

## CONTRIBUTION TO THE KNOWLEDGE OF *RAMARIOPSIS* *SUBARCTICA* (CLAVARIACEAE, BASIDIOMYCOTA)

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**Abstract.** Although general knowledge of *Ramariopsis subarctica* Pilát has advanced in the past four decades, there is still little understanding of how the species is distributed and which aspects of the environment determine its distribution. This paper presents the first Polish collections of the species. Hitherto unknown in Poland, *R. subarctica* is reported from two localities in subalpine belts of the West Tatra Mts and Karkonosze Mts. The morphology of newly collected basidiomata of the fungus is described, illustrated and commented, and some basic chemical parameters of its habitat in the Karkonosze Mts are given. All available published material relevant to the global distribution and ecology of *R. subarctica* is reviewed.

**Key words:** arctic and subalpine habitats, biogeography, clavarioid fungi, *Clavulinopsis subarctica*, distribution, ecology, taxonomy

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### INTRODUCTION

All members of the genus *Ramariopsis* (Donk) Corner probably have evolved a biotrophic nutritional mode (Birkebak *et al.* 2013). Macroscopically the fungi are distinguished by their small to medium-sized, branched or rarely unbranched basidiomata, often with a distinct stem and usually slender, cylindrical branches. Microscopically they can be distinguished mainly on the basis of their echinulate or verrucose to almost smooth spores showing cyanophilous ornamentation, and the presence of clamps at the basidia and hyphae (Knudsen & Shiryayev 2012b). Fungi of the genus *Clavulinopsis* Overeem are superficially similar but have smooth basidiospores as a rule (Knudsen & Shiryayev 2012a) and differ fundamentally in spore wall ultrastructure (Pegler & Young 1985). Recent phylogenetic analyses of nuclear ribosomal large subunit RNA (nrLSU) sequences support the monophyly of *Ramariopsis* species with ornamented spores, clamps in trama and branched

basidiomata (subgen. *Ramariopsis*), and suggest a paraphyletic origin of the remaining taxa with (almost) smooth spores (Kautmanová *et al.* 2012). Different generic and infrageneric concepts of *Ramariopsis* and allied taxa are presented by various authors (e.g., Corner 1950, 1970; Petersen 1978; Jülich 1984, 1985; Hansen & Knudsen 1997; Krieglsteiner 2000; Olariaga & Salcedo 2012). Even though molecular methods have been applied, many problems remain unsolved (García-Sandoval *et al.* 2005; Dentinger & Mclaughlin 2006; Kautmanová *et al.* 2012). According to Kirk *et al.* (2008), *Ramariopsis* is represented by ca 44 species worldwide. As of October 2016, *Index Fungorum* included 40 valid species in *Ramariopsis*. In this paper we prefer to use the generic concept of *Ramariopsis* proposed by Knudsen and Shiryayev (2012b).

Depending on the systematic treatment, 7–9 species of *Ramariopsis* are known in Europe (Domański 1984; Jülich 1984, 1985; Krieglsteiner 2000). Five species of this genus were

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found previously in Poland: *Ramariopsis crocea* (Pers.: Fr.) Corner [syn. *Clavulinopsis crocea* (Pers.) Jülich], *R. kunzei* (Fr.) Corner [syn. *Clavulinopsis kunzei* (Fr.) Jülich], *R. pulchella* (Boud.) Corner [syn. *Clavulinopsis pulchella* (Boud.) Jülich], *R. subtilis* (Pers.: Fr.) Corner [syn. *Clavulinopsis subtilis* (Pers.: Fr.) Corner] and *R. tenuiramosa* Corner (Schröter 1885–1889; Błoński 1890; Wojewoda 1974, 2003; Gumińska 1976, 1981; Kujawa & Gierczyk 2013; Nowicki & Gierczyk 2013a, b), all of them recorded from few collections and with only brief descriptions of characteristics.

This paper presents the first Polish records of *Ramariopsis subarctica* Pilát [syn. *Clavulinopsis subarctica* (Pilát) Jülich], with comments on the morphological variability of the species and its habitat requirements. We also give detailed information on the occurrence of the fungus along with the accompanying ecological conditions in the Karkonosze Mts, which may be useful in understanding the role, status and ecological requirements of *R. subarctica* in mountainous regions of Central Europe. We also summarize the available ecological and distributional data for *R. subarctica* worldwide.

