North American Fungi

Clavarioid-type fungi from Svalbard:
Their spatial distribution in the European High Arctic

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Abstract: The list of fungi with club or coralloid-type ('clavarioid') basidiomes from the Svalbard archipelago presented here includes 22 species from 7 genera in several families of Basidiomycota. Nineteen of them are new for the region. Genera include *Artomyces, Clavaria, Clavulina, Macrotyphula, Multiclavula, Ramaria* and *Typhula.* A quantitative analysis is also presented on the distribution of these fungi on Svalbard in comparison to similar taxa in other high Arctic regions, such as the Novaya Zemlya Isles (Russia) and Yamal Peninsula (Russia). Data suggest that for fungi with 'clavarioid' basidiomes richness and diversity decreases with high latitude (towards colder regions) and also with distance from the warm influence of the Gulf Stream. This study found that fungi with club type basidiomes are a primary component of the non-gilled Basidiomycota in the Arctic region which is depauperate in 'poroid', 'thelephoroid' and 'hydnoid' fungi.

Key words: Arctic, clavarioid fungi, club fungi, coral fungi, diversity, ecology, Novaya Zemyla Isles, Russia, Svalbard, tundra, Yamal Peninsula

Introduction: Svalbard is a major European high-Arctic archipelago located deep within the Arctic Circle at the north-western edge of the Barents Sea at 74°–81°N and 10°–30°E, and is 657 km north of the most northerly point on the Norwegian mainland, halfway to the North Pole. The archipelago consists of five main islands (Spitsbergen, Nordaustlandet, Edgeøya, Prins Karls Førland, Barensøya) and about 150 lesser ones. The largest island is Spitsbergen.

The total land area is roughly 60,000 km² of which 60% is presently covered by glaciers. In spite of its extreme northerly position, Svalbard shares some features common to Atlantic islands. First, the climate over parts of the archipelago is relatively oceanic. The warm North Atlantic Current reaches the west coast of Spitsbergen, which results in a relatively mild climate in the western and central parts of the archipelago (Jónsdóttir 2005), while cold Barents Sea waters impact the East coast and southernmost tip of Spitsbergen. The climate of western Svalbard can be termed arctic-oceanic; in contrast, the eastern cost of the island is influenced by cold currents from the north and in total, the yearly growth period is six to ten weeks (Birks et al. 2004).

The Arctic is by definition a treeless landscape often referred to as one entity composed of tundra ecosystems that are simple and fragile due to the harsh climate and low energy budget. In reality, the Arctic spans areas with more than a threefold difference in length of the growing season and a ten-fold difference in mean July temperatures, a heterogeneity that has long been recognized by people living, working or traveling in the Arctic. Furthermore, the relative simplicity of Arctic ecosystems in general, and Svalbard ecosystems in particular, has recently been confirmed with an extensive accounting of the vascular plants, algae, cyanobacteria and fungi (Elvebakk & Prestrud 1996). However this includes very scarce information on fungi with club/coralloid basidiomes ('clavarioid').

Although details of the evolutionary affinities of fungi with club/coralloid ('clavarioid') basidiomes (Basidiomycota) are still debated (Hibbett et al. 2007), they appear to constitute an ecologically and phylogenetically diverse group. However, as an assemblage they are characterized by coral- or club-like basidiomes and include about 700 species (Kirk et al. 2008). Historically most were placed in the Aphyllophorales (as non-gilled fungi) and have since been assigned to various families that are not closely related to one another, i.e. Auriscalpaceae (*Artomyces pyxidatus*), Clavariaceae (*Clavaria argillacea, C. falcata*), Clavulinaceae (*Clavulina cinerea, Clavulina coralloides*), Gomphaceae (*Ramaria abietina*), and Typhulaceae (*Macrotyphula, Multiclavula, Typhula*). Most macrofungi in the Arctic are in Agaricales and non-gilled groups are rare or absent. This disparate group represents macrofungi with a convergent evolution towards club-shaped basidiomes instead of gills. Some are probably cosmopolitan in distribution, but a number of species appear confined to the tropics or subtropics and others have been collected only in temperate or boreal regions (Corner 1950, 1970, Parmasto 1965a, Berthier 1976, Petersen 1973, Shiryaev 2006a).

The group is also ecologically diverse and contains four different trophic groups of macromycetes: saprotrophic, mycorrhizal, parasitic and basidiolichens (Corner 1950, Petersen 1967, Berthier 1976, Agerer et al. 1996, Hoshino et al. 2003, Nouhra et al. 2005, Moncalvo et al. 2006, Shiryaev 2006a, 2006b). Most of what is known about the assemblages of these fungi and their associations with particular types of terrestrial ecosystems has been derived from studies carried out in boreal and temperate regions of the world. Although club and coral fungi are known to occur in the Arctic and sub-Arctic, species in these high-latitude regions of Europe have received very little study (Lange 1957, Kobayasi et al. 1967, Knudsen et al. 1993,

Mukhin and Knudsen 1998, Borgen et al. 2006, Hoshino et al. 2003, Shiryaev 2006a, 2010). Only a few articles mention the high Arctic mycota of the club and coral fungi i.e. reports from Novaya Zemlya Isles (Shiryaev 2006b) and the northern Yamal Peninsula (Shiryaev 2008a, 2010).

Although the vascular plant flora of Svalbard is limited, the Cryptogam flora (including bryophytes, fungi and lichens) consists of a comparatively high number of species for a high-Arctic region (see Elvebakk and Prestrud 1996, Jónsdóttir 2005). A report on the mycota of Svalbard (altogether with Bjørnøya Island) dealt mainly with Agaricales (Gulden and Torkelsen 1996). Twenty-two species from 16 genera of "Aphyllophorales" are known (Gulden and Torkelsen 1996, Kosonen and Huhtinen 2008), including only three with club or coralloid basidiomes i.e. *Ramaria abietina* (Pers.) Quél. (Skifte 1994), *Typhula culmigena* (Mont. & Fr.) Berthier (Huhtinen 1987) and "snow mold" *T. ishikariensis* S. Imai (Hoshino et al. 2003).

