Phytotaxa 299 (2): 234–235
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.299.2.7

Schistidium relictum (Grimmiaceae, Bryophyta), a new moss species from Northwest North America and Siberia

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Abstract

Schistidium relictum is described as a new northwest North American and Siberian species of moss. Important distinguishing characters include dull, nearly black plants, with stems densely and evenly foliated, weakly spreading leaves that usually lack awns, and the mostly 1-stratose distal leaf laminae with 2(–3) -stratose margins. The species has a remarkable disjunct distribution pattern with most of the sites where it has been found having been unglaciated during the Pleistocene glaciations. It is restricted to areas with occurrence of calcareous bedrock, especially limestones. It appears to be rather isolated genetically based on molecular studies of total ITS. It is sister to the large clade, 'Apocarpum', which consists of species which probably embody its closest known extant relatives.

Key words: biogeography, internal transcribed spacer (ITS), mosses, phylogeny, Pleistocene glaciations, *Schistidium*

Introduction

Historically, *Schistidium* Bruch & Schimper (1845: 93) has been a difficult genus to resolve taxonomically (Blom 1996, McIntosh 2007, McIntosh *et al.* 2015). Past floristic treatments have varied from region to region, and names that have been applied to specimens at both the species and varietal levels have been as inconsistent as the characters used to differentiate the taxa (McIntosh 2007). However, initiated by the landmark treatment of the *S. apocarpum* (Hedwig) Bruch & Schimper (1845: 99) complex in Norway and Sweden (Blom 1996), numerous *Schistidium* species have been recently recognized (e.g., Blom 1996, 1998, Blom and Darigo 2009, Blom *et al.* 2016, McIntosh *et al.* 2015). The majority of these would have once been considered within the broad and uncomfortable species concept of *S. apocarpum*, although a few were lodged within other broadly defined species, such as *S. rivulare* (Bridel) Podpêra (1911, 207) and *S. confertum* (Funck) Bruch & Schimper (1845: 99). Discussions in other works have helped clarify confusion regarding key characters useful in species recognition and include Deguchi (1979), Blom (1998), and McIntosh (2007). A great amount of genetic research has also contributed to the understanding of species concepts as well as species relationships within *Schistidium* (e.g., Goryunov *et al.* 2007, Ignatova *et al.* 2009, Hofbauer *et al.* 2016). As a result, although more species will be described in the coming years, *Schistidium* is currently comprised of about 130 species.

The name *Schistidium relictum* has been used previously by H. H. Blom to name numerous herbarium collections during his earlier research (Blom 1996). Also, it was published as a provisional name by Ignatova *et al.* (2009) in a key to the Russian species of *Schistidium*. Because this species and its name have not, to date, been described, this name has been considered a 'manuscript name'. This article describes *S. relictum*, thus validating that name.

 Accepted by Matt von Konrat: 18 Jan. 2017; published: 21 Mar. 2017

Materials and Methods

Two of the authors, T. T. McIntosh and E. A. Ignatova, examined the *Schistidium relictum* specimens available in their regional herbaria, whereas H. H. Blom, both during his earlier work (Blom 1998) and recently, examined the great majority of the specimens listed below. In all cases, microscopic examination involved describing and measuring the characters listed in the following description.

Voucher specimens of *Schistidium relictum* are deposited in many herbaria, i.e., University of Alaska (ALA), University of Alberta (ALTA), National Herbarium of Canada (CANM), University of Michigan (MICH), Moscow University (MW), Tsitsin' Main Botanical Garden (MHA), University of Newfoundland (NFLD), New York Botanical Garden (NY), Norwegian University of Science and Technology (TRH), University of British Columbia (UBC), and University of California (UC).

The distribution map (Fig. 2) was made in ArcMap using a Fuller projection.

For the phylogenetic research, ITS1-5.8SrRNA-ITS2 sequences were obtained from four specimens collected recently in northern Siberia. Specimen data and Genbank accession numbers are listed in Appendix 1 (results shown in Fig. 3). Extractions of DNA and laboratory protocols were essentially the same as in Gardiner *et al*. (2005), using White *et al.* (1990) primers L and B. Amplified DNA fragments were sequenced in the Center of Collective Use "Genom" in Moscow. New sequences were included in the alignment used for broader analyses (Goryunov *et al.* 2007; Ignatova *et al.* 2010; Milyutina *et al.* 2010), and aligned manually in Bioedit (Hall 1999). Trees were rooted on *Schistidium sordidum* following a previous analysis, where this species appeared basally in an analysis of chloroplast DNA (Ignatova *et al.* 2009). Analyses were conducted under a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Huelsenbeck *et al.* 2001) with 5.8S analyzed with HKY+I model, and ITS1 and ITS2 with a GRT+I+G model, the model selection by ModelgeneratorV.85 (Keane *et al.* 2006). Three parallel runs were completed, each with five chains and 10,000,000 generations (25% burnin), with trees sampled every 1000 generations, a temp parameter value of 0.015.

