious (Drummond et al. 2012) and manually edited. Consensus sequences were

extracted and compared by generating Geneious alignment with default settings.

Despite *Cryptomyces maximus* having a fruit body traditionally included in the discomycetous type of ascoma, its morphology in many ways reminds one more of a diatrypeaceous or xylariaceous fungus (e.g. *Diatrype*; *Biscogniauxia*). Thus we have chosen to use the terms ecto- and entostroma (as in stromatic pyrenomycetes) rather than ectal- and ental excipulum as used in the discomycetes.

Results

Stroma – development and morphology

Cryptomyces maximus appears in branches or smooth and thin stems of living willows (*Salix* spp.) as irregular dark or black swellings in the host periderm. Hence the British vernacular name Willow Blister. Those are the stromata, proliferating along the length of the stem or branch. The black parts are surrounded by a more or less continuous orange or yellow zone, resembling a halo (Fig. 1b-d). The stromata are slightly convex, being thickest in the middle and gradually thinner towards the edges. They develop individually, or may grow close to each other and coalesce, forming oval patches of infections, attaining a length from less than a centimetre up to about 20 cm, and a width of 0.4–5 cm according to the diameter of the affected part of the host. They rarely completely circumscribe the branch or stem. Still immature stromata, are covered by the unruptured host periderm. On maturing the stroma pushes the periderm apart, which splits off irregularly and rolls back, taking with it some of the dark brown stroma surface. This peeling off starts in the thickest, most mature part of the stroma.

The stroma develops in the upper part of the cortex. It is stratified in several different layers distinguishable only with a light microscope. However, with the naked eye or a hand lens three main layers may be differentiated: an upper dark brown stratum freed from the periderm followed by a thin, pale brown zone, which is the upper part of the hymenium, sitting upon a thick (ca 0.5 mm) white entostroma. Below the entostroma is the brown or greyish brown cortex intruded by hyphae and dark brown fungus deposits.

A thin cross section, perpendicular to the long axis of the branch, of dry, almost fully mature stroma with the thin periderm (ca 30 µm) still attached, unveils a quite complex structure, con-



Fig. 1. *Cryptomyces maximus*. a = habitat of the species in Tromsø, Kroken 21.IX.2011. b= mature stroma; Tromsø, Gamvika 13.VII.2008. c = mature stroma; Evenes, Kvanndalen 26.VIII.2011 (= later coll. Granmo 65/11). d = overmature stroma (Granmo16/08). Photos: a Rämä; b-d Granmo.

sisting of many different layers and types of tissue (Fig. 2). Starting from the very outside or top, their sequence, texture and thickness (in parentheses) are as follows:

(a) the thin, glassy (hyaline) cuticle of the periderm (5–10 µm); (b) an upper layer of three to four rows of periderm cells (15–20 µm), of which one or two rows are filled with an orange substance (the colour in Fig. 2 is distorted). Just below these coloured cells the upmost part of the dark brown ectostroma begins with (c) a zig-zag line of dense, dark stroma substance (2.5–5 µm), followed by a (d) *textura angularis* (ca 40 µm), incrustated with dark brown substance; (e) a palisade of septate cells, each ca 2.5 µm wide and with rather thick walls, similar to a *textura porrecta* (35–60 µm). The tissue below this palisade of cells is very dark, consisting of an upper part with discernible cells of *textura angularis-globulosa* (80–90 µm). At the base of this tissue the cell type becomes indiscernible and much incrustated due to numerous dark brown granules. This incrustated stratum appears to be the main part of the later epithecium.

When the lobes of the periderm roll back on maturing, the ectostroma seems to rupture in the lower half of (f1+f2), leaving just a thin part of it as layer (f2), while the rest crumbles away or adheres to the backward bent periderm. The hymenium is covered by an epithecium (f2) 25–70 µm. Its surface is dull and granular due to dark brown particles (3–12 µm in diam). The hymenium (g) 220–300 µm, is pale brown, more brownish in its upper part, becoming nearly hyaline downwards. Besides asci, whose apices may be at different heights in the hymenium owing to successive maturing, there are interascal threads in abundance, attached at the base while their upper parts are wound in the epithecium. The white entostroma (h) below the hymenium occupies the largest part of space between the periderm and cortex, and varies in thickness between 350–600 µm when dry, or 450–750 µm after being soaked in water. The subhymenial part of it is a small-celled *textura angularis-globulosa*, beneath which is a massive *textura intricata* made up of 2.5–4.5 µm wide, septate, sometimes branched, thin-walled hyphae. Towards the middle of the entostroma the tissue has several swollen cells (10–15 µm in diam), and becomes intermingled with large-celled *textura angularis* (15–20 µm in diam). In the middle of the entostroma the tissue

is more loose, with intercellular spaces. Towards its base the tissue type again changes to *textura angularis-globulosa* with both small and larger cells. The hyphae have scattered swellings, and are running mainly in the direction of the cortex. Entostroma without hymenium also propagates below the orange or yellow parts of the periderm.

Both at the base and sides of the entostroma, where the periderm still persists, broad hyphae with swellings can be seen penetrating the periderm cells and cortical cells. We suppose these hyphae are nourishing hyphae exploiting the host's nutrients. In the cortex both hyphae and host cells are orange or reddish brown. The entostroma has its base on the greyish brown cortex. In old stromata the white entostroma also dries up and withers off, leaving remnants of it and the dark epithecium particularly at the edges of the former stroma, now surrounded only with desiccated flaps of periderm.

In any willow invaded by the fungus the whole area influenced has a periderm with orange or yellow orange cell rows. However, in places where the dark stromata are developing, the orange colour is completely masked by the more or less black, underlying stroma colour (Fig. 1c).