The theory of plant life forms (Raunkier 1934) has been rarely used for Cryptogams (Friesian system and its modifications), but even scant information provides an opportunity to better understand the convergence of form in fungi, and to describe such mycotas and their importance in ecosystems (Parmasto 1965b). Fungal life forms (fruiting bodies as reproductive organs) may be more dependent on current environmental and local hydrothermal conditions than are vascular plants (primarily vegetative organs). Therefore, studies of the life forms of fungi are possibly more meaningful for examining evolutionary process, coevolution of fungi with plants (Karatygin 1993) and the theory of species than is phytocoenology (Parmasto 1965b).

The primary aim of this study was to assemble taxonomic, ecological and biogeographical data on fungi with club/coralloid basidiomes reported and/or represented by specimens from Svalbard. In addition, the following specific questions were

addressed: (1) what species of club or coral fungi actually occur in this European high-Arctic region (2) which taxonomic and trophic groups comprise the mycota of such regions (3) how does the Svalbard mycota compare to that of other European high-Arctic regions and (4) are there longitudinal changes in European high-Arctic mycota related to oceanic versus continental climate? It should be made clear that results are based solely on basidiome occurrence.

Materials and Methods

STUDY AREA: According to a recent study of the relationship between climatic and vegetation characteristics, whole Arctic ecosystems can be divided into five subzones (A–E), with A the coldest and E the warmest subzone (hereafter referred to as "zones"). These subdivisions provide a framework for both the Pan Arctic Flora Project (Elvebakk et al. 1999) and the Circumpolar Arctic Vegetation Mapping project (CAVM Team 2003, Walker et al. 2005) and this framework was also applied in this paper. According such subdivisions, the Svalbard archipelago includes three of the coldest zones: **A** (Arctic desert), **B** (northern Arctic tundra) and **C** (middle Arctic tundra). The strong influence of warm ocean currents on terrestrial ecosystems is obvious from the irregular shifts between the different zones (Jónsdóttir 2005).

The vascular plant flora of Svalbard includes about 170 native species and a few introduced species (Jónsdóttir 2005). In addition, at least 373 species of bryophytes, 606 lichen species, 705 fungi, and just over 1,100 terrestrial, freshwater and marine algae and Cyanobacteria are recorded (Elvebakk & Prestrud 1996). The vegetation of western Svalbard lies largely within the A and B zones with some C zone vegetation in the inner-fjord areas. There is a sparse, low-growing cover in much of the outer-fjord areas of *Salix polaris* Wahlenb., *Cerastium arcticum* Lange, *Saxifraga cernua* L., *S. cespitosa* L., *S. oppositifolia* L., *S. hirculus* L., *Luzula arcuata*

(Wahlenb.) Sw., *L. alpino-pilosa* (Chaix) Breistroffer, and *Poa arctica* R. Br. typical for the B zone (Birks et al. 2004). The very open A zone of the extreme north and areas at an elevation above about 100 m lack *Salix polaris* but *Papaver czekanowskii* Tolm. is locally frequent along with *Poa arctica* R., *Phippsia algida* Soland R. Br., *Luzula* spp., *Cerastium arcticum* Lange, *C. regelii Ostenf., Saxifraga* spp., *Sagina intermedia Fenzl.* and a range of bryophytes and lichens. In the inner-fjord areas the vegetation belongs to the C zone with locally frequent *Betula nana* L., *Dryas octopetala* L., *Cassiope tetragona* (L.) D. Don*, Salix reticulata* L.*, S. polaris*, *Saxifraga oppositifolia, S. hirculus, S. nivalis* and extensive moss-dominated carpets. The A zone includes areas with mean temperatures for the warmest month of 3°C or less, whereas the B zone is within the range of 3–5°C and the C zone 5–7°C (Birks et al. 2004). The studies of Svalbard club and coral fungi were carried out in western and central parts of Spitsbergen along the Isfjorden, in three different areas: Pyramiden, Barentsburg and Longyearbyen (Fig. 1). These areas include three

Fig. 1. The Svalbard archipelago and investigated area of Isfjorden (black rectangular): Nordenskiöld Land (Barentsburg, Longyearbyen) and Dickson Land (Pyramiden).

whole bioclimatic subzones, and moreover, contain the major biomass of decaying woody material in central Spitsbergen as they have been central areas of human activity. Pyramiden has been a Russian-run mining settlement from the beginning of the 20th century. Mining activity ceased in 1999 and the settlement was deserted afterwards. About ten square kilometers were surveyed. On Nordenskiöland the area between Barentsburg and Longyearbyen was surveyed. The areas surrounding Longyearbyen are close to several mines. These mines have remained relatively intact during the past 50 years. Barentsburg is the Russian-run settlement of inhabitants. There is no road connecting Longyearbyen and Barentsburg, but on the shore between the two towns there are several small deserted settlements, telephone poles and an experimental drilling station with numerous aggregations of decaying timber. The area covers more that 83 square kilometers. The studied area is one of the richness in vascular plants species on Svalbard (Jónsdóttir 2005).

FIELD SURVEY: The fieldwork took place in July and August of 2008 in cooperation with amateurs (from Ekaterinburg) who worked in Barentsburg. The collected material is deposited in the mycological Herbarium of the Institute of Plant and Animal Ecology of the Russian Academy of Science, Ekaterinburg (SVER). The following references were used for species identification: Corner (1950, 1970), Parmasto (1965a), Berthier (1976), Hansen and Knudsen (1997), Franchi and Marchetti (2001). Names of fungus species and authors follow *Index Fungorum* (2009) and for vascular plants Czerepanov (1995).

QUANTITATIVE ANALYSIS: As much as possible areas with identical types of substrata (habitats) were examined in each subzone. Abundance estimation of i-th species was calculated as the ratio of the number of i-th species registration units compared to the general number of registration units (Novozhilov 2005). Each

sample (registration unit) of i-th species is understood to be a group (colony, cluster) of i-th species fruiting bodies situated not less than 15 m (for soil- and litter-inhabiting fungi) from other similar groups. Basidiomes of i-th species within a group, irrespective of their quantity and size, are considered one registration unit. For wood-inhabiting fungi, a species found on one substrate (stump, trunk) was considered as one registration unit, regardless of the quantity or size of fruiting bodies (Mukhin 1993). Also, the literature defines the i-th species with rather exact occurrence records (area or vicinities of settlement, a substrate) accepted as one registration unit. In virtually all cases, this could be identified without difficulty. The method used in collecting specimens involved removing most of the fruiting body along with a portion of the substrate upon which they occurred.