Taxonomic Treatment

Schistidium relictum T.T. McIntosh, H.H. Blom, and E. A. Ignatova *sp. nov.*, FIG. 1.

Diagnosis: Schistidium relictum is a distinctive species, readily separated from other species of *Schistidium* by a number of gametophytic characters including dull, nearly black plants, with stems densely and evenly foliated, weakly spreading leaves that usually lack awns, the mostly 1-stratose distal leaf laminae with 2(–3) -stratose margins, a papillose distal abaxial surface of the costa, and a differentiated alar group of enlarged subquadrate cells delimited from adjacent cells. Also, its strongly differentiated perichaetial leaves are much larger than adjacent stem leaves, often hiding the sporophyte in lateral view. Also, its peristome teeth are long and curved.

Type:—CANADA. British Columbia: Mile 445, Alaska Highway, outcrop above creek, 59°05´N 125°49´E, 886 m, 26 August 1967, *F. Boas 67071* (holotype UBC! B106018, isotype TRH!).

Plants medium-sized to large, dull, nearly black or dark-brown, new growth yellow-brown, forming compact or loose mats, tufts, or cushions, sometimes partially buried in sand or silt. Stems (1.0–)1.5–2.5(–3.5) cm, dark, upper stems simple or branched (branching is less common in North American plants), usually somewhat curved, occasionally straight, arching-horizontal, ascending, or erect, densely and evenly foliate and somewhat 'columnar-like', with broad central strands. Stem leaves (1.2–) 1.4–1.8 (–2.0) mm long, 0.5–0.7(–1.1) mm wide, ovate-lanceolate, occasionally lanceolate or ovate-triangular, straight or slightly secund, sometimes in ± spiral rows, sharply keeled distally, broadly concave proximally, most leaves darker in the distal 1/2, when dry erect-appressed and sometimes with recurved apices, when wet patent to erecto-patent and recurved, 1-stratose, not decurrent; *margins* weakly recurved from base to about 2/3 (–4/5) of the leaf, smooth or papillose(-denticulate) distally, especially evident in young leaves, 2(–3) stratose distally in 1 or 2 rows; *apices* acute, rarely somewhat rounded; *awns* usually absent, when present short, to 0.1 mm, hyaline, terete, weakly denticulate or spinulose, usually not decurrent; *costae* strong, dark-coloured throughout, percurrent, dorsal surface often papillose distally, especially in young leaves, strongly bulging on abaxial surface for much of leaf length, in transverse section rounded near apex, broadened-elliptic, asymmetric and unevenly bulging

medially and proximally, 2–3 cells thick; *distal laminal cells* (6–)8–9 µm wide, irregular in shape, short-rectangular or more or less isodiametric, occasionally oblate, walls moderately thick to thick, not sinuose, with small corner thickenings, smooth or with scattered, low papillae on the dorsal surface; *medial laminal cells* (8–)9–13 µm wide, short-rectangular, walls moderately thick, sinuose; *basal cells* 12–16 µm wide, rectangular or short-rectangular, thick-walled, weakly sinuose; *alar cells* differentiated as an area of enlarged and clear cells that are more or less isodiametric, short-rectangular, or, occasionally, rectangular especially along the margins, the alar region is 1–5 rows wide and 3–6 cells high (but smaller and less defined in North American material). Perichaetial leaves paler than stem leaves, (2.1–)2.3–3.2 mm, broadly ovate or oblong with a triangular distal portion, erect, broadly acute, often with a short awn. Sexual condition gonioautoicous. Sporophytes common, immersed in perichaetial leaves or about 1/8 to 1/3 exposed. Seta (0.15–)0.3(–0.4) mm. Capsule urn reddish-brown to dark brown, short-cylindrical, (0.7–)0.8–1.0(–1.2) mm, sometimes slightly narrowed towards the mouth, shiny, occasionally striolate when dry; exothecial cells short-elongate or ± isodiametric, usually irregular in shape, sometimes 5 sided, sometimes oblate, rarely in lines, thin-walled or slightly and unevenly thickened, walls often curved; rim the same colour as capsule wall or darker and redder. Stomata (0–)2–6 at base of capsule. Peristome erect or patent, reflexed when dry, curved, not twisted along axis, 250–450 µm, reddish-brown, usually densely papillose with very short papillae, usually perforated with slits, sometimes with small terminal prongs. Operculum usually short-conic, rostrate, rostrum straight or oblique. Spores yellowish, 9–12 (–14) µm, finely granulose.