## MATERIAL AND METHODS

### SAMPLING

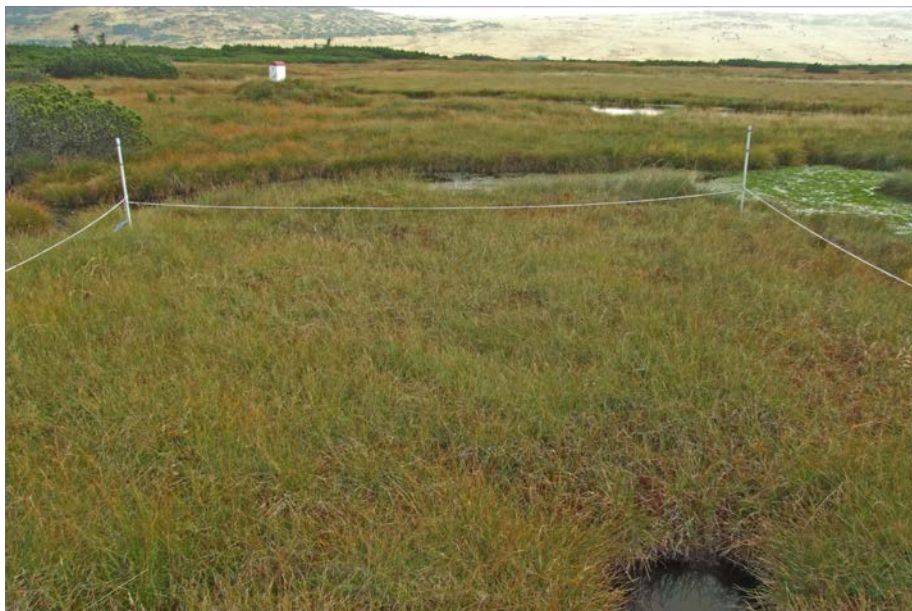
Originally this paper was planned to be based on material collected in the Polish part of the Karkonosze Mts, where comprehensive ecological studies of subalpine mires are being conducted by one of the authors (PP). At a late stage of our research, however, it emerged that one earlier gathering of *R. subarctica* originating from the Polish part of the Tatra Mts is housed at SVER herbarium. The specimens from the Tatra Mts represent the first authentic Polish record of *R. subarctica* documented by voucher material. Because the location data for the material from the Tatra Mts is sketchy, and due to time restrictions, it was not possible to compile a dataset describing the Tatra site conditions comparable in quality and scope to the data for the Karkonosze Mts. Here we base the site description and ecological characteristics on the accurate data collected from the Karkonosze Mts. The studied fungi are deposited in the WRSL and SVER collections.

### ENVIRONMENTAL STUDY IN THE KARKONOSZE MTS

The investigated mire lies on Równia pod Śnieżką, a subalpine plateau. It is situated at 1437 m a.s.l. (Ignaciuk 2006). In order to characterize the ecological conditions, water samples were taken from the nearest bog hollows and collected into 100 ml acid-washed polyethylene bottles. Water pH and conductivity were measured in the field with a HI 991300 pH-meter. Both parameters were standardized at 20°C. Conductivity was corrected according to Sjörs (1950). The collected water samples were filtered through a glass-fiber filter and stored at 4°C. We determined the content of Na, K, Ca and Mg by atomic absorption spectrometry (GBC Avanta), and  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$  and  $\text{SO}_4^{2-}$  with a flow-injection analyzer (FIA analyzer, MLE). In order to characterize the vegetation in which the sampled specimens occurred, we made a phytosociological relevé in a 25 m<sup>2</sup> plot, following the methodology of Braun-Blanquet and scoring cover on a 7-point scale. Nomenclature follows Kucharski and Kopeć (2007) for plant communities, Mirek *et al.* (2002) for vascular plants, Ochyra *et al.* (2003) for bryophytes, and *Index Fungorum* (Kirk 2016) for fungi except for *Ramariopsis* (Knudsen & Shiryayev 2012b).