Material used in the analysis consisted of 110 specimens (registration units) of 'clavarioid' (club/coral basidiomes) fungi: for the Arctic desert (**A**) there are 10 specimens, for the northern Arctic tundra zone (**B**) 23 and for middle Arctic tundra (**C**) 77. Some specimens belonging to genera *Clavaria* and *Typhula* remain unidentified. They most probably represent unknown taxa and will be formally described later. They are excluded from consideration.

Species diversity was calculated using Shannon's diversity index H' = −Σ P_i log P_i, where P_i is the relative abundance (the proportion of the number of records represented by a particular species, Magguran 2004). Dominance was calculated using Simpson's index D = Σ P_i^2. The assemblages of species associated with the different study areas (β-diversity) were compared using a Chao-Søerensen similarity index (C_s) and this calculation was based solely on the presence or absence of species: $C_s = 2c / (a + b)$. Here, *a* is the total number of species in the first dataset being considered, *b* is the total number of species in the second dataset and *c* is the number of

species common for both dataset. The program Statistica 6.0. was used for the cluster analysis. Additional parameters were also used, such as a 'Clavarioid' Index (CLI) calculated as the species richness of fungi with club and coral basidiomes over the total richness of 'Aphyllophorales' (here defined as non-gilled macromycetes) for a data point. The Cryophilic Index (CrI) reflects the share of "Cryophilic species" in comparison to the total richness of club and coral fungi for a point.

Taxonomic parameters were calculated as the percentage of the mono-species genera (MSG) out of the total number of genera and the percentage of the three basic genera (BG) found in all of Northern Eurasia (***Typhula*** *s.l.* [*Typhula*, *Pistillina*, *Pistillaria*], ***Ramaria*** and ***Clavaria*** s.l. [*Clavaria*, *Clavulinopsis*, *Ramariopsis*]) over the total richness of 'clavarioid' fungi in the studied area. To estimate the prevalence of boreal or temperate features, the ratio between *Typhula* (boreal genus) and *Ramaria* (temperate genus) species (T/R) and specimen frequency levels (T_F/R_F) was used. Also, an estimation of the effects of extreme Arctic cold (continental) conditions were calculated as ratios between club and coral life forms for both species (Cl/Co) and specimen frequency levels (Cl_F/Co_F). Overall, the effects of different ecological conditions were calculated using substrate preferences (litter and soil) for both species (Lit/So) and specimen frequency (Lit_F/So_F) levels (Shiryaev 2006).

Other sites and their abbreviations used in the analysis of the distribution of 'clavarioid'-type fungi in the European high-Arctic (includes A–C zones) are: Novaya Zemlya Isles, Russia **(NZ)** (Shiryaev 2006a 2006b) and Yamal Peninsula, Russia **(YP)** (Shiryaev 2006a, 2008a, 2010), both close to the European-Asian border.

Results and Discussion: Except for the three species known from the papers of Huhtinen (1987), Skifte (1994) and Hoshino et al. (2003), no other records of fungi with club and coralloid

basidiomes are known for Svalbard. This study presents the first comprehensive survey for the region. The high number of occurrences of fungi with club and coralloid basidiomes is a surprise for such an extremely cold high-latitudinal region. Based on our own collections and data from the literature, twenty-two species (belonging to 7 genera) are reported from Svalbard, including 19 species that are new for the region. The species are listed in Table 1.

[Also noted is an additional species with a non-gilled basidiome, *Thelephora terrestris* Ehrh. (Thelephoraceae) that was discovered on Svalbard for the first time; it was at the base of alive/dead *Salix reticulata* near Barentsburg.]

SPECIES RICHNESS: The richest genus, *Typhula* contains 13 species (59% of the total) and all other genera include only one (*Artomyces*, *Macrotyphula*, *Ramaria*) or two species (*Clavaria*, *Clavulina*, *Multiclavula*). The overall species/genus ratio is 3.1 (Tab. 2). Only four species are common with more than 10 specimens or registration units): *Typhula crassipes* Fuckel*, T. culmigena* Mont & Fr.) Berthier, *T. lutescens* Boud, *T. variabilis* Riess. They make up only 18% of species richness, but account for 55.5% of the total specimens (Tab. 1); other taxa are rare. *Typhula ishikariensis* was previously mentioned by Hoshino et al. (2003) for Svalbard. All determined species have wide distributions (cosmopolitan, holarctic, Eurasian) in the northern hemisphere (Berthier 1976; Shiryaev 2006a) that include arcto-alpine, boreal or multi-zonal distributions. Many are typical pioneering species (Shiryaev 2006b).

ZONE A: Only five species (two genera) were collected in the most extreme bioclimatic subzone (Table 1): *Typhula* is the richness genus (4 species, 80% of all species) in zone A with only one other species (in *Multiclavula*) reported. The lowest levels of richness and diversity (S/G = 2.5; H' = 1.50) and higher dominance (D = 0.240)

were recorded here in comparisons to other subzones (Table 2). Grass decomposers (sclerotial *Typhula*) comprise 90% of specimens for trophic groups and only one specimen was found on soil (basidiolichen *Multiclavula*). The occurrence of these genera in zone A is not surprising since they are also reported from the Polar Urals and the Novaya Zemlya region by Shiryaev (2006b) who found *Multiclavula corynoides* (Peck) R.H. Petersen, *Typhula lutescens* and *T. phacorrhiza* (Reichard) Fr. about 10 m from a glacier on: naked soil, dead petioles of pioneer vascular plants, and mosses, respectively. Remarkably, *T. phacorrhiza* has a fruiting body that can be over 10 cm in length and its sclerotia are deeply buried in ice-cold moist mosses near waterfalls coming from the glacier. Only the club form was found in the present study. In summary, only the most adaptive groups (potentially sclerotial and symbiotic basidiolichens) were found in the coldest zone.