Additional specimens examined:—CANADA. British Columbia: Summit Lake, 3 mi beyond N end, 58°35′N 124°40 E, *Schofield 66179* (UBC); Mt. St. George, 5300–5900 ft., 58°37′N 124°43′E, *Vitt 11240* (ALTA); Wokkpash Lake, SW shore, Mt. Roosevelt-Churchill Peak area, 58°45′N 124°85′E, *Schofield*, *Vitt & Horton 66451* (ALTA), *66619* (ALTA, UBC); Muncho Lake area, Alaska Highway post 444.9 at Peterson Creek Bridge No 4, 58°52′N 125°49′E, *Vitt & Andrus 3023* (ALTA); Rocky Mts., Haworth Lake, 3800 ft., 58°47′N 125°07′E, *Vitt 20096* (ALTA, with *Schistidium trichodon*); Yukon: Northern Ogilvie Mts., Nahoni Range, 65°37′N 139°06′E, *Vitt 12963* (ALTA, with *Schistidium boreale*); Northern Ogilvie Mts., Nahoni Range, 4600–4700 ft., 65°37′N 139°03′E, *Vitt 13073 (*ALTA); Northern Ogilvie Mts., Nahoni Range, 65°38′N 139°03′E, *Vitt 13378* (ALTA, NFLD); Northern Ogilvie Mts., Nahoni Range, 3900–4100 ft.,65°37′N 139°02′E, *, Vitt 13130*, *13156* (ALTA); mountain S of Mt. Klotz, at headwaters of Ogilvie River, 65°20′N 140°06′E, *Vitt 7482* (ALTA); Mackenzie Mts., Bonnet Plume Range, Wrightii Lake, ca 7.5. mi SE of Fairchild, 3300–4400 ft., 65°54′N 133°33′E, Horton 6701 (ALTA), Vitt 16977 (ALTA); Bonnet Plume Range, Riparium Lake, 4800–5200 ft., 64°46′N 133°23′E, *Horton 6559* (ALTA); South Richardson Mts., Doll Creek area, 66°05′N 135°48′E, *Ritchie 7045* (CANM); Peel River Watershed, Mt. Reception, site 36, 65°37′N 135°30′E, *Bird & Benson 30496* (CANM); N.W.T.: Inuvik, SE of Airport Lake along stream, *Packer & Lemay 205* (ALTA, with *Grimmia teretinervis*); Mackenzie distr., Nahanni Range, just N of peak at 3598 ft., 61°43′N 123°20′E, *Vitt 20290* (ALTA, NY); Nahanni Range, 62°13′N 123°22′E, *Horton 10403* (ALTA); Mackenzie distr., Ram Range, 61°43′N 123°53′E, *Vitt 20390* (ALTA); Campbell Hills, 68°14′N 133°15′E, *Scotter 28358* (ALA, + *Schistidium submuticum subsp. arcticum*); Gibson Ridge, Chick Lake, 1300 ft., 65°49′N 128°15′E, *Gubbe & Burr 616A* (ALTA); South Nahanni River Natl. Park, Deadman Valley, 61°19′N 124°35′E, *Steere 76-325* (NY); Kraus Hot Springs, 61°15′N 124°03′E, *Steere 76-291* (NY), *Scotter* 22530 (NY); Virginia Falls, 61°38′N 125°42′E, *Scotter 22349, 22259, 22260* (NY); Nunavit: Devon Island, 75°40′N 84°40′E, *Vitt 5354* (ALTA); U.S.A. Alaska. Central Yukon River district, White Mts., limestone ridge, *Gjærevoll 18.VII.1953* (TRH), *Gjærevoll 28.VII.1953* (TRH); Chandalar Quad., Brooks Range, Sukapak Mt., *Spatt 631* (ALTA); base of Sukapak Mt., 610 m, 67°36′N 149°45′E *Murray 77-121* (ALA); Mountains NW of Walker Line, upper Kopuk River, above W end of Walker Lake, 67°10′N 154°30′E, *Jordal 4041* (MICH); Survey Pass Quad., vicinity of confluence of Alatna and Nahtuk rivers, 1200 ft., 67°25′N 153°43′E *Murray 73-42* (ALA); vicinity of Ambresvajun Lake (= Last Lake), 1159 m, 68°38′N 143°41′E, *Batten 75-43c* (ALA); Endicott Mts., Arrigetch Creek valley, 3400 ft., 67°26′N 154°05′E, *Cooper CB-161,* 4500 ft., 67°26′N 154°00′E, *Cooper CB-165* (ALA); Okpilak Lake vicinity, 69°25′N 144°03′E, *Murray 8625* (ALA); Toolik Lake, *Wallace 18.VII.1976* (ALA); Arctic Village, White mountain W of Chandalar River, 68°08′N 145°32′E, *Steere & Iwatsuki 74-293* (NY); RUSSIA (ASIA): West Siberian Arctic, Yamalo-Nenetzky Autonomous District, Yunto Lake, 67°40′N, 68°00′E, 10.VIII.1993, *Czernyadjeva 58* (LE, MW); Krasnoyarsk Territory: Taimyrsky Autonomous District, State Biosphere Natural Reserve Taimyrsky, Medvezh'ya (Bear's) River, slope of a limestone ridge along the right bank of Kotuy River, 70°58′N, 102°49′E, *Fedosov 05-672 & 05-718* (MW); Taimyrsky Autonomous District, right bank of Maimecha River 14 km downstream of Chopko Creek mouth, 70°50′N, 100°57′E, 30.VI.2009, *Fedosov 09-46* (MW); Republic Sakha/Yakutia: Bulun District, lower course of Lena River, Kharaulakh Mt. Ridge, Ogonnior-Yurege Creek, 170 m, 71°25′N, 127°25′E, 09.VII.2006, *Pisarenko op04672* (MW); Tompo District, Sette Daban Mt. Ridge, right bank of Segenyakh (Rosomakha, or Wolverine) Creek upstream Magadan Hwy, 470 m. 63°02′N, 137°57′E, 17.VII.2015, *Ignatov & Ignatova 15-538* (MHA, MW).

