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Bullatosporium taxicola, a new genus and species in *Mytiliniaceae* (*Pleosporomycetidae*, *Dothideomycetes*) from western Norway

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Abstract: The new genus and species *Bullatosporium taxicola* are described from dead wood of *Taxus baccata* in western Norway. Despite some morphological resemblance with *Hysteriaceae*, including low ascomata with a thick carbonized peridium and mainly five-septate ascospores, multigene analysis of the five molecular markers SSU, ITS, LSU, *TEF1-α* and *RPB2* revealed an affinity to *Mytiliniaceae*. The new species formed a strongly supported sister clade to the remaining strains of *Mytiliniaceae*. Dichotomous keys to genera of *Mytiliniaceae* and to hysterioid species with phragmospores in Fennoscandia are provided to aid identification.

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INTRODUCTION

Fungi belonging to the family *Mytiliniaceae* (*Mytiliniales*, *Dothideomycetes*) can be found on wood, bark, resin, cones, twigs and needles of conifers (Barr 1990, 1975, Boehm *et al.* 2009a, b). As such, they can be quite prominent in boreal forests, especially in areas with older trees.

While bearing some resemblance to fungi in *Hysteriaceae* by having slit-shaped rather than pore-shaped openings, *Mytiliniaceae* typically differ from fungi of this family by having fragile, thin-walled ascomata, which are erect and conchate as opposed to the thick-walled, low and lip-shaped ascomata of *Hysteriaceae* (Boehm *et al.* 2009b). Duby (1862) accommodated these fungi in a section of the then widely construed family *Hysteriaceae*, but Kirschstein (1924) proposed the separate family *Mytiliniaceae*. Subsequently, Luttrell (1953, 1973) suggested a wide concept of *Hysteriaceae*, but Barr (1979) maintained the two-family distinction. *Mytiliniaceae* has been variously associated with *Melanommatales* (Barr 1987, 1990), *Chaetothyriomycetidae* (Eriksson 2006) and *Pleosporales* (Lumbsch & Huhndorf 2007, Boehm *et al.* 2009a, b), but the family is currently considered as the only order of *Mytiliniales* of the *Pleosporomycetidae*, *Dothideomycetes* (Boehm *et al.* 2009a, b). According to Wijayawardene *et al.* (2018), the currently accepted genera in *Mytiliniaceae* are *Actidium*, *Halokirschsteiniothelia*, *Lophium*, *Mytilinidion*, *Ostreola*, *Peyronelia* (asexual morph), *Pseudocamaropycnis*, *Quasiconcha*, *Septonema*, *Taeniolella* and *Zoggium*. Of these, all of the genera with known sexual morphs have mytilinioid ascomata except the maritime genus *Halokirschsteiniothelia*,

which has subglobose ascomata with papillate ostioles. The ascospores vary from one- to multiseptated and can be hyaline or light brown.

While surveying fungi in old-growth forest remnants in western Norway, we encountered an unknown fungus on *Taxus baccata* with some morphological characters suggesting an affinity to *Hysteriaceae*, including low ascomata with a thick carbonized peridium and four- to six-septate brown ascospores. After molecular analysis it proved to belong to *Mytiliniaceae* but forming its own strongly supported clade within the family. We here present the new genus *Bullatosporium* to accommodate our species and discuss the phylogenetic relationships within the family based on five molecular markers. Genus and species taxonomy are provided alongside a dichotomous key to the genera of *Mytiliniaceae* with sexual morphs. A key to hysterioid species with phragmospores in Fennoscandia is also provided to further aid identification.

MATERIALS AND METHODS

Sampling and morphological investigation

During October 2018, May 2019, November 2021 and June 2023 we collected hysterioid ascomata from dead wood of living *Taxus baccata* in the oceanic lowlands of Møre and Romsdal and Vestland counties in western Norway.

Ascomata were rehydrated with autoclaved water and studied using a Nikon SMZ 745T stereomicroscope and a Nikon Eclipse Ci-L or a Zeiss Axio Imager A2 compound microscope.

Images of ascomata were captured with a NIKON DS-Fi2 or Tucsen DigiRetina 16 camera, using stacking software Lite Helicon Focus 8 v. 8.2.2. Microslides were created with contents of the ascomata mounted in sterile water or 5 % KOH. Photomicrographs were produced using a Zeiss AxioCam 503 camera and measurements were made with Zeiss AxioVision v. 4.9.1 software (Carl Zeiss AG), and images were processed in GIMP v. 2.10.34 (Kimball & Mattis 1996).

Cultivation techniques

For pure culture isolation from ascospores, hymenial material was transferred into a sterile water droplet on a micro slide and transferred with a sterile pipette onto Petri dishes containing malt agar (MEA: 3 % malt extract, 1.5 % agar in water) and antibiotics (0.25 % Streptomycin, 0.1 % Tetramycin, 0.5 % Ampicillin). Petri dishes were incubated at 20 °C for spore germination and checked daily for growth under a dissecting microscope. Germinated spores were transferred individually onto MEA plates (without antibiotics), their growth monitored, contaminants removed, and pictures taken. Isolates have been deposited at the Westerdijk Fungal Biodiversity Centre (CBS-KNAW), Utrecht, The Netherlands. Freshly collected specimens have been deposited in the Fungarium of Oslo, University of Oslo (O).

DNA extraction and sequencing

Genomic DNA was extracted from cultures by placing filamentous fungal hyphae from cultures in lysis buffer solution, and sent to Eurofins Genomics, Germany for DNA isolation, amplification, and Sanger sequencing of the ribosomal DNA regions of internal transcribed spacer (ITS) containing ITS1, 5.8S and ITS2, a fragment of the 28S large subunit ribosomal DNA (LSU) and translation elongation factor 1-alpha (*TEF1- α*).