Details of the hymenium

The asci (Fig. 3c) are cylindric-clavate, 207–285 × 19–28 µm, with a sporal part of (147–)165–200(–232) µm, while the stipe-like part is 30–85 µm. The rest of the ascus is filled with hyaline sap, becoming orange in Lugol's reagent. No blue or red reaction is seen in the ascus apex, neither with Lugol's nor with Melzer's reagent, either with or without KOH pretreatment. The eight ascospores are uniseriate or obliquely uniseriate, or biseriata in the upper half of the ascus.

Ascospores (without the slimy perispore) are 28–39.5 × (12–)13.5–19.5 µm, mean 34.5 × 15.8 µm, hyaline, ellipsoid to ovoid, with a 2–2.5 µm thick hyaline perispore (Fig. 3c-d). The perispore is always more pronounced and durable at the spore ends than at the sides, and hardly noticeable on the sides of mature spores (Fig. 3d). In water the pale yellowish grey spore content appears grainy. In Lugol's reagent the content becomes brownish orange, the spore wall darkens and attains a hardly visible tinge of blue. Pro-

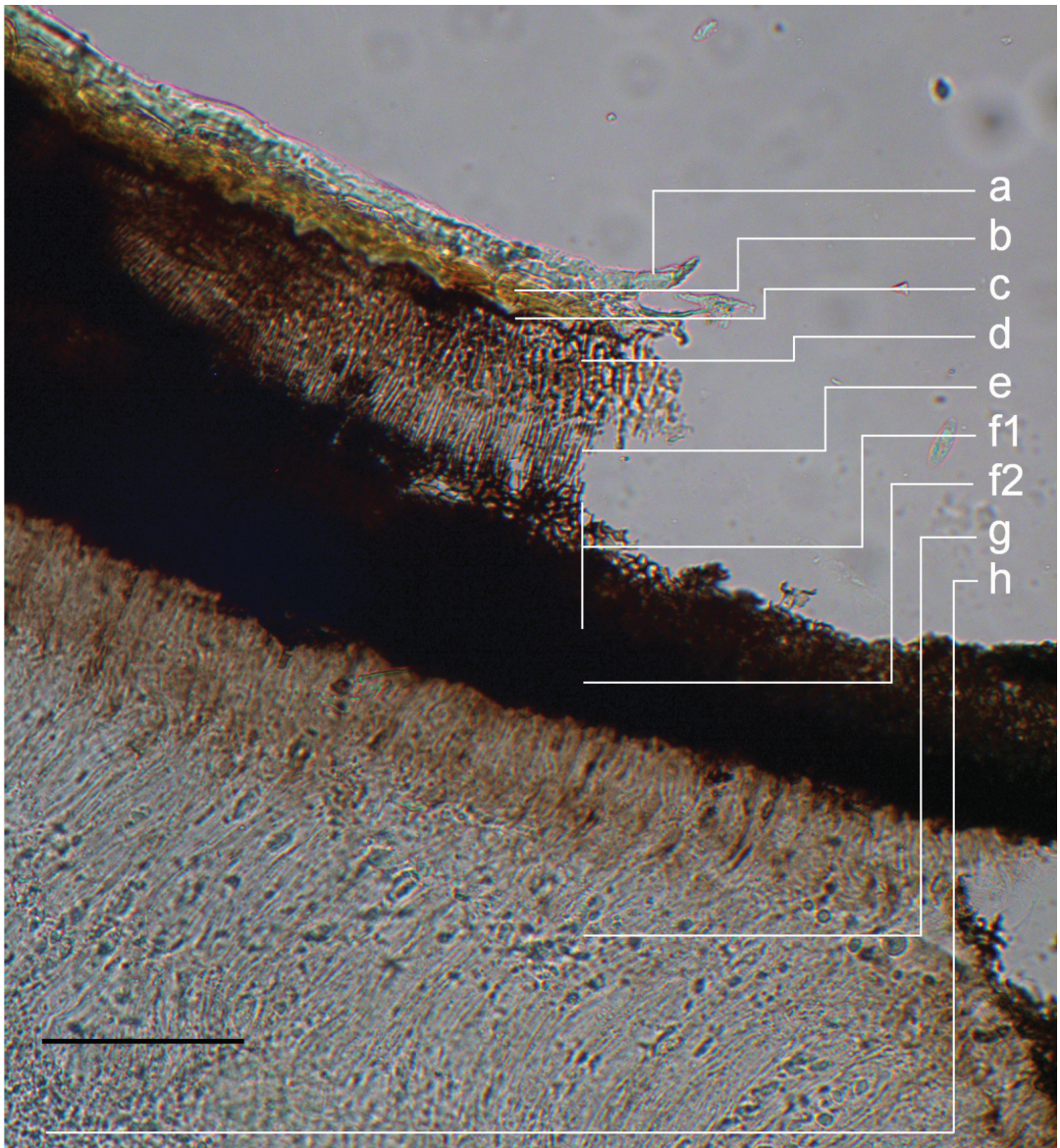


Fig. 2. *Cryptomyces maximus*. Transverse section of an almost mature stroma Granmo 4/08. a = cuticle of periderm, b = coloured periderm cells. c-f2 = ectostroma, c = zig-zag line of dark stroma material, d = incrusted tissue of *textura angularis*, e = palisade of *textura porrecta*, f1 = *textura angularis-globulosa* with thick walls, f2 =heavily incrusted epithecium, g = hymenium (with brownish upper part), h = white entostroma. Scale = 100 µm. Photo: Granmo.

longed treatment (30 minutes) in 10 % KOH generates 2-4 evaginations of the perispore.

Interascal threads seem to occur in bunches in between the asci. These are 2–3 µm wide, septate, profusely branched, widened to 5 µm at the ends, and often strongly wavy, winding

themselves in between the brown matter of the epithecium (Fig. 3b, 4a). In addition there appear to be free paraphyses whose apices push up into the epithecium. They are simple and filamentous, 1.5–2 µm broad, with at least one septum and a clavate apex ca 5 µm wide (Fig. 4b).