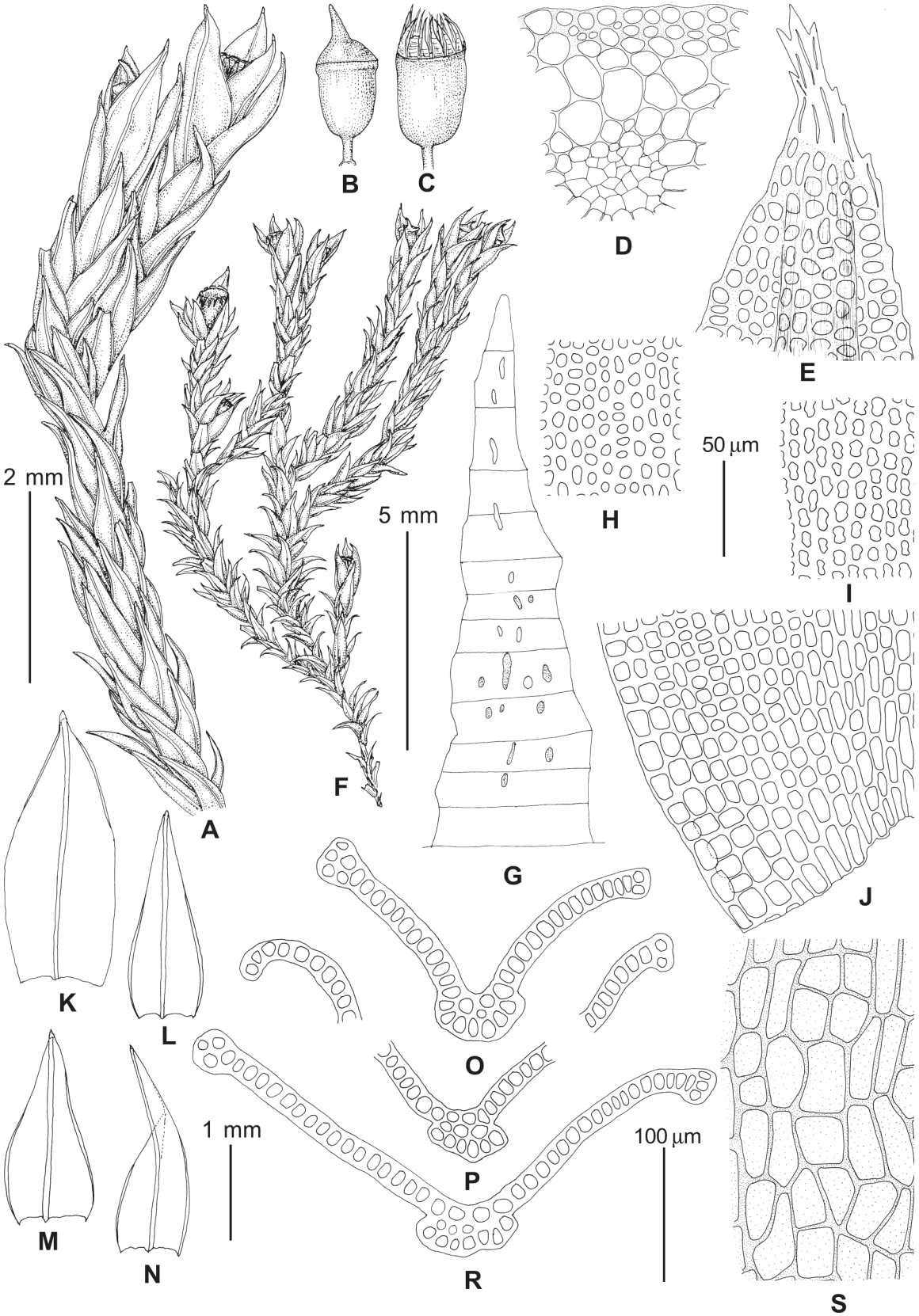

FIGURE 1. *Schistidium relictum.* **A, F.** Habit. **B–C.** Sporophytes, with and without operculum. **D.** Stem section. **E**. Cells of stem leaf apical portion with hyaline tip. **G.** Peristome tooth. **H.** Upper laminal cells**. I.** Median laminal cells. **J.** Basal laminal cells. **K.** Perichaetial leaf. **L–N.** Cauline leaves. O–R. Leaf transverse sections. **S**. Exothecial cells. **Scale bars**: 5 mm for F; 2 mm for A–C; 1 mm for K–N; 100 µm for D, G, O–R; 50 µm for E, H, I–J, S.