Sequence alignment and phylogenetic analyses

Sequence editing, assembly and concatenations were done using Geneious Prime v. 2023.0.4 (Kearse *et al.* 2012) and deposited in GenBank (Table 1), and the alignments were uploaded to figshare (www.figshare.com; doi: 10.6084/m9.figshare.25305109). Sequence data from Boehm *et al.* (2009a) and additional sequences of species from *Mytiliniaceae* were downloaded from GenBank. Preliminary alignments were made using Muscle v. 5.1 (Edgar 2022) with standard settings as incorporated in Geneious Prime. All alignments were inspected and manually adjusted.

Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI). Substitution models for each locus were determined based on the AICc model selection criterion (small-sample-size corrected version of Akaike information criterion) as implemented in PartitionFinder v. 2.1.1 (Lanfear *et al.* 2016). The search was set to “all” and branch lengths set to “linked”. The ML analyses were performed on aligned sequences using RAxML v. 8.2.11 (Stamatakis 2014) as implemented in Geneious. Rapid Bootstrapping and search for best-scoring ML tree algorithms were used and Bootstrap analyses obtained by 10 000 bootstrap replications. To examine topological incongruence among data sets, ML bootstrapping analyses were carried out on each of the single-gene data sets. Topological incongruence was assumed if conflicting

tree topologies were supported by ≥ 70 % ML support. Since topological incongruence could not be observed, maximum likelihood (ML) bootstrapping analyses were carried out on the concatenated four-locus dataset using the same settings as for the single-gene analyses. The BI analyses were performed with MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001) with substitution models for different regions selected with the AICc parameter. Metropolis-coupled Markov chain Monte Carlo (MCMC) runs were performed for 1.1 M generations with trees sampled every 200 generations. Convergence of the MCMC procedure was assessed and effective sample (EES) size scores > 200 checked by using the MrBayes build in Tracer v. 1.6 (Rambaut *et al.* 2018). The first 10 % of trees were discarded as burn-in, and the remaining trees were used to calculate 50 % majority rule trees and to determine Bayesian posterior probabilities (BPP) for individual branches. Output trees were edited with Inkscape v. 1.2.2 (Harrington *et al.* 2003).

RESULTS

Phylogenetic analyses

We obtained consensus sequences from two strains of the ITS, LSU and *TEF1- α* markers (Table 1). The concatenated alignment for *Mytiliniaceae*, *Hysteriaceae* and *Gloniaceae* comprised 5 716 nucleotide characters, including gaps (SSU: 1–1 656; ITS1, 5.8S and ITS2: 1 657–2 140; LSU: 2 141–3 556; *TEF1- α* : 3 557–4 759; *RPB2*: 4 760–5 716). In total, the alignment was composed of 23 strains of the *Mytiliniaceae*, 21 strains of *Hysteriaceae*, nine of *Gloniaceae*, three *incertae sedis* and the following six *Pleosporales* outgroup taxa: *Bipolaris maydis* (CBS 134.39), *Byssothecium circinans* (CBS 675.92), *Cochliobolus heterostrophus* (CBS 134.39), *Delitschia winteri* (CBS 225.62), *Leptosphaeria maculans* (DAOM 229267) and *Pleospora herbarum* (CBS 191.86).

The maximum likelihood (ML) analysis of the combined datasets yielded the best scoring trees for *Mytiliniaceae* had an MLn of -32451.808911 (Fig. 1). Also, the Bayesian inference (BI) analysis showed congruence with the topology of the ML analyses, and for simplicity, only the ML tree is shown. Values for both ML bootstrap above 50 % and Bayesian posterior probabilities (BPP) higher than 0.90 are given at the nodes. The alignments had 52.16 % undetermined nucleotide gaps.

Representatives from the order *Pleosporales* formed a fully supported clade and outgroup to all included taxa from *Hysteriaceae* (*Hysteriales*), *Gloniaceae* (*Gloniales*) and *Mytiliniaceae* (*Mytiliniales*) (ML 100 % and BPP 1). The clade comprising *Mytiliniaceae*, *Gloniaceae* and *Hysterographium* is highly supported (ML 100 % and BPP 1) as sister group to *Hysteriaceae*. *Mytiliniaceae* receives high support as sister group to *Gloniaceae*, and the *Mytiliniaceae*-*Gloniaceae* clade is sister group to the *Hysterographium* clade, but these sister-group relationships are not significantly supported.

Our analyses showed support for one new genus within *Mytiliniaceae* comprising a new species, represented by the strains CBS 151403 (α 21-004) and CBS 151402 (α 21-005), respectively (see Fig. 1). Also, the morphology of this group is consistent and distinct from the other genera within *Mytiliniaceae*. Within *Mytiliniaceae* the genera *Mytilinidion* and *Lophium* are both highly polyphyletic and are in need of revision. The genus *Pseudocamaropycnis* lacks support for