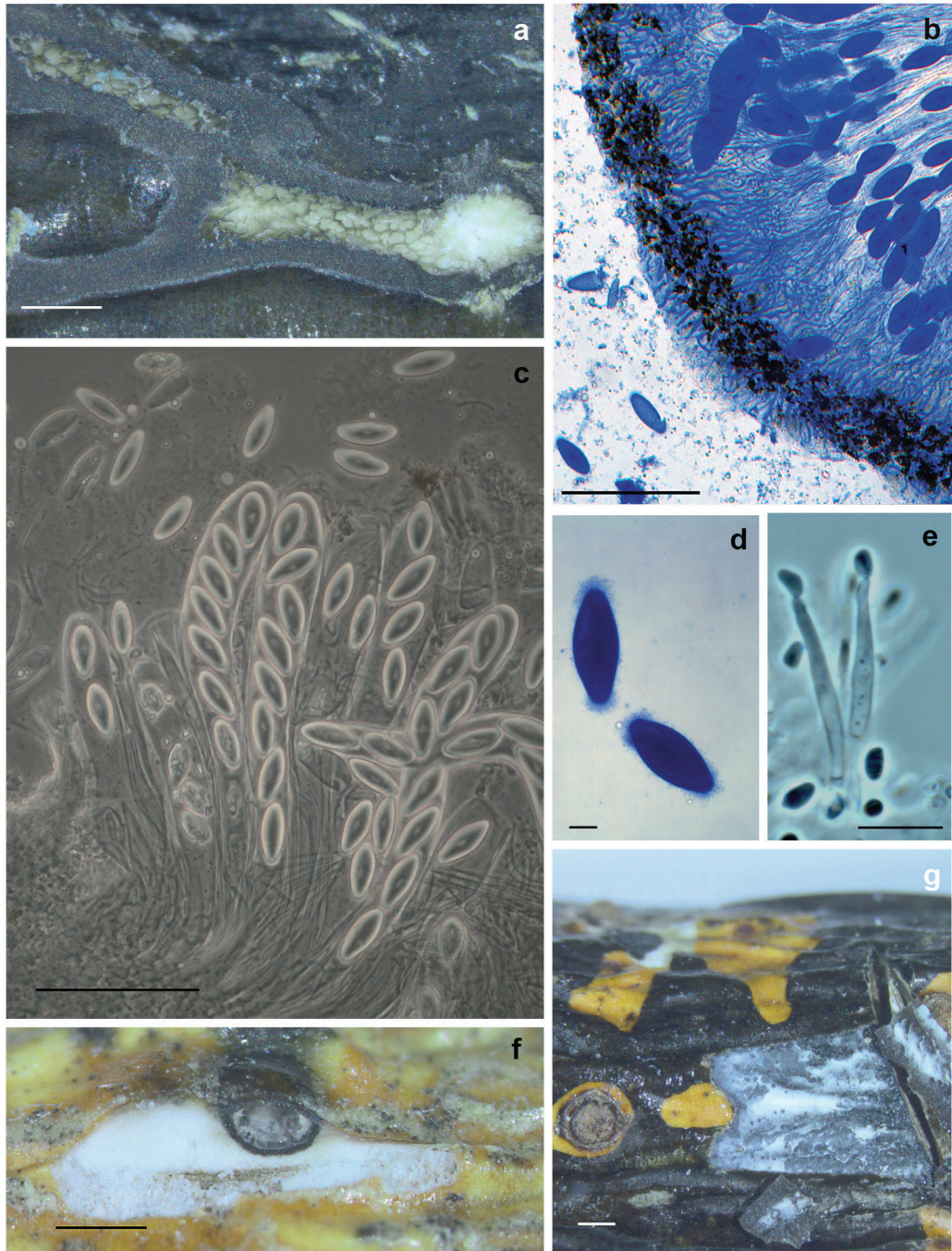


Fig. 3. *Cryptomyces maximus*. a = angular loculi in the dry hymenium freed from ectostroma (Granmo 18/08), b = transverse section of epithecium, and hymenium with numerous interscal threads (Granmo 4/08, in lactic acid cotton blue), c = asci and spores (Granmo 4/08, phase contrast), d = two spores showing slimy perispore (Granmo 4/08, in lactic acid cotton blue), e = anamorph with conidia and two conidiohores, f = cavity/acervulus of anamorph in upper part of entostroma (Granmo 9/08), g = yellowish conidial mass in acervulus beneath removed part of periderm (Granmo 4/08). Scale = 500 µm, except b, c = 100 µm, d, e = 10 µm. Photos: a, f, g Mathiassen; b-e Granmo and Rämä.

When studying the hymenial layer from above in a dry immature stroma totally freed from ectostroma including epithecium, an interesting feature is observed. At this stage the development of asci has been halted and the hymenium has mainly dried up, leaving only thin tissue remnants, standing curtain-like, bounding angular cavities much like a honeycomb between ento- and ectostroma (Fig. 3a). The curtains or walls consist of palisades of perpendicular hyphae reminiscent of the interascal threads, 2–3.5 μm wide. They have a few septa, and may be somewhat dilated in the upper half. This indicates that hymenial tissue which exist from an early stage is compressed or dissolved on ascal development, thus giving space for bundles of asci in pocket-like locules.

Anamorph stage

Below the blackened, wrinkled parts of the periderm, where no further stroma has ve developed, there are numerous cavities or acervuli. The bottom of empty acervuli is white or bluish white. But very often they are filled with a yellowish grey mass of conidia (Fig. 3g). The conidia are produced from a palisade of short, simple, erect conidiophores (Fig. 3e). The conidia seem to be forced out and reach the surface of the periderm, either through the lenticels or other small fissures. In early summer innumerable conidia and a shiny viscous mucus may cover the whole periderm above and around the stromata. At this stage the stromata may have a distinct sweet honey-like odour.