### MORPHOLOGICAL STUDY

The description of macro- and micromorphological characters of *Ramariopsis subarctica* is based on the collection from the Karkonosze Mts (WRSL: PeP-2014-001). The macroscopic description is based on study of fresh material and photos. Micromorphological characters were observed from dried material with a Nikon Eclipse E-400 light microscope fitted with a Nikon digital camera (DS-Fi1). Freehand sections of rehydrated pieces of basidiomata were examined in 5%  $\text{NH}_3 \cdot \text{H}_2\text{O}$  reagent with 1% Phloxine B, and reactions in Melzer's reagent and Cotton Blue were also tested. Image-grabbing and biometric analyses were made with NIS-Elements D 3.1 imaging software. Dimensions of microcharacters were given as (minimum) 10–90 percentile (maximum) values ( $n$  = sample size). Statistical computations employed Statistica (StatSoft). Spore length/width ratio is reported as Q. For basidiospore size measurements, randomly selected mature spores were measured without the hilar appendix and excluding ornamentation. Basidia length was measured excluding sterigmata. Details of hymenial elements were drawn freehand on tracing paper over photographs at 4000×. Morphological terminology follows Hansen and Knudsen (1997). Herbaria abbreviations follow *Index Herbariorum* (Thiers 2017).



**Fig. 1.** Locality of *Ramariopsis subarctica* Pilát on a subalpine plateau in the Karkonosze Mts. The vegetation is dominated by *Eriophorum vaginatum* and *Sphagnum russowii*. Równia pod Śnieżką in the Karkonosze Mts, 4 Sept. 2014.

## RESULTS

### FLORISTIC CHARACTER AND SITE CONDITIONS IN THE KARKONOSZE MTS

The vegetation in which *Ramariopsis subarctica* was recorded presents the typical composition of the *Sphagno robusti-Empetrum hermaphroditii* community (Fig. 1). Plant species coverage in the relevé was as follows: herb layer c – *Eriophorum vaginatum* 3, *Andromeda polifolia* 2, *Carex pauciflora* 2, *Deschampsia flexuosa* 1, *Vaccinium myrtillus* 1, *Vaccinium uliginosum* +, *Oxycoccus palustris* +, *Calluna vulgaris* +; moss layer d – *Sphagnum russowii* 5, *Polytrichum strictum* 2, *Sphagnum lindbergii* 2, *Sphagnum compactum* 1, *Plagiothecium laetum* +. The herb layer is scattered, with sedges dominating and a small share of dwarf shrubs. Apart from small shares of *S. lindbergii* and *P. strictum*, the moss layer is dominated by *S. russowii*. Both layers are meager, with no more than 14 plant species altogether. The habitat of *R. subarctica* in this area can be characterized as acid and oligotrophic, with water in the surrounding bog hollows at pH 3.86 and conductivity at 3  $\mu$ s.

The habitat is poor in nutrients (K 0.428 mg/l, Na 0.498 mg/l,  $\text{NO}_3^-$  0.005 mg/l,  $\text{NH}_4^+$  0.03 mg/l,  $\text{PO}_4^{3-}$  0.023 mg/l,  $\text{SO}_4^{2-}$  10.3 mg/l) and minerals (Ca 0.568 mg/l, Mg 0.107 mg/l).

### THE SPECIES

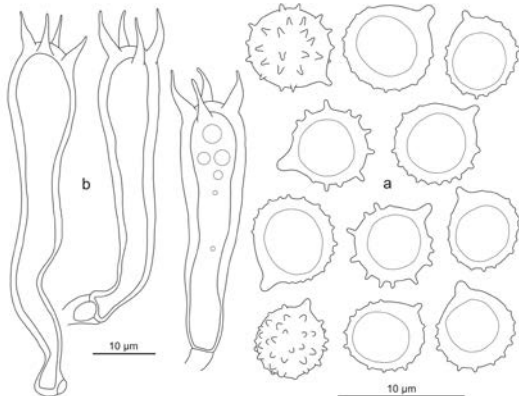
***Ramariopsis subarctica* Pilát** Figs 2 & 3  
Česká Mykol. 25(1): 10. 1971.