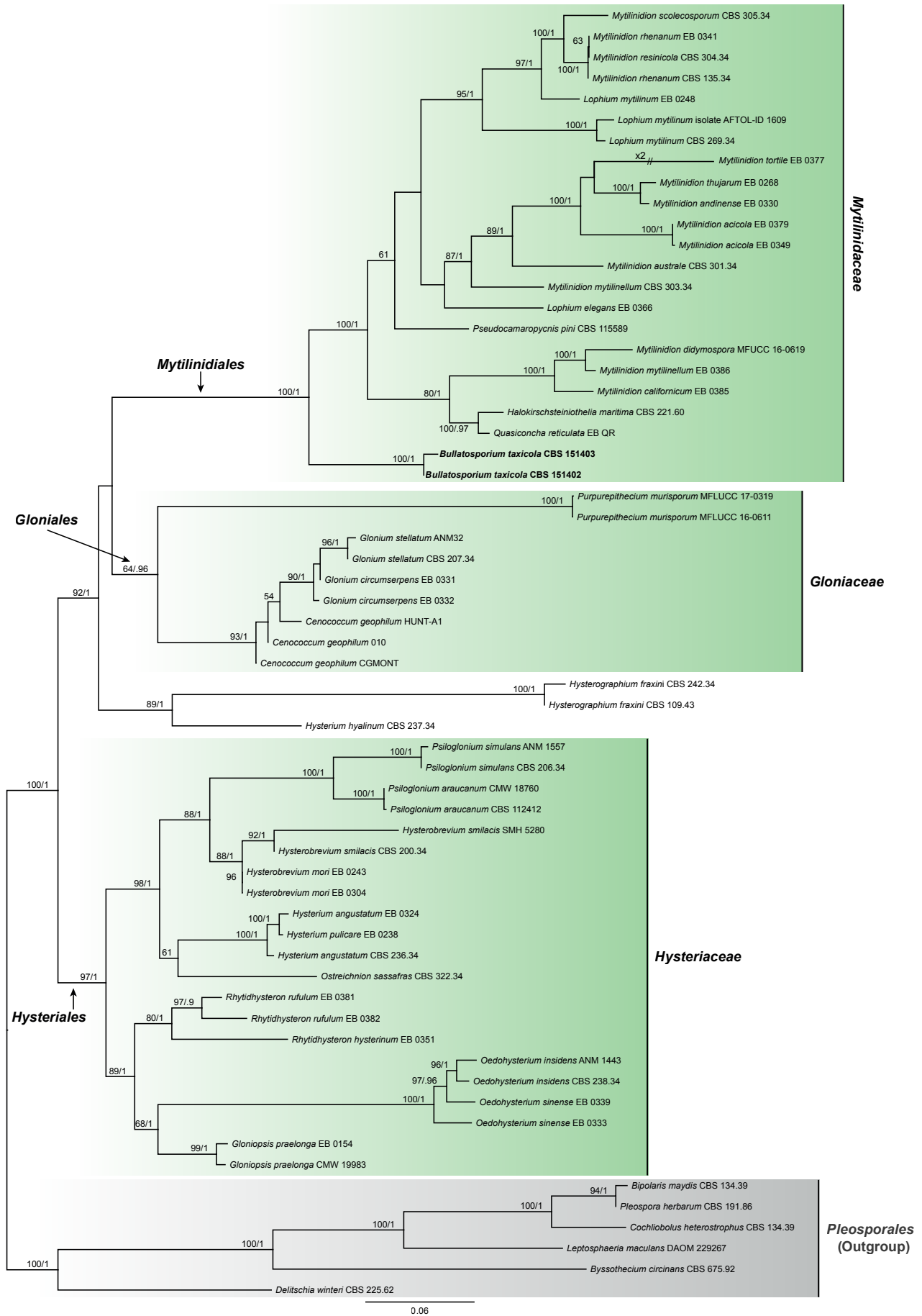


Fig. 1. Maximum likelihood phylogeny of *Mytiliniaceae*, *Gloniaceae* and *Hysteriaceae* based on SSU, ITS, LSU, *TEF1- α* and *RPB2* combined sequence data revealed by RAxML (MLn = -32451.808911). Numbers above branches indicate Maximum likelihood RAxML bootstrap values above 50 % and Bayesian posterior probabilities higher than 0.90 at first and second position, respectively. Newly obtained strains are shown in bold. Shortened branches are marked with crossing lines and indications (x2) of how many times the branch has been shortened. Branch length equals substitutions per site.

Table 1. Fungal taxa, strains and GenBank accessions used of *Hysteriaceae*, *Mytiliniaceae* and *Gloniaceae* along with representatives from *Pleosporales* as outgroup. The sequences generated in this current study are indicated in bold.