Conidia can also be formed in cavities in the entostroma beneath small black patches occurring in the yellow or orange zone. These cavities are reminiscent of pycnidia, about equally high and broad (300–500 μm), but may be long and pipe-like (Fig. 3f). They are situated in the upmost part of entostroma in immature stroma lacking hymenium. The roof of these closed cavities is the blackened periderm, while the sides and bottom are demarcated by a zone (25–40 μm thick) of brown cells of the same texture as the surrounding entostroma. The cavities probably have some kind of opening to the outside, but we have not seen any. The conidia are formed in the same way as in the acervuli previously described.

The conidiophores are about $35 \times 3 \mu\text{m}$, hyaline, smooth, with 1–2 septa. The conidiogenous cell is a phialide, 15–20 μm long, 2.5 μm wide at base, tapering to less than 1 μm at the conidiogenous locus, where a blastic conidium arises (Fig. 3e). The liberated conidia are hyaline (yellowish in mass), ovoid or ellipsoid, (3.5–)4–5(–6) \times 2–2.5(–3) μm , and adhering to each other.

Through time different types of conidial fungi have been reported connected with *Cryptomyces maximus* (see below). Further, some other fungi with their anamorphs (e.g. *Godronia fuliginosa* (Pers.: Fr) Seaver, *Nectria* sp.) are apparently often associated with the species. Because of this an analysis of nuclear DNA was performed on the sexual and asexual morphs reported herein. DNA sequences of the fungal barcode region ITS (Schoch et al. 2012) were only 2 (of 450) base pairs different between the morphs (on two individual samples), thus confirming them to be the same organism (GenBank Acc. Nos. JX014412 and JX014413).

Distribution and ecology

The present distribution of *Cryptomyces maximus* in Norden is shown on the map (Fig. 5).

Young, still quite smooth stems and smooth branches both on young and older trees seem to be the more susceptible parts for this pathogen. Judging from the date of collected vouchers, and from our own observations, the species may be found all year round. At least in North Norway the fungus seems to need at least two summer seasons to mature. It is most easily discovered in the early summer, when the stromata are in their most colourful stage. Towards the autumn the yellow or orange colours fade somewhat, and the black parts of the stromata occupy more space at the expense of the more coloured ones. We have observed the species at a height of 0.5 to 3 m on standing, living trees. The diameter of the infected host parts may be from 4 cm down to 2 mm.

As already mentioned the cells in the greyish brown cortex below the entostroma are invaded by hyphae. In scars where withered off stromata previously have been growing, the cortex is left unprotected. The cortical cells close to the wood are dark brown and completely infiltrated with thick hyphae, sometimes creating a dense cylin-

der around the wood. At this time we normally can observe clear signs of wilting of the branch or stem above the scar (cp. also Rostrup 1902). With time the cortex may also wither off, leaving the bare wood without any sign of the causal pathogen. In such places the wood is dried out and of a less diameter than in the fresh part of the stem. Some trees apparently may recover from the first infections, leaving only a scar or depression circumscribing the naked cortex without periderm. Hence another British vernacular name for the fungus, Twig Girdling.

Several different species and hybrids of *Salix* act as hosts for the pathogen. In Norden *S. myrsinifolia*, *S. phylicifolia*, and *S. × smithiana* (*S. lanceolata*) seem to be the most common hosts. Occasionally also smaller species of *Salix* may be invaded, such as *S. repens* (Denmark) and *S. arbuscula* (Sweden). Outside Norden, several other species of *Salix* act as hosts (Farr & Rossman 2011).

Aside from the obligatory connection to *Salix*, the habitat seems to play a great role in deciding where *Cryptomyces maximus* is likely to be found. Humid localities are clearly preferred (Fig. 1a). According to our observations in North Norway, bushes of *Salix* close to water, such as rivers, brooks and wet ditches are the best places to search for the fungus (Granmo 2011). The edges of wet mires are also promising sites. However, willows that have been browsed by the European elk (*Alces alces*) in the winter rarely house *C. maximus*, regardless of site. The cause for this can be both the drying out of the injured bushes and a reduced production of assimilatory products, on which the fungus may depend to develop.

Discussion

Stroma

The best previous descriptions of *Cryptomyces maximus* (or *Rhytisma maximum* Fr.: Fr.) have been provided by Tulasne & C. Tulasne (1865), Höhnel (1917), and Arx & Müller (1954). These authors have recognized the uppermost, thick dark layer connected with the periderm, according to von Höhnel even more than 200 µm in thickness, and the white interior, i.e. the entostroma. Some details are provided about these

layers, for example by Arx & Müller, but are not easy to interpret. Rostrup (1902) noticed that the interior white stroma swells in humid weather and becomes jelly-like.

Nannfeldt (1932) based his analysis of *Cryptomyces maximus* on an immature specimen from Vestergren's exsiccate nr. 530 (wrongly as nr. 540). His description of the stomatal layers and presumed asci is hard to understand (Nannfeldt 1932). Most probably the hyaline "Pallisadenschicht" he refers to is the still immature hymenium developing in the uppermost part of the entostroma. He claims to have seen ascogoneous hyphae and ascus initials a little above the base of these hyphae. About the dark covering layer (Fig. 2c-f), mentioned by the Tulasnes (1865) and Höhnel (1917), he stated he "...konnte nicht einmal irgendwelche Spuren einer derartigen Decke beobachten." Nevertheless Nannfeldt has drawn (Fig. 30a) a thin dark covering upon the palisade layer.