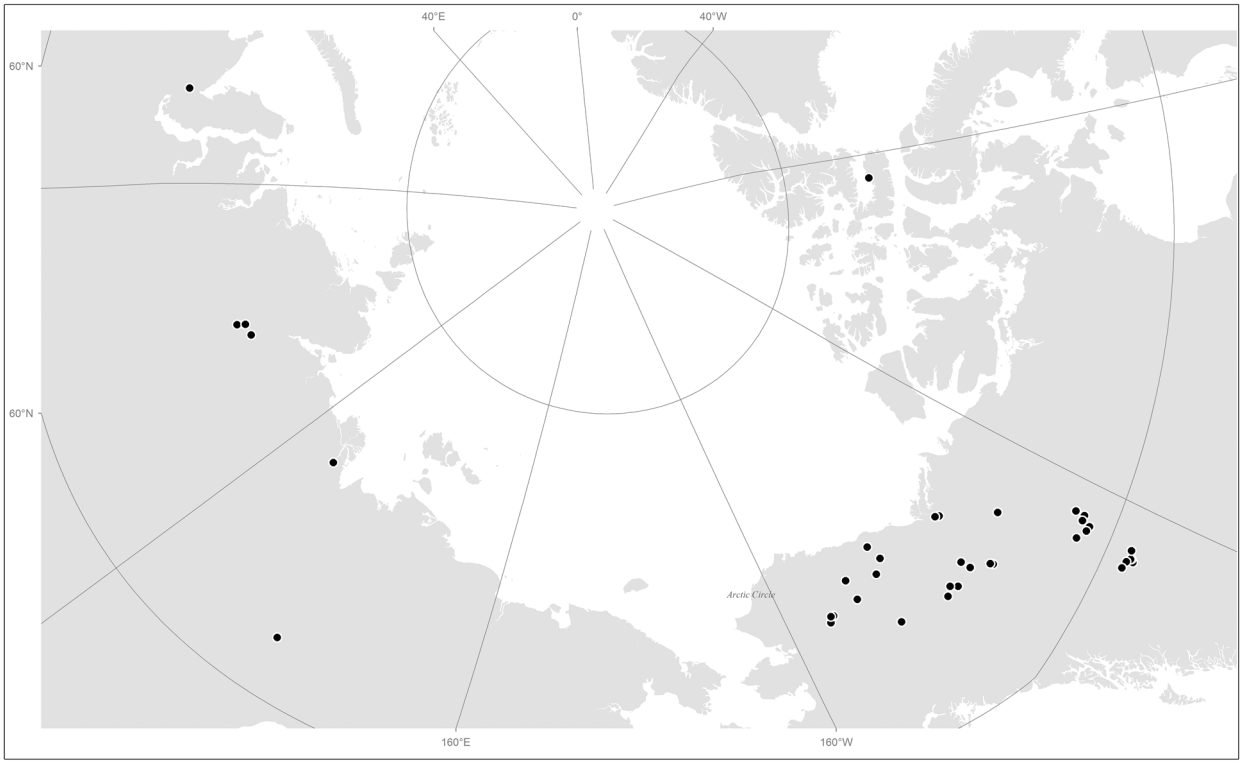

FIGURE 2. Global distribution of *Schistidium relictum*.

Etymology:—The epithet *relictum* refers to a distribution pattern that suggests that *S. relictum* survived large parts of the Pleistocene glaciations *in situ* as a relict.

Distribution and Habitat:—*Schistidium relictum* is known from northwest North America and northern parts of Siberia in Asian Russia (Fig. 2). Its elevation range is from ca 100–470 m in Siberia and ca 50–1700 m in North America. The species has a remarkable disjunct distribution pattern with most of the sites where it has been found having been unglaciated during long periods of the Pleistocene glaciations (e.g., Svendsen *et al*. 2004). We hypothesise that the species persisted in ice-free refugia north of the continental ice sheets during the Pleistocene, the huge Beringian refugium being the most important one (e.g., Hultén 1937, Schuster 1983). Its present distribution pattern probably indicates a low degree of migration in the Holocene following the retreat of the inland ice sheets.

Schistidium relictum is restricted to areas with occurrence of calcareous bedrock, especially limestones. It has been collected on dry ledges, walls, and boulders but also on periodically irrigated rocks on river banks, and occasionally on mineral soil. According to specimen labels and field data, there is a rather large variation in habitats from windswept ridges with little snow cover to adjacent to snow beds to moist sheltered sites in creeks and along rivers. Based on species admixtures in herbarium specimens, it grows with other Grimmiaceous calciphytes including *Schistidium submuticum* subsp. *arcticum* H.H.Blom, *S. frisvollianum* H.H.Blom, *S. boreale* Poelt, and *Grimmia teretinervis* Limpr.