Taxa	Family	Strain no.	GenBank accession no.						Reference
			SSU	ITS	LSU	<i>TEF1-α</i>	<i>RPB2</i>		
<i>Bipolaris maydis</i>	<i>Pleosporales</i>	CBS 134.39	—	—	AY544645	—	—	Lutzoni et al. (2004)	
<i>Bullatosporium taxicola</i>	<i>Mytiliniaceae</i>	CBS 151403/α21-004	—	PP516536	PP516533	PP514386	—	This study	
<i>Byssothecium circinans</i>	<i>Mytiliniaceae</i>	CBS 151402/α21-005	—	PP516535	PP516534	PP514385	—	This study	
<i>Cenococcum geophilum</i>	<i>Pleosporales</i>	CBS 675.92	AY016339	OM337536	AY016357	GU349061	DQ767646	(AFOL 1735) GenBank	
	<i>Gloniaceae</i>	HUNT A1	L76616	—	—	—	—	LoBuglio et al. (1996)	
	<i>Gloniaceae</i>	CGMONT	L76617	—	—	—	—	LoBuglio et al. (1996)	
	<i>Gloniaceae</i>	010	L76618	—	—	—	—	LoBuglio et al. (1996)	
<i>Cochliobolus heterostrophus</i>	<i>Pleosporales</i>	CBS 134.39	AY544727	DQ491489	AY544645	DQ497603	DQ247790	(AFOL 54) GenBank	
<i>Delitschia winteri</i>	<i>Pleosporales</i>	CBS 225.62	DQ678026	—	DQ678077	DQ677922	DQ677975	Schoch et al. (2006b)	
<i>Gloniopsis praelonga</i>	<i>Hysteriaceae</i>	EB 0154/CBS 123337	FJ161154	—	FJ161195	FJ161103	—	Boehm et al. (2009b)	
	<i>Hysteriaceae</i>	CMW 19983	FJ161152	EU552133	FJ161193	—	—	Boehm et al. (2009b)	
<i>Glonium circumserpens</i>	<i>Gloniaceae</i>	CBS 123342/EB 0331	FJ161168	—	FJ161208	—	—	Boehm et al. (2009b)	
	<i>Gloniaceae</i>	CBS 123343/EB 0332	FJ161160	—	FJ161200	FJ161108	FJ161126	Boehm et al. (2009b)	
<i>Glonium stellatum</i>	<i>Gloniaceae</i>	CBS 207.34	FJ161140	MZ570257	FJ161179	FJ161095	—	Boehm et al. (2009b)	
	<i>Gloniaceae</i>	ANM 32	—	—	GQ221887	—	—	Mugambi & Huhndorf (2009)	
<i>Halokirschsteiniothelia maritima</i>	<i>Mytiliniaceae</i>	CBS 221.60	—	—	GU323203	GU349001	—	Schoch et al. (2009)	
<i>Hysterium angustatum</i>	<i>Hysteriaceae</i>	CBS 236.34	GU397359	—	FJ161180	FJ161096	FJ161117	Boehm et al. (2009a,b)	
	<i>Hysteriaceae</i>	EB 0324/CBS 123334	FJ161167	—	FJ161207	FJ161111	FJ161129	Boehm et al. (2009b)	
<i>Hysterium hyalinum</i>	<i>Incertae sedis</i>	CBS 237.34	FJ161141	—	FJ161181	—	—	Boehm et al. (2009b)	
<i>Hysterium pulicare</i>	<i>Hysteriaceae</i>	EB 0238/CBS 123377	FJ161161	—	FJ161201	FJ161109	FJ161127	Boehm et al. (2009b)	
<i>Hysterobrevium mori</i>	<i>Hysteriaceae</i>	EB 0304/CBS 123336	FJ161164	—	FJ161204	—	—	Boehm et al. (2009b)	
	<i>Hysteriaceae</i>	EB 0243/CBS 123335	FJ161162	—	FJ161202	—	—	Boehm et al. (2009b)	
<i>Hysterobrevium smilacis</i>	<i>Hysteriaceae</i>	CBS 200.34	FJ161138	—	FJ161177	—	—	Boehm et al. (2009b)	
	<i>Hysteriaceae</i>	SMH 5280	GU323183	—	GQ221912	—	GU371784	Mugambi & Huhndorf (2009); Schoch et al. (2009)	
<i>Hysterographium fraxini</i>	<i>Incertae sedis</i>	CBS 109.43	FJ161132	—	FJ161171	FJ161088	—	Boehm et al. (2009a,b)	
	<i>Incertae sedis</i>	CBS 242.34	—	—	FJ161189	—	—	Boehm et al. (2009b)	
<i>Leptosphaeria maculans</i>	<i>Pleosporales</i>	DAOM 229267	DQ470993	—	DQ470946	DQ471062	DQ470894	Spatafora et al. (2006)	
<i>Lophium elegans</i>	<i>Mytiliniaceae</i>	EB 0366	GU323184	—	GU323210	—	—	Schoch et al. (2009)	
<i>Lophium mytilinum</i>	<i>Mytiliniaceae</i>	AFTOL-ID 1609	DQ678030	—	DQ678081	DQ677926	DQ677979	Schoch et al. (2006b)	
	<i>Mytiliniaceae</i>	CBS 269.34	DQ678030	EF596817	DQ678081	DQ677926	DQ677979	Schoch et al. (2006b)	
	<i>Mytiliniaceae</i>	EB 0248/CBS 123344	FJ161163	—	FJ161203	FJ161110	FJ161128	Boehm et al. (2009b)	
<i>Mytilinidion acicola</i>	<i>Mytiliniaceae</i>	EB 0379	GU397362	—	GU397346	—	GU397355	Boehm et al. (2009a)	

Table 1. (Continued).

Taxa	Family	Strain no.	GenBank accession no.					Reference
			SSU	ITS	LSU	TEF1- α	RPB2	
	<i>Mytiliniidiaceae</i>	EB 0349	GU323185	—	GU323209	—	GU371757	Schoch et al. (2009)
<i>Mytilinidion andinense</i>	<i>Mytiliniidiaceae</i>	EB 0330/CBS 123562	FJ161159	—	FJ161199	FJ161107	FJ161125	Boehm et al. (2009b)
<i>Mytilinidion australe</i>	<i>Mytiliniidiaceae</i>	CBS 301.34	—	MH855533	FJ161183	—	—	Boehm et al. (2009b); Vu et al. (2019)
	<i>Mytiliniidiaceae</i>	EB 0385	GU323186	—	GU323208	—	—	Schoch et al. (2009)
<i>Mytilinidion californicum</i>	<i>Mytiliniidiaceae</i>	MFUCC 16-0619	MH535891	—	MH535902	—	MH535877	Jayasiri et al. (2018)
<i>Mytilinidion didymospora</i>	<i>Mytiliniidiaceae</i>	CBS 303.34	FJ161144	—	FJ161184	FJ161100	FJ161119	Boehm et al. (2009b)
<i>Mytilinidion mytilinellum</i>	<i>Mytiliniidiaceae</i>	EB 0386	GU397363	—	GU397347	—	GU397356	Boehm et al. (2009a)
<i>Mytilinidion resinicola</i>	<i>Mytiliniidiaceae</i>	CBS 304.34	FJ161145	MH855535	FJ161185	FJ161101	FJ161120	Boehm et al. (2009b); Vu et al. (2019)
	<i>Mytiliniidiaceae</i>	CBS 135.34	FJ161136	—	FJ161175	FJ161092	FJ161115	Boehm et al. (2009b)
<i>Mytilinidion rhenanum</i>	<i>Mytiliniidiaceae</i>	EB 0341	GU323187	—	GU323207	—	—	Schoch et al. (2009)
<i>Mytilinidion scolecosporum</i>	<i>Mytiliniidiaceae</i>	CBS 305.34	FJ161146	MH855536	FJ161186	FJ161102	FJ161121	Boehm et al. (2009b); Vu et al. (2019)
	<i>Mytiliniidiaceae</i>	EB 0268	GU323188	—	GU323206	—	—	Schoch et al. (2009)
<i>Mytilinidion thujarum</i>	<i>Mytiliniidiaceae</i>	EB 0377	GU323189	—	GU323205	—	—	Schoch et al. (2009)
<i>Mytilinidion tortile</i>	<i>Mytiliniidiaceae</i>	CBS 238.34	FJ161142	—	FJ161182	FJ161097	FJ161118	Boehm et al. (2009b)
<i>Oedohysterium insidens</i>	<i>Hysteriaceae</i>	ANM 1443	GU323190	—	GQ221882	—	GU371785	Schoch et al. (2009); Mugambi & Huhndorf (2009)
	<i>Hysteriaceae</i>	EB 0333/CBS 123345	FJ161169	—	FJ161209	—	FJ161130	Boehm et al. (2009b)
<i>Oedohysterium sinense</i>	<i>Hysteriaceae</i>	EB 0339	GU397364	—	GU397348	GU397339	GU397357	Boehm et al. (2009a)
<i>Ostreichnion sassafra</i>	<i>Hysteriaceae</i>	CBS 322.34	FJ161148	—	FJ161188	—	FJ161122	Boehm et al. (2009b)
<i>Pleospora herbarum</i>	<i>Pleosporales</i>	CBS 191.86	DQ247812	MH861935	DQ247804	DQ471090	DQ247794	Schoch et al. (2006a); Spatafora et al. (2006); Vu et al. (2019)
	<i>Mytiliniidiaceae</i>	CBS 115589	—	KU728518	KU728557	KU728594	—	Crous & Groenewald (2016)
<i>Pseudocamaropycnis pini</i>	<i>Hysteriaceae</i>	CBS 112412	FJ161133	—	FJ161172	FJ161089	FJ161112	Boehm et al. (2009b)
<i>Psiloglonium araucanum</i>	<i>Hysteriaceae</i>	CMW 18760	FJ161151	—	FJ161192	—	—	Boehm et al. (2009b)
	<i>Hysteriaceae</i>	CBS 206.34	FJ161139	—	FJ161178	FJ161094	FJ161116	Boehm et al. (2009b)
<i>Psiloglonium simulans</i>	<i>Hysteriaceae</i>	ANM 1557	—	—	GQ221873	GQ221920	—	Mugambi & Huhndorf (2009)
	<i>Gloniaceae</i>	MFUCC 16-0611	KY799175	—	KY799173	KY887666	KY799176	Jayasiri et al. (2017)
<i>Purpurepithecium murisporum</i>	<i>Gloniaceae</i>	MFUCC 17-0319	—	—	KY799174	KY799177	KY887667	Jayasiri et al. (2017)
	<i>Mytiliniidiaceae</i>	EB QR	—	—	GU397349	—	—	Boehm et al. (2009a)
<i>Quasiconcha reticulata</i>	<i>Hysteriaceae</i>	EB 0351	—	—	GU397350	GU397340	—	Boehm et al. (2009a)
<i>Rhytidhysterium hystrinum</i>	<i>Hysteriaceae</i>	EB 0381	GU397366	—	GU397351	—	—	Boehm et al. (2009a)
<i>Rhytidhysterium rufulum</i>	<i>Hysteriaceae</i>	EB 0382	—	—	GU397352	—	—	Boehm et al. (2009a)