Anamorph

The Tulasne brothers (1865, as *Rhytisma maximum*) described and drew very beautifully a conidial stage connected with *Cryptomyces maximus*. They stated that these "spermatia or microstylospores are generated in enormous quantities on the top of the crust under the somewhat loosened epidermis." Their figures (Tab. 16, Fig. 11-12) of conidiogenous cells and conidia, measuring $5 \times 3 \mu\text{m}$, are fully in accordance with our observations. The same can be said about their observation that the "... spermatia or microstylospores [=conidia] are expelled through fissures or inconspicuous pores in the cuticle in the shape of viscous liquid or violaceous glue; and smear the matrix as if with shining tears". We have not seen, however, that some asci "...project beyond the surface of the hymenium, standing out for a great distance, and looking like 'hyaline papillae'. This peculiar feature may probably be seen by continual observations of the living fungus in situ.

Vleugel (1908) also observed sterile stromata of *Cryptomyces maximus* from Sweden with ovoid one-celled conidia, similar to those we have observed. Höhnel (1925) named the conidial stage *Cryptomycella maxima* Höhn., based solely on the description and figures of the Tulasnes. Un-

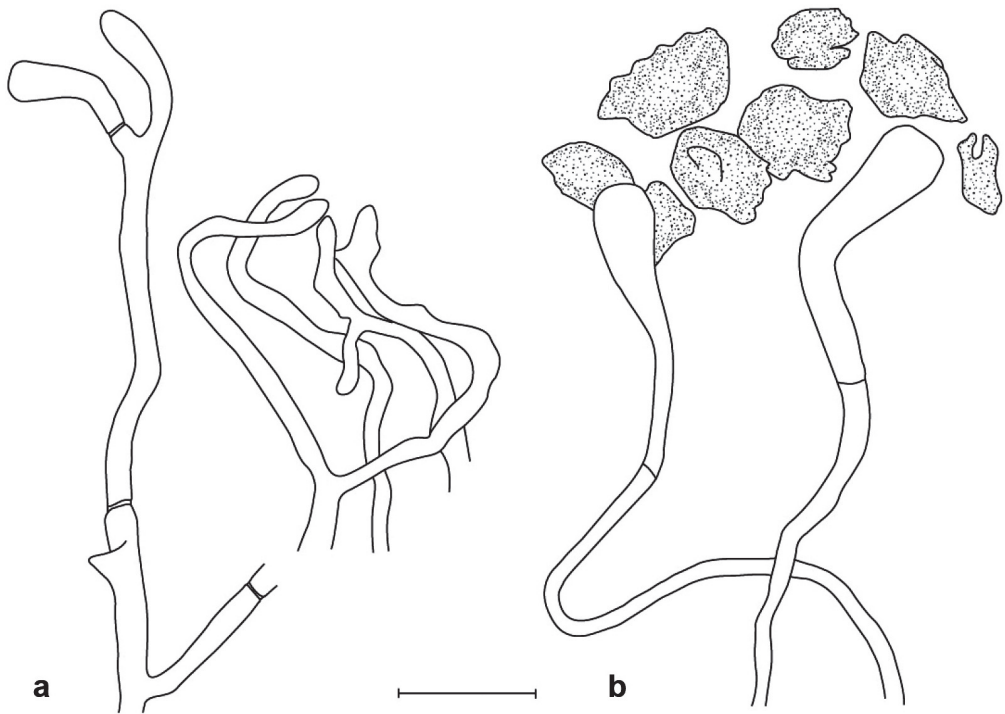


Fig. 4. *Cryptomyces maximus*. a = interascal threads, b = paraphyses covered by epithelial incrustations (Granmo 24/08). Scale = 10 μ m. Drawing: Granmo & Mathiassen.

fortunately his type of the genus *Cryptomycella* Höhn., *C. pteridis* (Kalchbr.) Höhn., was said to be the conidial stage of *Cryptomyces pteridis* (Rebent.) Rehm, a quite different fungus now known as *Cryptomycina pteridis* (Rebent.: Fr.) Höhn., which makes the combination *Cryptomycella maxima* doubtful and possibly untenable.

Rostrup (1902) said the surface of the stroma in parts becomes rough due to pycnidia with "aflange Knopceller" (i.e. oblong conidia), 15–20 μ m long and 6 μ m broad. We will not speculate if this observation might represent a synanamorph of *Cryptomyces maximus*. He had earlier (Rostrup 1899) described a pycnidial fungus which produced hyaline, fusiform, 4-celled, sometimes slightly curved conidia, and named this presumed anamorph *Pilidium fuliginosum* (Fr.: Fr.) Auersw. It was repeated as the anamorph of *C. maximus* by Lind (1913). This latter pycnidial fungus is most likely the anamorph of *Godronia fuliginosa* (Fr.: Fr.) Seaver, i.e. *Topospora fuliginosa* (Pers.) M. Morelet, sometimes seen associ-

ated with *Cryptomyces*. *Pilidium fuliginosum* is in fact a synonym of *Cenangium fuliginosum* Fr.: Fr., both of which now considered as synonyms of the valid name *Godronia fuliginosa* according to Eriksson (2009).

Some authors have placed *Cryptomyces* in a family of its own, Cryptomycetaceae (Arx & Müller 1954, Eriksson 2009). However, Minter (1994) stated that the anamorphs of Cryptomycetaceae and Rhytismataceae are similar, "... so it is clear that the two families are very close." This has been confirmed for two species in these families in a phylogenetic study by Lantz et al. (2011). They showed *C. maximus* to be a sister species of *Rhytisma andromedae* in a larger core group of Rhytismatales.