ZONE B: The number of species found in zone B is higher than for A zone, but the number of genera remains the same (Table 1) and diversity is also slightly higher (S/G = 3.0; H' = 2.04). As in zone A, only litter (on herbs and grasses) and soil inhabiting taxa are present. The four species found here are ecologically similar to those in zone A, however two exist together in a narrow ring of substrate absent in A zone i.e. *Clavaria argillacea* Pers. and *Multiclavula vernalis* (Schwein.) Corner grow together on soil with *Salix polaris* and *Empetrum nigrum*, both of which are absent in zone A. Conversely, *Typhula micans* (Pers.) Berthier and *T. sclerotioides* (Pers.) Fr. prefer dead petioles of herbs that do occur in the A zone but these fungi were not found in that zone. Either (1) their distribution is limited by climatic conditions and/or their own ecology or (2) sampling was insufficient. Also, only the club form was found for these species. Only cold adaptive taxa i.e. potentially sclerotial *Typhula* and symbiotic basidiolichens *Multiclavula* were found in zone A and B.

Table 1. Check-list and ecological data on 'clavarioid'-like fungi of Svalbard.

SPECIES	GF	NS	CAVM ZONES			NOTES
			C	B	A	
Artomyces pyxidatus (Pers.) Jülich	Co	1	1w	–	–	on spruce log – building materials
Clavaria argillacea Pers.	Cl	5	3 s	2 s	–	
Clavaria falcata Pers.	Cl	2	2 s	–	–	
Clavulina cinerea (Fr.) J. Schröt.	Co	4	3 s / 1 w	–	–	on soil, once on wood base of inhabited house in contact with soil
Clavulina coralloides (L.) J. Schröt.	Co	2	2 s	–	–	
Macrotyphula juncea (Alb. & Schwein.) Berthier	Cl	2	2 ll	–	–	on fallen leaves of *Betula nana*
Multiclavula corynoides (Peck) R. H. Petersen	Cl	7	4 Bs	2 Bs	1 Bs	
Multiclavula vernalis (Schwein.) Corner	Cl	4	3 Bs	1 Bs	–	
Ramaria abietina (Pers.) Quél.	Co	2	2 ll	–	–	on litter under *Betula nana* and *Vaccinium uliginosum*
Typhula caricina P. Karst.	Cl	2	2 lg	–	–	on dead petioles of *Carex misandra, Luzula arctica*
Typhula chamaemori L. & K. Holm	Cl	3	3 ll			on dead leaves of *Rubus chamaemorus*
Typhula crassipes Fuckel (syn. *Pistillaria bulbosa* Pat.)	Cl	**16**	8 lg/2 ll	4 lg	2 lg	mostly on dead grasses and herbs: *Campanula uniflora, Papaver dahlianum, Polygonum viviparum, Silene sp.*, seldom on fallen leaves of *Betula nana* and *Salix polaris*
Typhula culmigena (Mont. & Fr.) Berthier	Cl	**11**	7 lg	3 lg	1 lg	on dead grasses and herbs: *Campanula uniflora, Eriophorum scheuchzeri, Cerastium arcticum, Poa alpina, Polygonum viviparum*
Typhula graminum P. Karst.	Cl	1	1 lg	–	–	on dead parts of *Deschampsia caespitosa*
Typhula incarnata Lasch ex Fr.	Cl	1	1 p	–	–	parasite on *Deschampsia alpina*
Typhula ishikariensis S. Imai	Cl	1	1 p	–	–	according Hoshino et al. (2003)
Typhula lutescens Boud.	Cl	**22**	13 lg/1 ll	5 lg	3 lg	on dead herbs: *Campanula uniflora, Papaver dahlianum, Ranunculus lapponicus*, seldom on dead leaves of *Betula nana*
Typhula micans (Pers.: Fr.) Berthier	Cl	2	1 lg	1 lg	–	on dead parts of *Pedicularis dasyantha, Polemonium boreale*
Typhula phacorrhiza (Reichard) Fr.	Cl	4	1 ll /3 m	–	–	
Typhula sclerotioides (Pers.) Fr.	Cl	4	3 lg	1 lg	–	
Typhula setipes (Grev.) Berthier (syn. *T. gyrans* Fr., *T. ovata* P. Karst.)	Cl	2	2 ll	–	–	
Typhula variabilis Riess	Cl	**12**	5 lg	4 lg	3 lg	on dead herbs *Campanula uniflora, Cerastium arcticum, Papaver dahlianum, Ranunculus lapponicus*

GF – growth form (Cl – club; Co – coral)

NS – total number of specimens (most richness in bold)

CAVM – zones by Walker et al. (2005). Species in each zone (no. specimens per each substrate type:

ll = on litter leaves, lg = on litter grasses, s = on soil, Bs = basidiolichens on soil, w = on large dead woody debris of trees or shrubs, m = on mosses, p = parasites on grasses.

ZONE C: Species richness is highest in zone C in Svalbard. All taxa collected in zones A and/or B also occurred in zone C. The number of species and specimens were 2 and 3.4 times higher here, respectively, than in B and A zones (Tab. 1) and included more genera. Diversity was highest here for all study areas in Svalbard (S/G = 3.1; H' = 2.79) and dominance was lowest (D = 0.081). In contrast to zones A and, all trophic groups occurred in zone C. The growth form ratio for the Svalbard study is 4.5 which is similar to that for the whole European Arctic Cl/Co = 5.0) and the frequency ratio is 5.41 compared to that for the whole European Arctic is Cl_F/Co_F = 7.5.