The distribution of *Schistidium relictum* in North American resembles that of *Andreaeobryum macrosporum* Steere & B.M. Murray, which also occurs along the ice free corridor between the Laurentide and Cordilleran ice sheets in the Yukon-Northwest Territoiry-northern British Columbia area (Pedersen *et al.* 2016). Further, *Schistidium relictum* was recently discovered in Yakutia, east Russia (Ivanova *et al*. 2016), and, interestingly, was collected at this site along the same creek as *Andreaeobryum macrosporum* from 500 to 1100 m elevation. Both species are likely not rare in the mountains of this area.

Differentiation and relationships:—*Schistidium relictum* is a distinctive species only likely to be confused with other blackish *Schistidium* species, in particular *S. andreaeopsis* and *S. boreale. Schistidium andreaeopsis* is a much larger plant with longer leaves (2.0–2.7 mm vs., on average, 1.4–1.8 mm) and wider distal leaf cells (10–12 μm vs. 8–9 μm). Also, its leaf cells are strongly sinuose to nodulose almost throughout and possess characteristic reddish walls, whereas they are esinuose or slightly sinuose in upper part of leaf and lack the reddish wall coloration in *S. relictum*. Sporophytes are unknown in *S. andreaeopsis*. The gametophyte of *S. boreale* is similar to *S. relictum*, but its leaf laminal cells are distinctly more densely and highly papillose and cells walls often reddish or orange. Also, the peristome teeth of *S. boreale* are shorter than those of *S. relictum* (220–330 μm vs. 250–450 μm).