We cannot know for certain if the rich amount of fragrant, limpid mucus on the affected branches at a certain state is produced by the fungus only, or also (or mostly) by the host as a result of the fungus infestation. However it may be, the scent of the mucus can be an enticement for in-

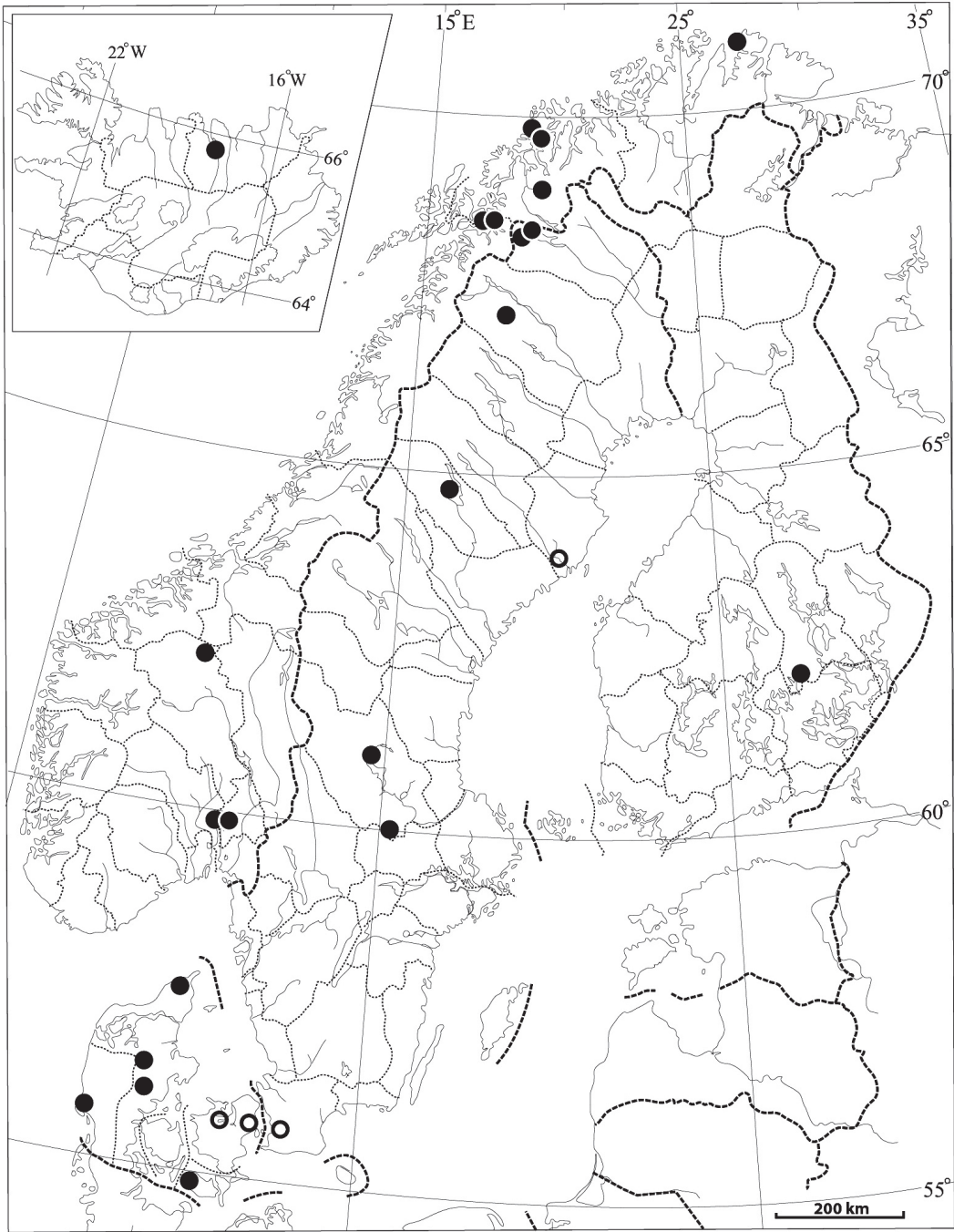


Fig. 5. *Cryptomyces maximus*. Nordic distribution until April 2012. ● = localities with studied specimens, ○ = literature records. Map: E. Høgtun ©, Tromsø University Museum, 2010.

Ernst Høgtun, Tromsø Museum - Universitetsmuseet 06.5.2001.bot

sects and thus help to disperse the conidia. One doesn't know if the conidia act as diaspores or as spermatia only.

Distribution

The known distribution of *Cryptomyces maximus* in Norden (Fig. 5) is the result of a small number of observations made by few mycologists during almost 200 years, and thus is unlikely to represent the actual distribution pattern of the fungus. For example large geographical areas of North Finland and Central Norway are without records. However, suitable hosts and habitats are present (see below), so the lack of records could simply be explained by the lack of mycological activity targeting to detect species like *C. maximus*.

The literary records of the species from Norden are scanty and quite old. The very first records (as *Rhytisma maximum*) are from Sweden (without location) by Fries (1823). In his exsiccate 'Scleromyceti suecia' he assigned it number 250. Later he mentioned the species from Skåne (Fries 1849: 371; cp. Notes to *Specimens studied*). Vleugel (1908) found immature stromata of *Cryptomyces maximus* in the vicinity of Umeå in August 1906, but his voucher could not be traced. Lind recorded the fungus on *Salix arbuscula* at Abisko in 1930 (Lind 1934), where Vestergren had found it in 1903. Eriksson (2009) provided key information about the species in Sweden. In 2009 the species was discovered in Åsele Lappmark (Artportalen 2012), about 80 years after previously found.

In Denmark, Rostrup, as a professional in plant pathology, observed and collected the fungus in the course of several years. His first herbarium voucher dates from 1874. He dealt with the species at least twice, once about an occurrence in Lolland (Rostrup 1899), the second in a textbook on plant pathogens (Rostrup 1902). Lind (1913) summarized most of the Danish localities known until then. The latest observation of the species was on a botanical excursion in Sjælland in 1912 (Lind 1913). For a century no further material has been collected in Denmark. The species is not known from The Faroe Islands.

The Norwegian records from 1825 (Oslo) and 1841 (Dovre) were reported by Rostrup (1904), and those from Målselv in 1926 by Jørstad (1928). After that the species was not observed

until 2008 (Granmo 2008). Four of the five recently discovered localities, all in North Norway, as well as the older ones, were treated by Granmo (2011).