SPECIES ON IMPORTED MATERIAL: Specific taxa found on Svalbard are associated with human activities . *Artomyces pyxidatus* Pers. Jülich is common in the whole forest zone of the Northern Hemisphere, but in treeless Arctic regions it is only found on imported wood used as construction material or fuel and once on driftwood (Shiryaev 2006a, 2006b, 2010). In Barentsburg it was picked up on a pine log in stage II decay by Renvall (1995) inside holes made by beetle larvae. Similar reports are known from other high-latitudinal regions such as Kolguev Island (Russia, Barents Sea) and the

Yamal Peninsula. In Barentsburg, *Typhula graminum* was collected on dead parts of cultivated *Deschampsia caespitosa* L.(Beauv.). It is a common boreal species with a wide distribution, but has never been found as a native element in A, B or C zones of the European Arctic. Perhaps, the regular traffic between Norway, Svalbard and Russia can spread fungi just as it has spread vascular plants. However, it is not known why other "southern" species do not appear on substrata introduced to high-latitude regions. For example, why aren't boreal fungi like *T. trifolii* found on introduced *Trifolium repens* or *Ramaria stricta* on imported wood? Both of the species collected near human activities in Svalbard have been found in similar situations in zone C of other Arctic regions (Shiryaev 2006a, 2006b, 2008a, 2010).

This study adds information to Ohenoja's (1971) contention that: "No Hydnaceae, Clavariaceae and Polyporaceae species have (yet) been found on (Svalbard)...but it is not impossible that the clavariolichens *Multiclavula vernalis* and *M. corynoides* may grow on Svalbard... and also *Clavaria argillacea* may well exist here". Clavarioid fungi have now been reported on Svalbard (including the three species mentioned

Table 2. Assemblages of 'clavarioid' fungi on various substrates from different bioclimatic (CAVM) zones of Svalbard and statistical parameters. S/G – species/genera ratio; Cl/Co – ratio club/coral growth forms (number of species); Cl_A/Co_A – ratio club/coral growth forms (frequency, number of specimens).

PARAMETER	TOTAL	CAVM ZONES		
		C	B	A
Total number of specimens	110	77	23	10
on litter	80	53	23	10
leaves	13	13	–	–
herbs and grasses	67	40	18	9
on soil	12	10	2	–
on wood	2	2	–	–
on mosses	3	3	–	–
basidiolichens on soil	11	7	3	1
parasites on grasses	2	2	–	–
Species	22	22	9	5
Genera	7	7	3	2
S/G	3.1	3.1	3.0	2.5
Cl/Co	4.5	4.5	All club	All club
Cl_F/Co_F	11.2	7.5	All club	All club
Shannon H'	2.79	2.79	2.04	1.50
Simpson D	0.097	0.081	0.146	0.240

by Ohenoja) as well as in other high-Arctic regions like Novaya Zemlya Isles (Shiryaev 2006a, 2006b) and Yamal Peninsula (Shiryaev, 2006a, 2008a, 2010) where their northern limit is the ice-caps in zone A. Moreover, a few "poroid" fungi have now been found, but "hydnoid" forms still appear absent on Svalbard.

TROPHIC GROUPS: Fungi with club and coralloid basidiomes consist of four main trophic groups: mycorrhizal, saprotrophic, parasitic and basidiolichens . For this study, the mycorrhizal trophic group is included in the litter, soil, and wood-inhabiting groups since this trophic type is not confirmed for these species in the Arctic.

In this respect, "saprotrophs" have the most diverse assemblage (18 species, all substrate specific, 94 specimens) that are distributed in all bioclimatic zones (Tab. 2). Whereas, symbiotic basidiolichens (2 substrate specific, 11 specimens, found in all zones) and parasites (2 obligate species, 2 specimens, found only in the C zone) have limited diversity. The 'saprotrophic' group as defined comprises 81.8% of all species and 85.5% of all specimens. The litter-inhabiting species (on fallen leaves and dead grasses) were highest in richness and specificity (3 genera, 13 species, 12 occurring exclusively on litter, 80 specimens) and were distributed in all three subzones. The soil-inhabiting group was second (2 genera, 4 species, 3 occurring exclusively here, 12 specimens) with reduced richness and fewer specialized species. Other substrates are species-poor, including those on: moss (1 genera, 1 obligate species, 3 specimens) and wood (2 genera, 2 species, 1 species exclusively here, 2 specimens), and both groups occur only in zone C. Overall, the species richness is comparable to that of other high-Arctic regions.

Litter-inhabiting species include those that (1) decay leaves and (2) occur on dead petioles of grasses and herbs. The latter includes the largest number of specimens (67) and has the richest biota (2 genera, 7 species, 6 exclusively here)

which grow in all bioclimatic zones. All species in common are in *Typhula* which grows on decaying grasses and herbs. In contrast, only 13 specimens were collected on decaying leaves but they are quite diverse (7 species). The relative richness (and thus importance) of the litter-inhabiting group increases in the northern direction: however in the forest-tundra this parameter includes 57±3% of all species while in zones C and D it reaches 85% (Shiryaev 2006a, 2010), and the number of specimens make-up 60-87% of the total.

MORPHOLOGICAL FORMS AND LATITUDINAL GRADIENT: A wider analysis of Svalbard fungi using the literature reveals interesting proportions of basidiomes in "Aphyllophorales" (except "Heterobasidiales"). According Gulden & Torkelsen (1996), Kosonen & Huhtinen (2008), and current work, the "clavarioid life form" makes up more than half (CLI = 0.53) of the whole compiled list, whereas "corticioid", "poroid" and "thelephoroid" fungi (life forms) are less diverse. Moreover, if we exclude species collected on manufactured imported wood, this parameter is higher (CLI = 0.91). Studies of Northern Eurasian ecosystems, have shown, that this parameter obviously decreases from north to south (t = 6.22; p < 0.001). For example, in the forest-tundra of Murmansk, Kola Peninsula CLI is 0.25 (Shiryaev 2009a) and in the boreal forests of Finland CLI is 0.14 (Kotiranta et al. 2009; Shiryaev 2009b). This parameter increases again to the south in the southern boreal and hemiboreal zones (Shiryaev 2009c) and towards the steppes and treeless areas (Rostov region, Russia) where CLI is 0.44, and also in semi-deserts. As in the Arctic and Boreal zones of Northern Eurasia, the 'clavarioid' life form Index (CLI) increases and strongly correlates (r = 0.9, p < 0.001) with decreasing tree and shrub richness both in northern (tundra) and southern (steppe) directions; it also increases to the East as climate becomes increasingly continental (East Siberian taiga and tundra).