Basidiomata 35–55 mm high and 25–40 mm wide, solitary, gregarious to caespitose, repeatedly 2–4 times branched (di- to trichotomous) with distinct fasciculate and confluent stems, rather elastic, cream at base, otherwise pale yellow to pale ochraceous; branches 1.6–3.5 mm thick, with rounded to slightly inflated, blunt tips, smooth to slightly tomentose (main branches). Stem 6–13  $\times$  2.0–2.5 mm, cylindrical, at base somewhat broader, more or less hidden in mosses, shortly tomentose. Context concolorous. Smell and taste not verified. Basidiospores (5.0) 5.5–7.0 (7.5)  $\times$  (4.5) 5.0–6.5 (7.5)  $\mu$ m, Q = (1) 1.0–1.1 (1.3) (n = 161) for the Karkonosze Mts, (5.1) 5.4–7.2 (7.7)  $\times$  (4.2) 4.6–6.2 (6.7) Q = 1.16 (n = 30) for the Tatra Mts,



**Fig. 2.** *Ramariopsis subarctica* Pilát on a *Sphagnum* mire. Równia pod Śnieżką subalpine plateau in the Karkonosze Mts, 4 Sept. 2014.

globose, subglobose to broadly ellipsoid, mostly 1-guttate, minutely spiny (echinulate) to verruculose, spines to 0.5  $\mu\text{m}$  high, cyanophilous, apiculus 0.6–1.3  $\mu\text{m}$  long. Basidia (33.0) 35.0–54.0 (57.5)  $\times$  (9) 9–11 (11)  $\mu\text{m}$  ( $n = 22$ ), mostly 4-spored, rarely 2-spored, mostly sclerified (in Karkonosze Mts material). Subhymenium and trama in main branches composed of 2–8  $\mu\text{m}$  thick, interwoven to somewhat parallel hyphae. Surface of sterile base covered by repent, cylindrical hyphae ca 2.0–4.5  $\mu\text{m}$  thick. Clamp connections present in all tissues.



**Fig. 3.** Micromorphological characters of *Ramariopsis subarctica* Pilát. A – basidiospores, B – thick-walled (sclerified) basidia (all from WRSL PeP-2014-001).

**SPECIMENS EXAMINED.** POLAND, SUDETY Mts, Karkonosze Mts: Równia pod Śnieżką subalpine plateau, on bank of *Sphagnum* mire among living mosses (*Sphagnum russowii*, *S. lindbergii*, *Polytrichum strictum*) and vascular plants (*Andromeda polifolia*, *Carex pauciflora*, *Eriophorum vaginatum*, *Oxyccocus palustris*), 50°44'N, 15°41'E, 1430 m a.s.l., 4 Sept. 2014, P. Pech PeP-2014-001 (WRSL); CENTRAL WESTERN CARPATHIANS, West Tatra Mts: in the vicinity of Dziurawe hillside, on bank of moss (also *Sphagnum*) and ericoid-dominated plant community, on mound rising above community floor, among mosses and creeping dwarf shrubs, together with *Clavaria sphagnicola* Boud., 49°14'N, 19°53'E, 1650 m a.s.l. 26 Sept. 2008, A. Shiryayev AGS 26918 (SVER).

**ADDITIONAL SPECIMENS EXAMINED.** NORWAY, FINNMARK (Nordkapp), 4 Aug. 2013, A. Shiryayev AGS 17032 (SVER); RUSSIA, URAL: Yamal-Nenets Autonomous District (Rai-iz massif): 2 Sept. 2006, A. Shiryayev AGS 203 (SVER); EAST SIBERIA: middle part of Yenisei river basin, 16 Aug. 2015, A. Shiryayev AGS 25951 (SVER); Tunguska River basin, 22 Aug. 2015, A. Shiryayev AGS 12687 (SVER).

## DISCUSSION

### TAXONOMY AND MORPHOLOGICAL VARIABILITY

On the basis of basidiospore ultrastructure studies, no close phyletic relationship between *Ramariopsis* and 'allied' genera was supported (Pegler & Young 1985). Therefore, Jülich's (1985) placing of the genus *Ramariopsis* in synonymy with *Clavulinopsis* and making of new combinations (including those for *Ramariopsis subarctica*) does not seem justified. Among European members of *Ramariopsis*, *R. subarctica* is recognized morphologically by its pale yellow to ochraceous basidiomata with rather thick branches (2–4 mm diam.) and the comparatively large basidiospores (>5.5  $\mu\text{m}$  wide on average) (Knudsen & Shiryayev 2012b). Macroscopically, both Polish collections well fit the published descriptions, and especially correspond to the species concept of Daun and Nitare (1987). Measurements of basidiospores from the Karkonosze Mts (PeP-2014-001), seem to differ from those of the Tatra Mts (5.1–7.7  $\times$  4.2–6.7  $\mu\text{m}$ ,  $Q = 1.16$  ( $n = 30$ ), AGS 26918), Finnmark (4.8–7.6  $\times$  4.0–7.0  $\mu\text{m}$ ,  $Q = 1.15$  ( $n = 30$ ), AGS 17032), Ural (5.3–7.9  $\times$  4.1–5.8  $\mu\text{m}$ ,  $Q = 1.3$  ( $n = 30$ ), AGS