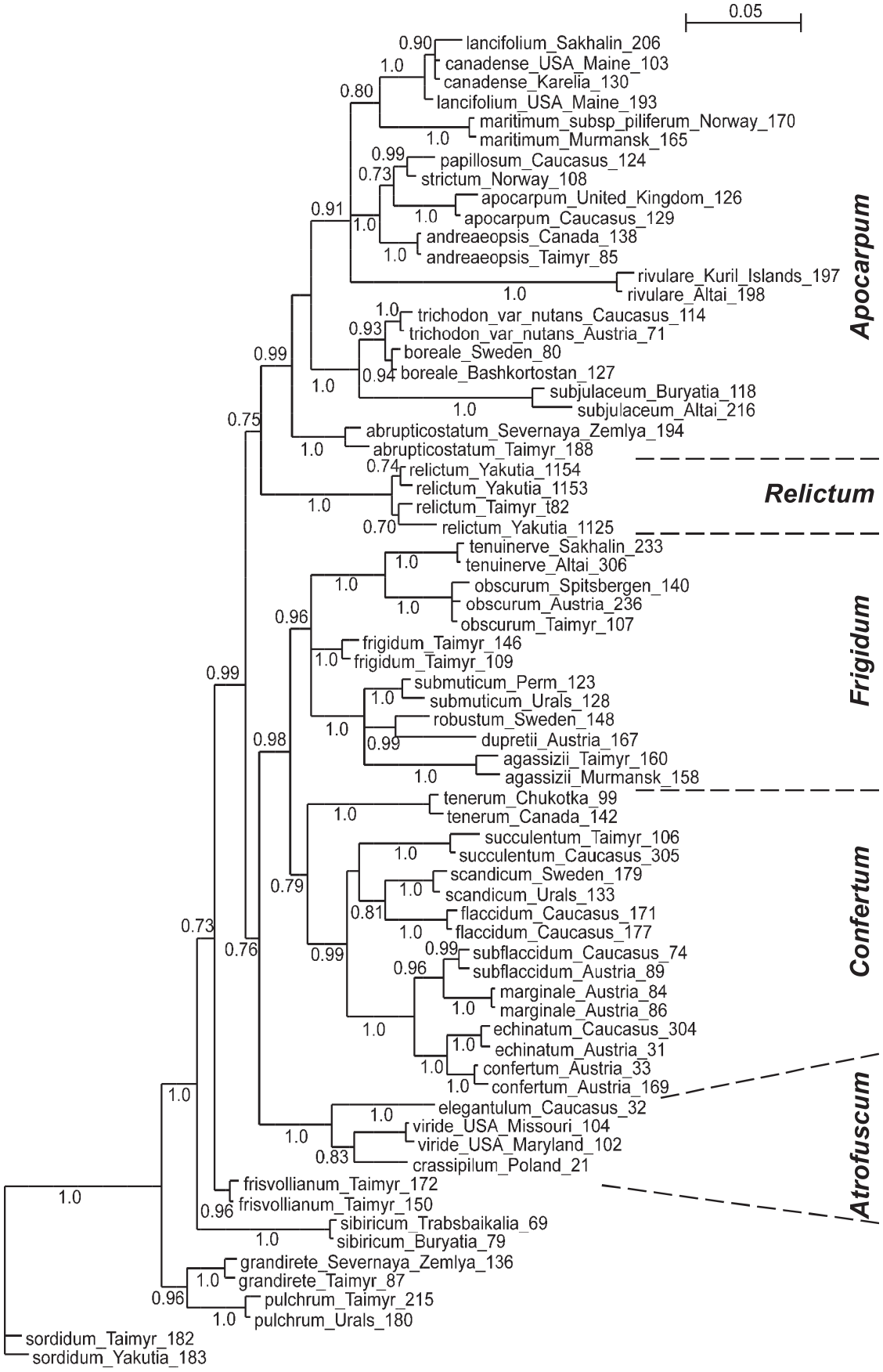

FIGURE 3. Illustration of genetic relationships of *Schistidium relictum* with selected species and species groups of *Schistidium* based on molecular studies of total ITS.

Schistidium relictum appears to be rather isolated genetically based on molecular studies of total ITS (Fig. 3). It is sister to the large clade, 'Apocarpum', which consists of species which probably embody its closest known extant relatives. *Schistidium relictum* shares the character states of long peristome teeth, papillose leaf costae, and denticulate upper leaf margins with several of these species. The tree in Figure 3 includes a basal paraphyletic clade formed by *S. pulchrum*, *S. grandirete*, *S. sibiricum*, and *S. frisvollianum*, and the main clade (PP=0.99) that includes all remaining species. The latter is subdivided into two clades, which, however, have low support. In contrast, high support is present for clades that correspond to the various sections, established by Blom (1996) based on morphological study, and clades from the previous broader analyses: *Atrofuscum*-clade (PP=1.00), *Frigidum*-clade (PP=0.96), *Confertum*-clade (PP=0.79, but P=0.99 for the main volume of this clade excluding *S. tenerum*), *Apocarpum*-clade (PP=0.99), and, in addition, the clade formed by four specimens of *S. relictum*. The latter retains the sister position to the *Apocarpum*-clade, and, even though with only moderate support (PP=0.75), indicates the isolated position of *S. relictum*.