Moreover, treeless versus forest areas include different proportions of club and coral growth forms (*Cl/Co*). For example, in the current study this ratio is 4.5 (average for the European Arctic = 5.0) which reveals the high relative richness of simple tiny club-like fruiting bodies (mostly *Typhula*) over multibranched fleshy coral-like species i.e. *Ramaria*, *Clavulina,* etc. In a southerly direction, this ratio decreases to 2.7 in forest-tundra and to 1.4 in southern boreal forests. Equilibrium (1.0) is reached in the hemiboreal and temperate zone where the coral form exceeds the number of club forms (*Cl/Co* = −2.5). In forest-steppe this ratio hovers around equilibrium and in the steppe zone, the club growth form dominates again (*Cl/Co* = 1.8).

Thus, the ratio of club/coral growth form changes in a north-south gradient suggesting this correlates with various life zones. Overall, the richness of the two life forms is statistically very different (t = 3.90, p < 0.001). The number of "saprotrophic" and parasitic groups also differs statistically (t = 4.41, p < 0.001). Distribution analysis of combined groups (life form/trophic group) shows that for the high Arctic, club-like litter-inhabiting fungi (*ClLit*) are the most common, whereas the grass and herb decaying group is the richest (Tab. 3). These are followed by club-like soil-inhabiting basidiolichens (*Multiclavula*) that are eco-morphologically adapted to extreme environments.

RELATIVE IMPORTANCE OF SVALBARD 'CLAVARIOID' FUNGI IN THE MYCOTA OF THE EUROPEAN HIGH ARCTIC : As shown in Table 4, our data from Svalbard fit well into patterns obtained in studies of other European high-Arctic regions such as Novaya Zemlya (Shiryaev 2006a, 2006b) and Yamal Peninsula (Shiryaev 2006a, 2008a, 2010). A comparison based on the adjusted indices of the Chao-Søerensen similarity index C_s shows the 'clavarioid' fungal biota of Svalbard to be most similar to that of Novaya Zemlya (C_s = 0.85) which has similar bioclimatic conditions (A–C zones) differing slightly from the Yamal Peninsula (C_s = 0.69) which has a wider biogeographic range (zones B–E and also forest-tundra) strongly influenced by boreal elements. Also, the Ob' river brings warm waters from southern regions (China, Kazakhstan, Altai, Southern Urals) that provide more favorable conditions for boreal plants and fungi. All species from zones A–D were also found in forest-tundra.

Of the 24 species of 'clavarioid' fungi known for

Table 3. Species richness of the 'clavarioid' mycota in three bioclimatic (CAVM) zones of Svalbard. abbreviation (−) means parameter is absent for this zone. Abbreviations of study zones as in Table 2.

SUBSTRATE	TOTAL		CAVM ZONES					
			C		B		A	
	Club	Coral	Club	Coral	Club	Coral	Club	Coral
On litter	3/12/78	1/1/2	2/12/51	1/1/2	1/6/18	−	1/4/9	−
leaves	2/6/11	1/1/2	2/6/11	1/1/2	−	−	−	−
grasses and herbs	1/7/67	−	1/7/40	−	1/6/18	−	1/4/9	−
On soil	2/2/7	2/2/5	1/2/5	2/2/5	1/1/2	−	−	−
On wood	−	2/2/2	−	2/2/2	−	−	−	−
On mosses	1/1/3	−	1/1/3	−	−	−	−	−
Basidiolichens on soil	1/2/11	−	1/2/7	−	1/2/3	−	1/1/1	
Parasites on grasses	1/2/2[7]	−	1/2/2	−	−	−	−	−
Total	4/18/101	3/4/9	4/18/68	3/4/9	3/9/23	−	2/5/10	−

Numbers represent: number of genera / number of species / number of specimens. Grey color highlights the richest and most frequent group in each zone and for Svalbard.

European high-Arctic regions (zones A–C), only eleven are regularly collecting in all three regions: *Clavaria argillacea, C. falcate Pers., Clavulina cinerea* (Fr.) J. Schröt., *Multiclavula corynoides, M. vernalis, Typhula crassipes, T. culmigena, T. incarnata* Lasch *ex Fr., T. lutescens, T. phacorrhiza* and *T. variabilis.* All also occur in the boreal zone where some reach their highest occurrence and are found on a wide range of substrates. Thus, it can be concluded that the high-Arctic 'clavarioid' mycota is basically a depauperate version of that found in the boreal region.

Practically all species known from the high-Arctic are multi-zonal (occurring from Mediterranean and steppe areas to tundra and Arctic deserts) in Eurasia. However, a few species recorded elsewhere as rare were fairly common in this study which indicates there is a certain degree of distinctiveness to the Arctic 'clavarioid' mycota.

Table 4. Pairwise comparisons of clavarioid mycota among three high-Arctic regions. The total of all specimens was used for calculation of the adjusted incidence-based Chao-Søerensen similarity indices (C_s).

	SV	NZ	YP
SV	–	**0.85**	0.69
NZ	17	–	0.76
YP	22	17	–

Abbreviations for study areas: SV – Svalbard, NZ – Novaya Zemlya, YP – Yamal Peninsula.

For example, *Multiclavula corynoides* and *M. vernalis* occur in zones A and B, respectively, and also in boreal forests, the southern taiga and high-mountainous terrain (the Alps, Carpathians, Caucasus, Ural, Tjan-Shan, Altai, Sajan). While both species appear to have characteristic Arcto-Alpine distributions, they are most abundant in other zones (E zone and forest-tundra). This is also true of other Arcto-alpine fungi such as *Ramariopsis subarctica* Pilát and *Typhula chamaemori* L. Holm & K. Holm (Shiryaev 2006a).