its accurate placement within the family. The sister group relationship of genera *Halokirschsteiniothelia* and *Quasichoncha* is highly supported and the placement of these two genera as a sister group to the clade comprising the three *Mytilinidion* species *Mytilinidion californicum*, *M. mytilinellum* and *M. didymospora* receives medium (ML) to maximum (BPP) support. The two strains of *Halokirschsteiniothelia maritima* 3124D and NWHC 45703-222_6SD, represented only by the ITS region, were omitted due to their lack of additional regional markers. Sequences from the genera *Hysteropatella* and *Glyphium* were omitted as recent molecular evidence shows that *Hysteropatella* resides within the *Patellariaceae*, and *Glyphium* resides within the *Chaetothyriales*, *Eurotiomycetes* (Lindemuth *et al.* 2001, Lutzoni *et al.* 2004, Lücking *et al.* 2004, Lumbsch *et al.* 2005, Schmitt *et al.* 2005, Geiser *et al.* 2006, Boehm *et al.* 2009a). The genera *Ostreola*, *Taeniolella*, *Peyronelia* and *Zoggium* all lack sequences in international databases.

Taxonomy

Mytilinidiaceae Kirschst., *Verh. Bot. Vereins Prov. Brandenburg* **66**: 28. 1924. MycoBank MB 81049

Type genus: *Mytilinidion* Duby, *Mém. Soc. Phys. Hist. Nat. Genève* **16**: 34. 1861. MycoBank MB 3389.

Sexual morph: *Ascomata* superficial, scattered to gregarious, black, sometimes less connivent, more appressed, hysteroioid, grouped in triangular or radiating star-shaped or astral arrangement, fragile, yet persistent, carbonaceous, globoid to obovoid, to strongly laterally compressed erect, bivalve shell-shaped structures, standing on edge, with lateral walls more or less connivent, and extended vertically to a prominent longitudinal keel or cristate apex; usually distinctly clam- or mussel shaped, rarely (*Halokirschsteiniothelia maritima*) subglobose ostiolate. *Peridium* fragile, thin- to rarely thick-walled, scleroparenchymatous, rarely of multiple layers. *Hamathecium* comprising narrow trabeculate pseudoparaphyses borne in a gelatinous matrix, often sparse to lacking at maturity. *Asci* 8-spored, rarely 4-spored, bitunicate, fissitunicate, cylindrical, with a broad, short pedicel, ocular chamber not well developed, borne on a basal cushion, centrally orientated within the centrum, rarely borne laterally. *Ascospores* overlapping 1–2-seriate or in one or two fascicles within the ascus, hyaline to pigmented yellow to dark brown, highly variable in septation, showing bipolar symmetry. *Asexual morph*: Primarily coelomycetous or less frequently hyphomycetous (Lohman 1932a, b, 1933a, b, Blackwell & Gilbertson 1985, Speer 1986).

Ecology: Saprobic on wood, bark, resin, cones, scales, needles, seeds, and roots of gymnosperms, much less frequently on angiosperms. Predominantly temperate (Northern Hemisphere) in distribution.

Notes: The ascomata range from globoid to obovoid to strongly laterally compressed, erect oyster- or bivalve shell-shaped (conchate) or hatchet-shaped (dolabrate) structures, standing on edge, usually with a prominent longitudinal keel or cristate apex. The hamathecium consists of narrow trabeculate pseudoparaphyses, borne in a gel matrix, which are often sparse to lacking at maturity (Zogg 1962, Barr 1987, 1990). The

bitunicate asci are borne in a basal, rarely lateral, orientation within the centrum, and contain eight, rarely four, ascospores, overlapping uniseriate, biseriate or in one or two fascicles. The ascospores range from scolecospores to didymospores to phragmospores to dictyospores, hyaline, soon yellow to dark brown in pigmentation, and generally showing bipolar symmetry in outline (Barr 1990).