In Iceland a voucher by G. Guðmundsson from Kollafjarðarnes (Northwest Iceland), 1897, was reported by Rostrup (1903), and referred to in the list of Hallgrímsson & Eyjólfsson (2004). The material (C), has been studied. It is hardly *Cryptomyces maximus*. The shining black stroma has several loculi with immature, small asci and most likely represents a pyrenomycete. The first and only reliable Icelandic record to date is that by Lundqvist in 1977.

In Finland there are four collections of *Cryptomyces maximus*, all from the same location, dating back to 1913. They have been distributed to four different herbaria (see below).

From other European countries the species is so far known from the Czech Republic (Rehm 1896), France (Tulasne & C. Tulasne 1865), Germany (Rehm 1896, Butin 1960, Farr & Rossman 2011), Portugal (Saccardo 1889, Farr & Rossman 2011), Ukraine (Farr & Rossman 2011), and the United Kingdom: England (Sowerby 1803, Dennis 1981), Wales (Harries 2008, 2009, 2010; Lantz et al. 2011), Scotland (Harries 2008, Farr & Rossman 2011), and Northern Ireland (Harries 2008). The species is also known from Canada: British Columbia, Alberta, Saskatchewan, Manitoba (Ginns 1986, Farr & Rossman 2011), and from southwestern United States: Utah and New Mexico (Farr et al. 1995, Farr & Rossman 2011).

Obviously the species has a wide distribution in the northern hemisphere, in highly different climatic regimes. The occurrences and observations are curiously scattered in space and time, in spite of the host genus *Salix* being common and wide-spread in this region of the globe. The northernmost locality in the world is in Finnmark, Norway, at lat. 70° 57' N, and long. 27° 30' E (Granmo 2008, 2011, Mathiassen & Granmo 2012).

Ecology

Some authors have commented on *Cryptomyces maximus* especially as a parasite (Rehm 1896, Rostrup 1902, Jørstad 1928, Butin 1960). Tulasne & C. Tulasne (1865) stated simply: "It is parasitic on living branches of *Salix alba* L. and

its allies, which it causes to wither and gradually kills.” Rostrup (1902) reported some damage by the fungus particularly on *S. alba* in some places in Denmark. In Germany, Butin (1960) said it was considered to do minor damage. According to our observations in North Norway, the fungus no doubt injures the affected trees, or parts of them, but owing to its scarcity apparently has no serious impact on *Salix*-populations as a whole.

Without knowing the ecology of a species one may search for it for a lifetime without success. However, only few authors have described the habitat where to find *Cryptomyces maximus*. For Germany Butin (1960) said that *C. maximus* prefers areas situated in ”... hohe Lagen (Alpen) oder kühlere Gegenden des Flachlandes.” The Tulasne brothers (1865) had made many of their observations at Chaville, near Versailles ”on the shores of forest ponds”, which is in close agreement with our observations on the common type of habitat.

On a world base *Cryptomyces maximus* is apparently a rare species, and the records for Norden suggest it to be quite rare in this area, too. We believe, however, that when the species becomes better known, far more localities will emerge in the future.

Red List status

International Union for the Conservation of Nature (IUCN), a global environmental organization, has not yet assessed the status of *Cryptomyces maximus* for the IUCN Red List (IUCN 2012). However, it has a provisional global assessment of ‘Critically endangered’ (CR) (IUCN 2010). It is not yet assessed in any Nordic Red List.

Specimens studied: **DENMARK.** Without locality, *Salix lanceolata*, VI.1899 Warming (C). **Eastern and northern Jylland:** Vrensted, Bagterp, *S. repens*, 6.VIII.1874 Rostrup (C). Glutsted Plantage, Kolpensig Planteskole, *S. daphnoides*, 5.IX.1901 Rostrup (C); Viborg, *S. lanceolata*, 2.II.1902 Lind (LD); same place, 5.VI.1903 Lind (C); same place, 4.VIII.1903 Lind (C, O). **Western Jylland.** Ål (= Oksbøl), *S. lanceolata*, V.1899 Warming (C). **Lolland.** Nakskov, Steensgaard, *S. alba*, 3.VIII.1898 unknown collector (C); same place, *S. alba*, VIII. 1901 Rostrup (C); same place and host species, 27.VIII.1903 Rostrup (LD). **FINLAND.** **Pohjois-Savo.** Joroinen, Lemmetti, *S. myrsinifolia* ssp. *myrsinifolia*, 23.V.1913