Overall, it is impossible to join species into a delineated Arcto-Alpine group because the ecological optimum of each species is not in the Arctic and all are widely distributed in both mountainous and boreal areas. One characteristic that possibly unites these species is their preference for cold habitats; accordingly, they could be considered a "Cryophilic group". The four species mentioned above occur on Svalbard (CrI = 0.18), but decrease on the southern end (zone E of the Kola Peninsula CrI = 0.14). The cryophilic elements mostly disappear in the middle boreal zone, but solitary specimens may be picked up by the sea, river shores and in Sphagnum bogs of the hemiboreal zones (Shiryaev 2006a; Kotiranta et al. 2009; Shiryaev et al. 2010). Perhaps, in such southern regions they should be considered Pleistocene relicts (Shiryaev, 2008c).

The complex of fungi with club/coralloid basidiomes (and perhaps other fungal groups) of high-Arctic regions can be considered a depauperate mycota of the taiga zone (Mukhin 1993, 2000; Nezdoiminogo 2003; Shiryaev 2006a, 2010; Zhurbenko 2009), and also of the tundra areas to the south (zones D and E) which have the lowest species richness (*S*), generic richness (*G*)), and diversity indices. In the two most northern, zones species richness is similar and within a limited interval (*S* = 4.5±0.5 sp. in zone A, 8.0±1.0 sp. in zone B), but jumps to 17.5±4.5 in zone C. (Tab. 5A). For comparison, in most southern Arctic areas (zone E) *S* = 28.5±3.5 (Shiryaev 2006a, 2010). In addition, the number of genera in zones A an B is similar (2 and 3, respectively) but is two times higher (*G* = 6±1) in zone C. Thus, species composition for the three high-Arctic zones is comprised of two clusters 1) most northern areas (zones A and B) and 2) the C zone. The absence of coral growth forms in zones A and B also distinguishes this group from the zone C group (Fig. 2).

Both the *S/G* ratio and diversity index increase from north to south (Tab. 5B). As a whole, these

parameters are considerably lower in high-Arctic regions, in southern areas of tundra, and also in the taiga (Shiryaev 2006a), confirming the hypothesis, that the mycota is more developed (diverse) in areas with more optimal hydrothermal conditions and high diversity of vegetation, and that there is a progressive simplification of the mycobiota under less favorable conditions (Odum 1971; Mukhin 1993; Shiryaev, 2006a). The zonal dynamics of the dominance index also confirms this (Tab. 5C).

Table 5. Species richness (A), diversity (B) and dominance (C) of 'clavarioid' fungi in the three regions of the European high-Arctic. (–) means that parameter is absent in this region. Abbreviations for study regions as in Table 4. Regions are placed in the table.

(A)

CAVM zone	SV	NZ	YP
A	5/2	4/2	–
B	9/3	8/3	7/3
C	22/7	17/6	13/5

Total number of species / total number of genera.

(B)

CAVM zone	SV	NZ	YP
A	2.5/1.50	2.0/1.38	–
B	3.0/2.04	2.6/1.90	2.3/1.82
C	3.1/2.78	2.8/2.63	2.6/2.33

Ratio species:genera in this point /Shannon (H') diversity index.

(C)

CAVM zone	SV	NZ	YP
A	0.240	0.256	–
B	0.146	0.159	0.181
C	0.081	0.095	0.117

Simpson's (D) dominance index.

Biogeographical studies of genus *Typhula* show a tendency for it's relative species richness and frequency to increase ($p < 0.001$) in the Polar direction, especially as continental conditions increase (Berthier 1976; Shiryaev 2006a, 2008b). In comparison to the temperate genus *Ramaria*,

the relative importance of genus *Typhula* in high-latitude regions is high (T/R = 13.0). This ratio decreases towards the southern boreal zone where it reaches equilibrium (1.0) and in native tropical environments *Typhula* is absent, but *Ramaria* richness increases.

CONTINENTAL CLIMATE (LONGITUDE) AND THE EUROPEAN HIGH ARCTIC 'CLAVARIOID' FUNGI: There is scant information on longitudinal changes in mycota. The three study sites comprise a west-east transect, where Svalbard has the most suitable hydrothermal conditions influenced by warm waters of the Gulfstream. Novaya Zemlya is situated on the north-eastern edge of the current which moderates the cold Siberian continental climate. To the north the Yamal Peninsula lies in the Kara Sea and has the most continental climate (of the three sites) with a long ice and snow cover period and poor vegetation.

Changes in richness and diversity can clearly be demonstrated across this gradient (Tab. 5). The hypothesis that the "mycobiota is more developed under more optimum hydrothermal conditions with a diverse vegetation appears to be supported here, although it should be noted that the study depends on 'fruiting conditions', and results may only reflect visibility of the fungi and not necessarily occurrence. Svalbard obviously has a milder climate in comparison than more eastern regions such as Novaya Zemlya and especially of Yamal Peninsula, and results do follow the expected longitudinal gradient in the present study of Arctic fungi (Tab. 6).

Taxonomical differences between Svalbard and the high-Arctic part of Yamal Peninsula (zones B and C) are clearly shown in Table 4 and are particularly obviously in zone C where the species richness of Svalbard is two times higher (as is that for genera). Changes in *S/G* ratio, both in diversity and dominance indices also show increases as continental climate increases from

west to east (Tab. 6). Overall, Svalbard and Yamal are statistically different ($t = 3.64$, $p < 0.001$) with Svalbard having a higher diversity of these fungi.

Arctic conditions that increase towards the eastern direction are correlated with an increase in the Cryophilic Index (CrI) which is two times higher for Yamal. The 'Clavarioid' Index (CLI) for Yamal is higher than for Svalbard ($p < 0.01$) and the growth form ratio on a species level (*Cl/Co*) also reflects the less favorable conditions; similarly, there is a difference in the ratio for growth form frequency (*Cl_F/Co_F*) ($t = 2.24$, $p < 0.05$). Taxonomical differences in *T/R* ratios were not significant.