Bullatosporium Andreasen & Nordén, *gen. nov.* MycoBank MB 852941.

Etymology: With reference to the bullate epispore.

Type species: *Bullatosporium taxicola* Andreasen & Nordén

Ascomata isolated to gregarious, variably erumpent to sessile, linear to almost subglobose, carbonaceous, black, hysterothecioid. *Ascoma apex* linear and curved, hysteroioid-like, carbonaceous and fragile. *Ostiolar canal* linear, periphysate. *Peridium* thick-walled, composed of dark brown cells of *textura angularis*, becoming lighter towards the inside, somewhat compressed. *Hamathecium* comprising filiform, hyaline, septate, guttulate, smooth cellular pseudoparaphyses. *Asci* bitunicate, fissitunicate, cylindrical, apically rounded, with a less developed ocular chamber, with 8 obliquely to irregularly biseriate ascospores, short stipitate. *Ascospores* hyaline when immature, becoming brown to dark brown at maturity, ellipsoid to oblong with rounded ends, with bullate epispore at the middle septum at least when immature, phragmospored, with 5–7 transverse septa, sometimes constricted at the central (primary) septum, guttulate, smooth-walled, lacking a mucilaginous sheath.

Ecology: Saprobic on wood (rarely bark) and dead branches of *Taxus baccata*.

Notes: The two strains CBS 151403/α21-004 and CBS 151402/α21-005 are nesting with maximum support as a sister clade to the remaining *Mytilinidiaceae* (ML 100 % and BPP 1). *Bullatosporium* is morphologically distinct from the remaining genera of *Mytilinidiaceae* by a thicker peridium and the unique epispore structure. Hence, our material represents a new genus and a taxon in its own right. The genus is most likely to be confused with fungi in the *Hysteriaceae* with phragmospores.

Bullatosporium taxicola Andreasen & Nordén *sp. nov.* MycoBank MB 852942; Fig. 2.

Etymology: With reference to the host species *Taxus baccata*.

Typus: **Norway**, Møre og Romsdal, Skodje, Ørnakken nature reserve, on dead wood of living *Taxus baccata*, 16 Nov. 2021, JB. Jordal & PG. Larsen (**holotype** O-F-270952, ex-holotype culture CBS 151402 = α21-005); Møre og Romsdal, Skodje, Ørnakken nature reserve, on dead wood of living *Taxus baccata*, 16 Nov. 2021, JB. Jordal & PG. Larsen (**paratype** O-F-270953, ex-paratype culture CBS 151403 = α21-004).

Additional material examined: **Norway**, Møre og Romsdal, Skodje, Ørnakken nature reserve, on *Taxus baccata*, 17 Oct. 2018, JB. Jordal (O-F-270954 – α21-001); Vestland, Kvam, Skeianeset, on *Taxus baccata*, 13 May 2019, JB. Jordal (O-F-270955 – α21-002); Møre og Romsdal, Molde, Otrøya W of Hagset, on *Taxus baccata* (three trees),