203) and East Siberia ( $5.2\text{--}8.1 \times 4.0\text{--}7.0$ ,  $Q = 1.25$  ( $n = 30$ ), AGS 12687) in their more subglobose than broadly ellipsoid shape. Moreover, we frequently observed over-refined (sclerified) basidia in the collection from the Karkonosze Mts. This type of basidia was also reported in *R. subarctica* by Daun and Nitare (1987), but they observed them only occasionally. It is worth noting that the presence of sclerified basidia is a more common phenomenon, occurring not only in Clavariaceae (e.g., Petersen 1971, 1979); it is also known in agarics (Bas 2003), for example.

#### POPULATION CONDITION, PHENOLOGY AND SUBSTRATE SPECIFICITY

*Ramariopsis subarctica* was found at the end of September 2008 in the Tatra Mts. The material from this area was collected during an ordinary autumn trip to the mountain range. Information on the total number of mature individuals was not then recorded, and care was not taken to record the specific substrate. In the Karkonosze Mts we made a search for *R. subarctica* when the species was noticed by chance in early September 2014 in several groups of basidiomata. In the next year it was only found growing solitary in the area in October. In two years fewer than 10 groups of basidiomata distributed over an area of ca 400 m<sup>2</sup> were recorded in the peat bog on the Równia pod Śnieżką subalpine plateau. There the occurrence of *R. subarctica* was confined to *Sphagnum* tufts and slightly raised parts of the mire. Our observations made at the locality revealed that its basidiomata had a preference for decaying thalli of *Sphagnum*, preferring to grow among *Sphagnum russowii* and *S. lindbergii*, in the close vicinity of *Polytrichum strictum*. This confirms the bryophilous character of *R. subarctica* with regard to habitat and substrate preferences as noted by Pilát (1971b) and subsequently supported by others (e.g., Daun & Nitare 1987; Vašutová *et al.* 2013). The appearance of *R. subarctica* in this period on mountain ranges in Poland seems consistent with Fenno-Scandinavian phenology, which shows a preference for late summer and early autumn months (Daun & Nitare 1987).

#### NOTES ON GENERAL DISTRIBUTION AND ECOLOGY

*Ramariopsis subarctica* is generally known from the Northern Hemisphere only, and it appears to be uncommon but widespread in arctic, tundra and boreal as well as subalpine regions of Asia, Europe and North America (Pilát 1971a, b, 1974; Daun & Nitare 1987; Shiryayev 2004, 2006; Borgen 2006; Knudsen 2006; Kotiranta *et al.* 2009; Voitk 2015; Table 1; Fig. 4).

In Europe, *R. subarctica* has its main occurrence in the northern part of the continent (especially north of 65°N), but it also reaches a certain level of frequency at lower latitudes, where it preferably grows in mountains in the subalpine zone (Daun & Nitare 1987; Vašutová *et al.* 2013). This is in line with Pilát's (1971a) characterization of this species as a glacial relict in Central Europe. Until now, the Central European distribution of *R. subarctica* apparently was restricted to very few refugia in the High Tatra Mts (Slovakia: Trojrohé pleso), West Tatra Mts (Poland: Dziurawe hillside), Karkonosze Mts (Poland: subalpine plateau Równia pod Śnieżką; Czech Republic: Prameny Labe, Prameny Úpy) and Hrubý Jeseník Mts (Czech Republic: site Vozka) (e.g., Vašutová *et al.* 2013; this study). The highest elevation recorded for *R. subarctica* in these regions is in the Tatras (1620–1650 m a.s.l.). Localities from the Karkonosze Mts are between 1370 and 1440 m a.s.l., and those from the Hrubý Jeseník Mts come from ca 1300 m (Pilát 1971a, 1974; Fellner & Landa 1991; Fellner 1996; Vašutová *et al.* 2013; this study). However, recently *R. subarctica* has also been reported from lowlands (<100 m a.s.l.) in Central Europe, from sites near Leck municipality (Süderlügum, Leckfeld-Nord) in the northern part of North Frisia (Schleswig-Holstein) in Germany (Lüderitz *et al.* 2016). There it grows in mossy and humid shrub habitat (inland dunes) with *Calluna vulgaris*, *Erica tetralix*, *Empetrum nigrum*, *Myrica gale* and *Salix repens* (Lüderitz *et al.* 2016).