Hintikka (H; duplicates in TUR and TUR-A not seen); same place and host species, V.1913 *Hintikka* (TROM ex H). **ICELAND.** **Norðaustur-Ísland.** (Nordurland vestra). Sudur-Thingeyjarsýsla, Fnjóskadalur, Vágaskógur Forest, twigs of *S. phylicifolia*, 31.VII.1971 Lundqvist 7131 (UPS). **NORWAY.** **Akershus.** Bærum, Bjerke, on *Salix*, X.1825 Sommerfelt (O, as *Rhytisma maxima*). **Oslo.** Oslo, Tøyen, on *S. phylicifolia*, 1840 Moe (O, as *R. maxima*). **Oppland.** Dovre, 1841 Moe (O). **Nordland.** Evenes, Veggfjell, southeast of Buhågen, *S. myrsinifolia* ssp. *myrsinifolia*, 6.VIII.2008 Granmo 15/08 (TROM); Veggfjell, at the west end of Kvanndalen, *S. myrsinifolia* ssp. *myrsinifolia* at the edge of a moist fen near a brook, 6.VIII.2008 Granmo 16/08, 18/08 (TROM); same place and host species, 12.VII.2009 Granmo 11/09 (TROM); Veggfjell, at the east end of Kvanndalen, *S. myrsinifolia* ssp. *myrsinifolia* in a damp depression near a brook, 6.VIII.2008 Granmo 19/08; same place and host species, 25.VI.2011 Mølster, G. Granmo & Granmo 1/11 (TROM); same place and host species, 25.IX.2011 Mølster & Granmo 65/11 (TROM). **Troms.** Målselv, Øverbjgd, west of Rostavatn, *S. myrsinifolia* ssp. *myrsinifolia*, 2.VIII.1926 Jørstad (O). Tromsø, Kvaløya, Gamvika, *S. myrsinifolia* ssp. *myrsinifolia* browsed by European elk in moist fen, 13.VII.2008 E.-T. & M. Andreassen, Mølster & Granmo 3/08 & 4/08 (TROM); same area and host specimen, now with necrotic scars, 1.VIII.2010 Granmo 2/10 (TROM); Kroken, *S. myrsinifolia* ssp. *myrsinifolia* along the edge of a drainage trench, 16.VII. and 25.VII.2008 Granmo 7/08, 8/08, 9/08 (with *Nectria* sp. and *Fusarium* sp.) (TROM); same place and host species, 4.X.2008 Granmo 24/08 (TROM); same place and host species, 8.X.2011 Mølster & Granmo 69/11 (TROM). **Finnmark.** Lebesby, Oksevågdaalen Nature Reserve, *S. myrsinifolia* ssp. *borealis* (Granmo 2011: erroneously as *S. glauca* × *phylicifolia*) in humid wood near a brook, 3.VII.2008 Granmo & Mathiasen 11765 (TROM). **SWEDEN.** **Dalarna.** Mora, *S. cinerea*, 22.VI.1905 Lind (C); Söderbärke, Malingsbo, *S. myrsinifolia* ssp. *myrsinifolia*, 19.VIII.1911 Sylvé (UPS, nr. 47 of exsiccate Lagerberg & Sylvé Skogens skade-svampar). **Lule Lappmark.** Jokkmokk, alpes Sarjekensis in silva betul. infra montem Låddepakte, *S. phylicifolia*, 1.VIII.1901 Vestergren (UPS, S, C; all from the exsiccate Vestergren Microm. rar. selecti 530, (cp. Vestergren 1909: 42)). **Torne Lappmark.** Jukkasjärvi, Abisko, *S. phylicifolia*, 17.VIII.1903 Vestergren (S); same place, *S. arbuscula*, VII.1930 Lind (C); Jukkasjärvi, Snuorätjärko in reg. subalpina, *S. myrsinifolia* ssp. *myrsinifolia*, 14.-16.VII.1928 Nannfeldt 1337 (UPS). **Åsele Lappmark.** Vilhelmina, Södra Tresund, twig of *Salix*, 19.VI.2009 Andersson (Artportalen 2012, photo).

Additional specimens studied: **FRANCE.** Lyon, *Salix* sp., VI.1875 ABP (C). **GERMANY.** **Bayern.** München, Isarauen, *S. incana*, IV.1899 Allescher (S two specimens of Rabh. F. Eur. 3676); Isarauen bei Grosshesselohe, *S. incana*, V.1899 Schnabl (S two specimens, C). **Brandenburg.** Triglitz in der Prignitz, *S. pentandra*, 30.XII.1909, 15.III.1910 Jaap (S), and 23.X.1915 Jaap (S, C). **Nordrhein-Westfalen.** Münster, an der Angel bei Angelmodde unweit Münster, *S. alba*, VII.1888 Tavel (S). **UNITED KINGDOM.** **England.** Kings-Lynn in Norfolk, living S.

fragilis, VI.1875 *Plowright* (S); same place, *Salix* spp., VII.1875 *Plowright* (S).

Literature records: DENMARK. Jylland. Baggesvogn, Viborg, *Salix caprea* × *viminalis* (no date), Lind. Sjælland. Tudsenes (= Tuse Næs), *S. fragilis*, Botanical excursion 2.VI.1912; Damhussøen, *S. alba*, (no date) *Rostrup*; Jægerkroen, *S. caprea* × *viminalis*, Botanical excursion 2.X.1910. All Danish specimens are reported by Lind (1913). SWEDEN. Surroundings of Umeå (Vleugel 1908).

Notes to specimens studied: (1) According to Norsk SoppDatabase (2010), there should be three additional vouchers from Bærum, Bjerke in 1825 and 1826 by Sommerfelt, of which one also has a *Nectria* (*N. episphaeria* det. Jørstad), another *Godronia fuliginosa*. There is also an additional collection from Målselv, Øverbygd 2.VIII.1926 by Jørstad on *Salix caprea* × *myrsinifolia* ssp. *myrsinifolia* which should be associated with *Godronia fuliginosa*, its anamorph *Topospora fuliginosa* (as *T. proboscidea*), and *Cyanophomella acervalis* (all: det. Jørstad). None of those have been examined. (2) In herb UPS there are two additional vouchers from Fries' hand which are synonyms of *Cryptomyces maximus* (Minter 1998), viz. *Rhytisma maximum* v. *ramealis* from Lund, Skåne, and *R. maximum* f. *minor* from Skåne (Svengunnar Ryman pers. comm.).

Acknowledgements: This investigation has been a part of the project "Sekksporesopper i Finnmark" (Ascomycetes in Finnmark) 2009-2011, granted by Artsdatabanken (The Norwegian Biodiversity Information Centre). The curator of the herbarium in Uppsala, Svengunnar Ryman, and of the herbarium in Copenhagen, Henning Knudsen, have provided valuable information on localities in Sweden and Denmark, respectively. Gyða Eyjólfsdóttir, Akureyri has provided information about the species in Iceland. Håvard Kauserud, Oslo aided in the DNA sequencing. Håkon Hovdenak, Bjarkøy has generously offered linguistic help. Ernest Emmett is specially thanked for a double-check of English language. Ernst Høgtun, Tromsø Museum has offered technical assistance with the illustrations. We express our gratitude to them all.

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