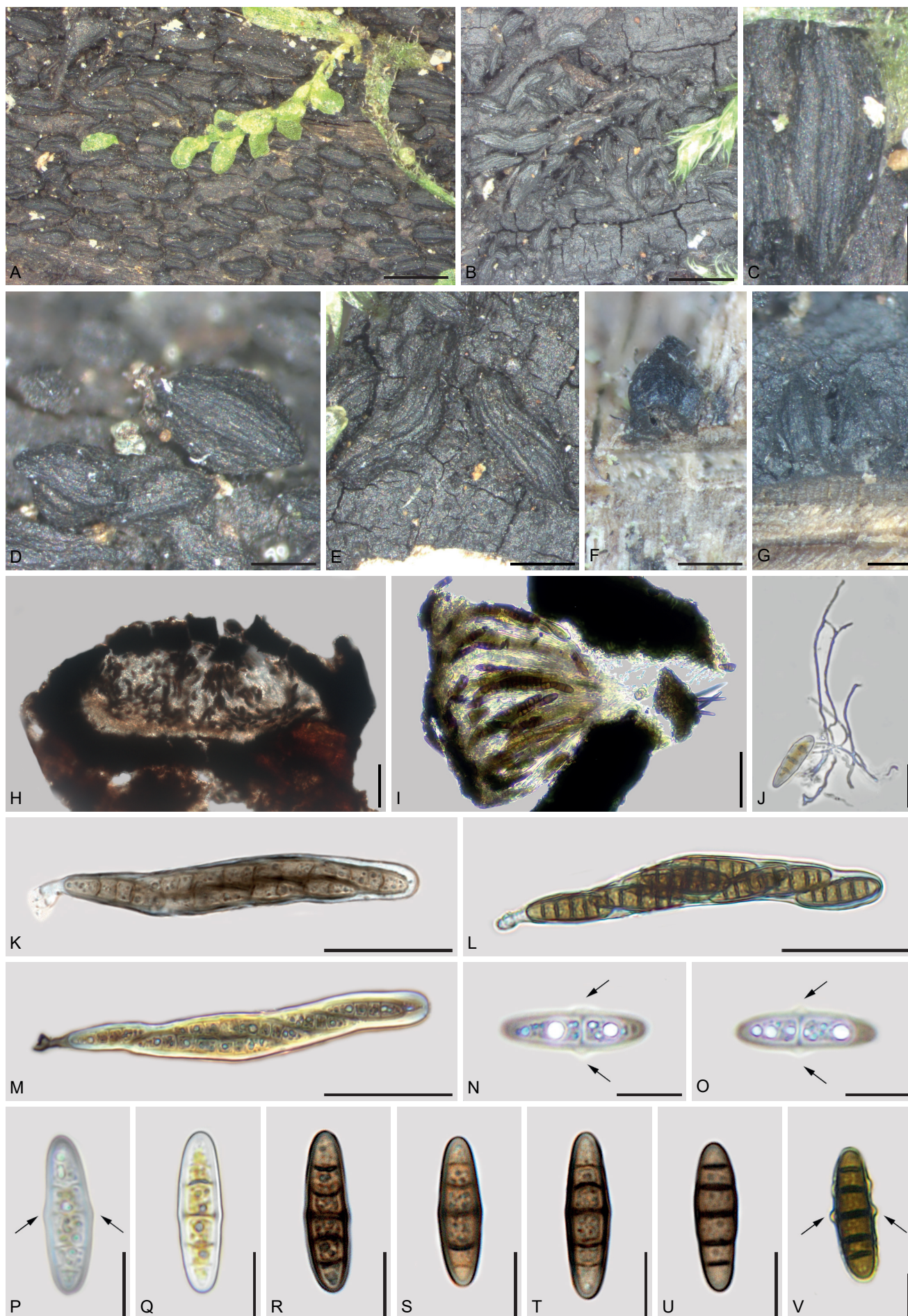


Fig. 2. *Bullatosporium taxicola*. **A–E.** Ascomata. **F, G.** Section of ascomata; **H, I.** Hymenium and peridium. **J.** Pseudoparaphyses. **K–M.** Asci. **N–Q.** Immature ascospores showing the bulging episporae. **R–V.** Mature ascospores. **A, C, E, V = O-F-270953**, paratype. **B, D, F–U = O-F-270952**, holotype. Scale bars: **A, B, D = 1 000 μ m**; **C, E–G = 100 μ m**; **H, I, K–M = 40 μ m**; **J = 20 μ m**; **N–V = 10 μ m**.

13 Jun. 2023, JB. Jordal & U. Hanssen (O-F-270956); Møre og Romsdal, Ålesund, Fylling, on *Taxus baccata* (18 trees), 14 Jun. 2023, JB. Jordal & U. Hanssen (O-F-270957).

Sexual morph: *Ascomata* (80–)225–1 025(–1 210) μm long ($n = 35$), isolated to gregarious, variably erumpent to sessile, linear to almost subglobose, carbonaceous, black, hysterothecioid, often staining the substrate around the ascomata black. *Ascoma apex* linear and curved, hysterothecioid, carbonaceous and fragile/brittle and easily falling apart when handled. *Ostiole* linear, periphysate. *Peridium* (43–)44–47(–48) μm thick ($n = 12$), thick-walled with dark brown cells, becoming lighter towards the inside, somewhat compressed, texture very difficult to discern, probably of *textura angularis*. *Hamathecium* comprising filiform, hyaline, septate, guttulate, smooth cellular pseudoparaphyses. *Asci* (91–)98–126(–146) \times (10–)12–14.5(–16) μm ($n = 30$), bitunicate, fissitunicate, cylindrical, apically rounded, with less developed ocular chamber, with 8 obliquely to irregularly biserial ascospores, short stipitate. *Ascospores* (20–)23–28(–35) \times (6–)7–8(–8.5) μm ($n = 75$), hyaline when immature, becoming brown to dark brown at maturity, ellipsoid to oblong

with rounded ends, with bullate episporium at the middle (primary) septum at least when immature, phragmosporous with 4–7 (typically 5) transverse septa, at over maturity constricted at the primary and secondary septa; guttulate, smooth-walled, lacking a mucilaginous sheath.

Culture characteristics: Ascospores germinated on MEA within 48 h. Germ tubes produced from several cells. Colonies reaching 2–3 cm diam after 4 wk at 20 °C, subcircular with irregular margins, black, turning (irregularly) grey in inner parts, reverse dark brown.

Ecology: On dead wood (rarely bark) and dead branches of living *Taxus baccata*. Often on trees injured by deer browsing.

Notes: The material is morphologically distinct from the remaining species of *Mytilinidiaceae* by the combination of a thick peridium and phragmospores with bullate episporium at the middle septum. Hence, our material represents a taxon of its own, which we describe as the new species *B. taxicola*. The species is most likely to be confused with fungi in the *Hysteriaceae*.

Key to the genera of the *Mytilinidiaceae* with sexual morphs

The key is based on Boehm et al. (2009a). The genera *Ostreichnion* and *Glyphium* along with the species *Mytilidium didymospora* are included in the key to effectuate identification of morphologically similar fungi, regardless of phylogenetic relationship. Genera where only the asexual morphs (*Septonema*, *Taeniolella*, *Pseudocamaropycnis*, *Peyronelia*, *Prostratomyces*) are known are not included.

- | | |
|---|--------------------------------|
| 1. Ascospores didymospores | 2 |
| 1. Ascospores phragmospores or dictyospores | 5 |
| 2. Didymospores hyaline to pale brown, asymmetric, cylindrical, one end tapering and another end rounded, smooth-walled, not constricted at the septa, 14–18 \times 2–4 μm | <i>Mytilidium didymospora</i> |
| 2. Didymospores pale brown, brown, olive- to reddish brown | 3 |
| 3. Didymospores 6–8 \times 5–5.5 μm ; brown, ellipsoid, symmetric, with coarsely reticulate wall | <i>Quasiconcha</i> |
| 3. Didymospores longer than 10 μm | 4 |
| 4. Ascomata not ostiolate, didymospores olive- to reddish brown, walls thin, smooth or delicately longitudinally striate, but not reticulated | <i>Actidium</i> |
| 4. Ascomata ostiolate, didymospores pale brown, ellipsoid, apices attenuated, constricted at the septum; only known from marine environments | <i>Halokirschsteiniothelia</i> |
| 5. Ascospores multi-septate, filiform, about equal in length to the ascus, in some cases at maturity longer than the ascus, often spirally arranged ... | 6 |
| 5. Ascospores variously septated, ellipsoid, fusoid, cylindrical, if filiform shorter than the ascus and not spirally arranged | 8 |
| 6. Ascomata conchate, solitary to gregarious, but never forming fused, ridge-like assemblages | <i>Lophium</i> |
| 6. Ascomata either forming rigid, fused band- or ridge-like structures or solitary, erect, dolabrate to ligulate | 7 |
| 7. Ascomata densely gregarious, forming band- or ridge-like assemblages | <i>Zoggium</i> |
| 7. Ascomata erect, dolabrate to ligulate in outline; often with subtending hyphal strands | <i>Glyphium</i> |
| 8. Ascospores dictyospores, or large and remaining 1-septate | 9 |
| 8. Ascospores transversely septate phragmospores or scolecospores | 10 |
| 9. Ascospores ellipsoid, shorter than 30 μm , with a single longitudinal septum, usually passing through the mid-cells, or spanning the entire length of the ascospore | <i>Ostreola</i> |
| 9. Ascospores ellipsoid or cylindrical, longer than 30 μm , with several longitudinal septa in cells or large and remaining 1-septate | <i>Ostreichnion</i> |
| 10. Ascospores without bullate episporium, peridium < 40 μm thick | <i>Mytilinidium</i> |
| 10. Ascospores often with bullate episporium, peridium (43–)44–47(–48) μm thick | <i>Bullatosporium</i> |