In the Tatra Mts, *R. subarctica* is reported from an open raised bog (with *Sphagnum*) and from a two-layer habitat formed by mosses (primarily *Sphagnum* species) and creeping dwarf

**Table 1.** Scheme of spatial distribution of *Ramariopsis subarctica* Pilát by latitudinal/altitudinal zone and geographical region (based on literature records and supplemented by unpublished data).

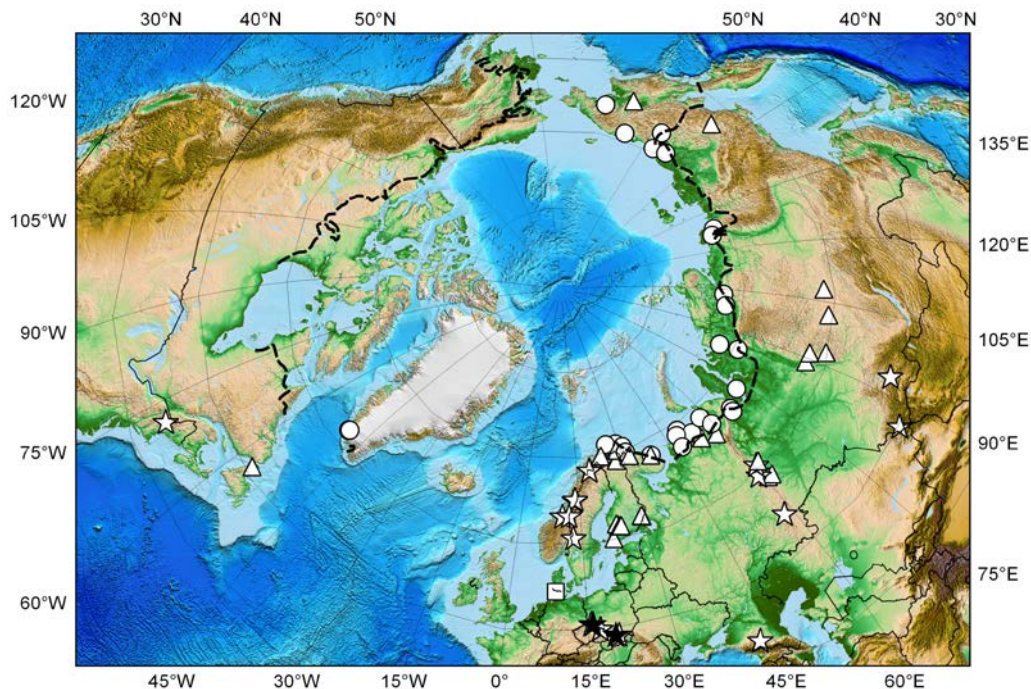
Geographical region	Latitudinal/Altitudinal zone							
	high arctic	low arctic /subalpine	forest-tundra	north boreal	middle boreal	south boreal	hemi-boreal	temoral
Greenland	–	+/-	+					
Scandinavia		+/+	+	+	+	+	+	–
Western Europe		/–						+
Central Europe		/+					–	–
Eastern Europe	+	+/	+	+	+	–	–	–
Caucasus Mts		/+					–	–
Ural Mts		/+	+	+	+	–	–	–
Altay-Sayans Mts		/+			+	–	–	
Western Siberia	–	+/	+	+	+	–	–	
Central Siberia	–	+/	+	+	+	–	–	
Eastern Siberia			+	+	+	+	+	
Far East (continental)		+/	+	+	+	–	–	–
Far East (oceanic)		+/	+	+	+	+	–	–