As mentioned before, most of the "high-Arctic" clavarioid species were found on decaying parts of vascular plants which decrease in richness and biomass as cold, continental conditions increase in the Arctic (Odum 1971; Walker et al. 2005). Accordingly, the richness of the Yamal mycota is two times poorer in both species and genera (Tab. 6) which is primarily a result of a decrease of litter-inhabiting species (Tab. 5). The number of soil and wood inhabiting species, as well as parasites remains relatively constant at low levels (Shiryaev 2010). Finally, it possible to say, that the share of club fungi that prefer grasses and clavarioid fungi in litter (*$ClLitg_F$*) increases in zone C from Svalbard to Yamal (Tab. 6) and especially towards the Western Taimyr Peninsula. These regions are relatively different ($\chi^2 = 3.93$, $p < 0.05$) and this increase is strongly correlated ($r = 0.79$, $p < 0.01$) with a decrease in mean maximum temperature of the warmest month (°C). Considerably more important might be July temperatures (Chapin et al. 1996) which on the western Spitsbergen reach 15° C and day time temperatures that sometimes rise to 25° C (Jónsdóttir 2005) and remain for some days.

IN SUMMARY: Clavarioid-type fungi dominate more than 90% (CLI = 0.91) the check-list of "Aphyllophorales" in native environments on

Svalbard and that for the European high-Arctic regions. Further, fungi with club-like basidiomes on litter (*ClLit*) are generally the richness group with the highest frequency. Within this group, the subgroup on dead grasses and herbs (*ClLitg*)

Table 6. Taxonomic and ecological comparison of the European high Arctic 'clavarioid' mycota: the most western region for the current study (Svalbard) and most eastern (Yamal Peninsula, B and C zones) using significance parameters for latitudinal gradient.

Parameter	Svalbard	Yamal
Longitude (mean E°)***	20	70
Number of species**	22	13
Number of genera*	7	5
*S/G***	3.1	2.6
T/R	0.59	0.61
MSG	43.2	60.0
BG·	77.0	69.2
CLI*	0.53	0.68
CLInat	0.91	0.93
CrI	0.18	0.31
Shannon H'**	2.79	2.33
Simpson D*	0.097	0.127
*Cl/Co***	4.5	5.4
*Cl_F/Co_F**	11.2	14.7
Lit, sp.***	13	7
Lit	73.1	75.2
Lit/So	2.3	2.0
Lit_F/So_F	3.48	3.50
ClLitg	54.3	54.5
$ClLitg_F$	61.4	68.3

S/G – species/genera ratio; *T/R* – Typhula/Ramaria ratio; MSG – percent mono- species genus; BG – percent basic genera; CLI – Clavarioid Index; CLInat. – Clavarioid Index for native ecosystems (except species on imported substrates artificial for tundra); CrI – Cryophilic Index; *Cl/Co* – club/coral growth form ratio (number of species); *Cl_F/Co_F* – club/coral growth forms ratio (frequency, number of specimens); Lit – percent of litter-inhabiting species; *Lit/So* – litter/soil inhabiting ratio (number of species); *Lit_F/So_F* – litter/soil inhabiting ratio (frequency, number of specimens); ClLitg – percent of club-like fungi on grasses and herb litter (number of species); *$ClLitgI_F$* – percent of club-like fungi on grasses and herb litter (frequency, number of specimens). Significance values are starred: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Not significant ($p > 0.05$), not starred.

dominated by the genus *Typhula* (potential sclerotial organisms) the richness and most frequent group. According, the whole European high-Arctic "Aphyllophorales mycota" should be eco-morphologically be named "fungi with club-like basidiomes on grasses and litter of herbs ", or taxonomically, "sclerotia-forming *Typhula* ". Domination of this group increases in the eastern direction with latitude and continental climate and also with latitude. This is also a reflection of the paucity or absence of other groups of aphyllophoraceous-type fungi such as those with poroid, hydnoid and thelephoroid basidiomes, although the latter might exist as mycorrhizae.

Undoubtedly, the high-Arctic clavarioid mycota is different from the low-Arctic and boreal-forest mycota. However differences in taxonomical, morphological, biogeographical and ecological parameters are also found between 1) zones A and B and 2) zone C; it is also possible to join most of the northern zones of each study area. An analysis of differences between Svalbard and the Yamal Peninsula suggests a possible taxonomical and biogeographical demarcation between the European and the Siberian part of the high-Arctic which might be addressed in future studies.
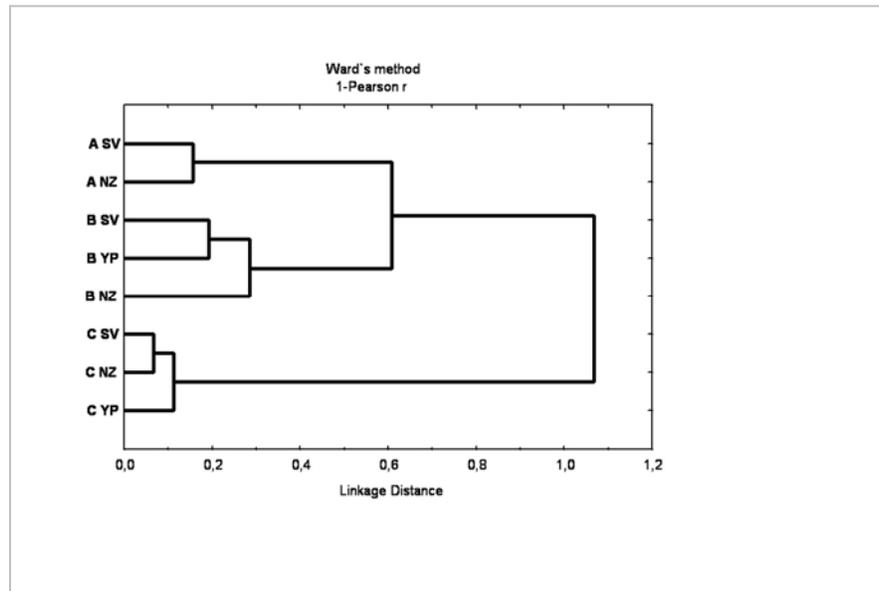

Fig. 2. Similarity of high Arctic clavarioid fungi regional mycotas. Abbreviations: A, B, C – CAVM zones (Walker et al., 2005). SV – Svalbard, NZ – Novaya Zemlya, YP – Yamal Peninsula.

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