Key to mytilinioid and hysteroiid species with phragmospores in Fennoscandia

The key is mainly based on Boehm *et al.* (2009a).

1. Peridium thin and papery. Ascospores yellow to reddish brown 2
1. Peridium thick and carbonaceous. Ascospores brown 6
2. Ascospores 3-septate, shorter than 16 μm . On small branches and needles of *Juniperus* *Mytilinidion decipiens*
2. Ascospores 3- or more septate, longer than 16 μm 3
3. Ascospores 3-septate, 16–22 \times 3–4 μm *M. mytilinellum*
3. Ascospores with more septa, or longer than 22 μm 4
4. Ascomata low, (usually < 100 μm) ascospores 3–5-septate. On twigs and needles of *Juniperus* *M. acicola*
4. Ascomata higher (usually > 100 μm), standing on edge. On various conifers 5
5. Ascospores 3–5-septate, 30–42 \times 3–5 μm *M. rhenanum*
5. Ascospores 7–9-septate, 32–38 \times 5–6 μm , slightly bent and asymmetric *M. gemmigenum*
6. Ascospores 3-septate 7
6. Ascospores with 4–7 septa and bulging epispore/gelatinous coating, 23–28 \times 7–9 μm . On dead wood, dead branches and bark of living *Taxus baccata* *Bullatosporium taxicola*
7. Hysterothecia partly open, exposing a disc. Exciple two-layered, the outer layer of black and thick-walled cells and the inner layer of thin-walled, pallid and compressed cells *Hysteropatella elliptica*
7. Hysterothecia closed. Exciple three-layered, the outer layer black and thick-walled and often the middle layer lighter in pigmentation, and the inner layer distinctly thin-walled, with pallid and compressed cells 8
8. Ascospores 20–40 \times 6–12 μm , usually with inner spore cells brown and end cells hyaline *Hysterium pulicare*
8. Ascospores 14–21 \times 4–8 μm , all cells usually brown *H. acuminatum*

DISCUSSION

Mytiliniaceae, phylogenetic reconstruction and genetic markers

Our phylogenetic analyses based on five molecular markers show strong support and monophyly of the three families of *Mytiliniaceae*, *Gloniaceae* and *Hysteriaceae*. The analysis also shows strong support for the three families' placement within and separation from other families within the *Pleosporomycetidae* (*Dothideomycetes*). *Bullatosporium gen. nov.* is placed with high backbone support (ML 100% and BPP 1) within *Mytiliniaceae*, a family which is separated from but shows close affinities to *Gloniaceae*.

The phylogenetic reconstruction of *Mytiliniaceae* is not entirely settled as the analysed dataset inferred less significant support for some genera, species and deeper nodes. The currently accepted genera *Lophium* and *Mytilinidion* are highly polyphyletic and need revision and lectotypification of type material for stabilization. We expect that the addition of further coding markers such as *TEF1- α* and *RPB2* for all taxa would enhance the resolution and support of deeper nodes and probably provide a more stable topology. Also, the addition of less conserved markers such as the ITS would improve delimitation of and support at the species level as at present this region is lacking for most species within the dataset.

Morphology

Peridium characters have traditionally separated *Mytiliniaceae* from *Hysteriaceae*, with the former having a thin papery one-layered peridium, and the latter displaying a complex three-layered, thick and brittle peridium (Boehm *et al.* 2009b). However, our fungus has a thick, opaque, one-layered peridium structure that may be derived from the regular *Mytiliniaceae* type.

The hamathecium of *Bullatosporium* consist of cellular pseudoparaphyses. This is another feature similar to *Hysterium*. Members of the *Hysteriaceae* have cellular pseudoparaphyses except for the genera *Ericboehmia* and *Ostreichnion* (Gardiennet *et al.* 2023), which share trabeculate pseudoparaphyses with the *Mytiliniaceae*.

The bulging epispore appearing in water mounts is a distinctive character and does, to our knowledge, not occur elsewhere within the treated families. The bulges, which are variable in number and appear mainly in immature ascospores, do not seem to have any apparent function.

Ecology and conservation

The new species was found only on *Taxus baccata* (ca. 35–40 trees) in Western Norway and our preliminary assumption is that it is host specific. We have opportunistically searched for the species on *Taxus baccata* also in the eastern part of southern

Norway but have not been able to find it there, it may therefore prefer the oceanic climate of Western Norway. It was found mainly on dead wood on living trees, both on the trunk and on dead branches, but sometimes also on old bark near tree wounds. *Taxus baccata* (listed as vulnerable on the Norwegian red list of species; Solstad *et al.* 2021) is in Western Norway often browsed by fallow deer and red deer, which are kept in unnaturally high densities for commercial hunting and prefer to feed on the trees, especially in winter. The deer often feed on the bark of the trees, which is a threat against their survival but may be a temporary advantage for *B. taxicola* by producing dead wood. The deer also feed on leaves, and recruitment of young *Taxus baccata* is largely prevented. In the future, *B. taxicola* can be negatively affected by the continued decline of its host in this area.

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