The compiled division of zonation follows Hämet-Ahti (1981), Bliss (1997), Körner (2003) and Huggett (2004).

shrubs (Vašutová *et al.* 2013; this study). In the Karkonosze Mts the fungus is known from various (tundra-like) peat bog communities of the class *Oxycocco-Sphagneteta* (e.g., *Chamaemoro-Pinetum mugo* and *Sphagno robust-Empetretum hemaphroditii*) and rarely of the class *Scheuchzerio-Caricetea fuscae* (Fellner 1996; this study). In the Hrubý Jeseník Mts, *R. subarctica* grows in phytocoenoses of the *Andromeda polifoliae-Sphagnetum magellanici* association (Vašutová *et al.* 2013). To complete the comparison, it should be mentioned that *R. subarctica* has frequently been characterized as a typical sphagnicolous and bryicolous species – strictly associated with mire habitats and occurring either among mosses (*Sphagnum* sp., *S. compactum*, *S. lindbergii*, *S. russowii*, *Plagiothecium curvifolium*, *P. laetum*, *Polytrichum strictum*) or on almost bare soil, often near living mosses and quite a number of accompanying vascular plants such as *Andromeda polifolia*, *Calluna vulgaris*, *Carex pauciflora*, *Deschampsia flexuosa*, *Eriophorum vaginatum*, *Oxycoccus palustris*, *Picea abies*, *Pinus mugo*, *Rubus chamaemorus*, *Vaccinium myrtillus* and *V. uliginosum* (Pilát 1971a, 1974; Fellner 1996; Vašutová *et al.* 2013; this study).

The distribution and ecology of *Ramariopsis subarctica* in Fenno-Scandinavia (Norway,

Sweden, Finland, Karelia and the Kola Peninsula of Russia) was exhaustively characterized by Daun and Nitare (1987) and supplemented by Kotiranta *et al.* (2009), Kotiranta and Shiryayev (2013) and Shiryayev (2013a, c). In general, records of the species are distributed across boreal, subalpine and arctic areas of the region. The literature data suggest that records of *R. subarctica* are not evenly distributed over the region. They are most frequent in the subalpine zone of Scandinavian mountains and in the low arctic zone (Daun & Nitare 1987; Kotiranta *et al.* 2009; Shiryayev 2013a). The highest records in Fenno-Scandinavia are from ca 600 m a.s.l. in Sweden to ca 850 m a.s.l. in Norway (Daun & Nitare 1987). The typical habitat of *R. subarctica* in Fenno-Scandinavia seems to be poor *Sphagnum* mires (with *Sphagnum fuscum*, *S. balticum*, *S. platyphyllum*, *S. nemoreum* and *S. teres*), intermediate fens in *Pinus-Betula* woodlands of the boreal structure type, or treeless areas of hypoarctic tundra type. *Ramariopsis subarctica* often occurs near living mosses (*Calliergon stramineum*, *Drepanocladus fluitans*, *Polytrichum strictum*, *Dicranum angustum*, *D. elongatum*, *D. fuscescens*, *D. scoparium*, *Pohlia nutans*, *P. shagnicola*) and vascular plants (*Baeothryon cespitosum*, *Betula nana*, *Drosera rotundifolia*, *Rubus chamaemorus*),



**Fig. 4.** Map showing world distribution of *Ramariopsis subarctica* Pilát, based on available literature records and supplemented by current studies. (dashed line – treeline, continuous line – country border, O – arctic record, Δ – boreal record, ☆ – subalpine record, □ – temperate record, ★ – new locality).

including ericoid species (*Andromeda polifolia*, *Calluna vulgaris*, *Empetrum hermaphroditum*). Ecological descriptions also indicate other habitat types such as snowbed vegetation with *Salix herbacea* and *Kiaeria starkei* most common (Daun & Nitare 1987; Walker *et al.* 2005; Kotiranta *et al.* 2009; Shiryayev 2013a, c).

Finds of *Ramariopsis subarctica* from Russian territory (over 40 reports) are the most published material on the species, but that is a small amount of data from such a vast area, and its geographical coverage is patchy due to incomplete penetration of the area for mycological studies. The westernmost finds of *R. subarctica* in Russia are from northern parts of Murmansk oblast (province) (Shiryayev 2009, 2013a), the Nenets Autonomous Region (Shiryayev 2012b), and the northern part of the Komi Republic (Shiryayev 2004, 2006). Further eastward there are records from the Yamal Peninsula (Shiryayev 2008) and Taymyr Peninsula (Shiryayev 2011). The easternmost finds are from

the Chukotka Autonomous Region (Shiryayev 2013b), Yakutia Republic (Shiryayev 2012a; Shiryayev & Mikhalyova 2013) and Magadan oblast (Govorova & Sazanova 2000) in the Far East. The southern distribution of the species follows records from the Caucasus Mts (Shiryayev 2014), Southern and Central Ural (Bashkiria Republic, Sverdlovsk region) (Shiryayev 2004), West Siberian Plain (Sverdlovsk region) (Shiryayev *et al.* 2009), through southern Siberia (Altai Mts, Sayan Mts) (Shiryayev 2014) and eastern Siberia (southern and central Krasnoyarsk Krai, northern Irkutsk Oblast) (Kotiranta & Shiryayev 2015; Shiryayev & Kudashova 2015; Shiryayev & Myzika 2015; Shiryayev & Kotiranta 2015). The available data indicate the highest frequency of *R. subarctica* in northern Russia, close to and beyond the tree line in both the European and Asian portions of low arctic and forest-tundra, while the southern part of its distribution range is rather discontinuous and seems to be shaped by the ecoclimate of higher

elevations. We suspect that this species is more widespread in the boreal zone than the available records would indicate (cf. Shiryayev & Mukhin 2010). The finds of *R. subarctica* are widely distributed across European and Asian Russia but appear to be habitat-limited. Although there is relatively little information on the specific vegetation type in which the fungus has been found (arctic tundra, taiga, subalpine tundra) it is by far most frequently recorded in association with more humid habitats (including bogs and margins of mires), preferably on or in mosses (including *Sphagnum*) (e.g., Shiryayev 2004, 2009; Shiryayev *et al.* 2009).

The few finds of *R. subarctica* from North America are very recent records from Canada (Voitk 2015) and the USA (Voitk & Voitk 2015). The latter (without clearly specified ecology and altitude range) is from Mt Washington (New Hampshire), and the former is from a raised *Sphagnum* bog in the L'Anse aux Meadows, a famous archaeological site of a Viking settlement on the northernmost tip of the island of Newfoundland (Newfoundland and Labrador Province). *Ramariopsis subarctica* is also known from Greenland (Borgen 2006; Borgen *et al.* 2006; Knudsen 2006), where the species was mostly observed within a hyperoceanic zone in dwarf-scrub heaths with *Empetrum hermaphroditum*, *Salix herbacea* and *S. glauca* south of 63°N.

## CONCLUSIONS

The described studies permit some general conclusions regarding the zonal distribution and ecology of *Ramariopsis subarctica*. Knowledge of the global distribution of *R. subarctica* has advanced during the past four decades but the geographical coverage of research on this species is incomplete. There are still major gaps in our understanding of its biogeographical patterns. For the time being its main documented distribution is in low arctic and forest-tundra areas, but the actual distribution may extend down farther to the southern boreal zone. This fungus reaches with some limited success into high arctic regions in the north and into hemiboreal (rarely nemoral) areas in the south. In the most southern (peripheral) regions, *R. subarctica*

is uncommon and restricted to mountainous subalpine belt areas. In general, the distribution of the species seems to be influenced by a combination of factors, the most important of which are its physiological adaptation to relatively cold and humid climate and its association with moss (peat moss) habitats. *Ramariopsis subarctica* is regarded as a glacial relict of mountain ranges of Central Europe. We found no significant differences in its phenology between the Central European subalpine and the Feno-Scandinavian subalpine or subarctic sites, with most records being from September. In Poland the recognized distribution of *R. subarctica* seems incomplete; its occurrence in other peat bogs of mountainous regions of the country seems highly likely, though it has not been found there yet. It remains to be seen whether it occurs in the more southern mountain ranges of Europe.

Our findings confirm prior observations that *R. subarctica* populations from different parts of its geographic range exhibit little variation of basidiomata morphology, though a range of cryptic phylogeographic structure at genetic level cannot be ruled out. Resolution of that question requires additional sequence data and comprehensive molecular studies.

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