Acknowledgments

Sincere thanks to the curators of the North American herbaria listed above for arranging loans to H.H. Blom during his previous studies of specimens of *Schistidium*, and to Line Walberg Larsen, Ås, for preparing the distribution map. Thanks also to Catherine La Farge for assisting in gathering herbarium data at the University of Alberta. The phylogenetic work was supported by Project 14-50-00029 (Scientific basis of the national biobank—depository of the living systems) funded by a grant from the Russian Science Foundation (RSF).

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APPENDIX 1

*Schistidium abrupticostatum*_Taimyr_188 HM053930; *S. abrupticostatum*_Severnaya_Zemlya_194 HM053928; *S. agassizii*_Murmansk_158 HM053878; *S. agassizii*_Taimyr_160 HM053879; *S. andreaeopsis*_Taimyr_85 HM053881; *S. andreaeopsis*_Canada_138 HM053882; *S. apocarpum*_Caucasus_129 DQ822033, HM031074; *S. apocarpum*_United_Kingdom_126 HM031076; *S. boreale*_Urals_127 DQ822024, HM031069; *S. boreale*_Sweden_80 HM053890; *S. canadense*_Karelia_130 DQ822016, HM031067; *S. canadense*_USA_Maine_103 HM053917; *S. confertum*_Austria_169 HM053891; *S. confertum*_Austria_33 JF262179; *S. crassipilum*_Poland_21 DQ822020, HM031073; *S. dupretii*_Austria_167 HM053894; *S. echinatum*_Austria_31 HQ890509; *S. echinatum*_Caucasus_304 HQ890508; *S. elegantulum*_Caucasus_32 DQ822022, HM031071; *S. flaccidum*_Caucasus_177 HM053896; *S. flaccidum*_Caucasus_171 HM053899; *S. frigidum*_Taimyr_109 HM053905; *S. frigidum*_Taimyr_146 HM053907; *S. frisvollianum*_Taimyr_150 HM053908; *S. frisvollianum*_Taimyr_172 HM053909; *S. grandirete*_Taimyr_87 HM053910; *S. grandirete*_Severnaya_Zemlya_136 HM053911; *S. lancifolium*_Sakhalin_206 HM053912; *S. lancifolium*_USA_Maine_193 HM053917; *S. marginale*_Austria_86 HM053919; *S. marginale*_Austria_84 HM053920; *S. maritimum*_Murmansk_165 HM053922; *S. maritimum*_subsp_*piliferum*_Norway_170 HM053923; *S. obscurum*_Taimyr_107 HM053900; *S. obscurum*_Austria_236 HQ890519; *S. obscurum*_Spitsbergen_140 HM053903; *S. papillosum*_Caucasus_13_124 DQ822012, HM031061; *S. pulchrum*_Urals_34_180 DQ822030, HM031053; *S. pulchrum*_Taimyr_215 DQ822031, HM031050; *S. relictum*_Taimyr_t82 KX522944; *S. relictum*_Yakutia_1154 KX522946; *S. relictum*_Yakutia_1125 KX522947; *S. relictum*_Yakutia_1153 KX522945; *S. rivulare*_Altai_198 HM053934; *S. rivulare*_Kuril_Islands_197 HM053936; *S. robustum*_Sweden_148 HM053938; *S. scandicum*_Urals_133 DQ822026, HM031054; *S. scandicum*_Sweden_179 DQ822027, HM031059; *S. sibiricum*_Buryatia_79 HM053883; *S. sibiricum*_Chita_69 HM053884; *S. sordidum*_Taimyr_182 HM053942; *S. sordidum*_Yakutia_183 HM053943; *S. strictum*_Norway_108 HM053944; *S. subflaccidum*_Austria_89 HM053945; *S. subflaccidum*_Caucasus_74 HM053946; *S. subjulaceum*_Altai_216_HQ890522; *S. subjulaceum*_Buryatia_118 HM053947; *S. submuticum*_Urals_128 DQ822011, HM031055; *S. submuticum*_Urals_123 DQ822010, HM031056; *S. succulentum*_Taimyr_106 HM053875; *S. succulentum*_Caucasus_305 JF280964; *S. tenerum*_Canada_142 HM053951; *S. tenerum*_Chukotka_99 HM053952; *S. tenuinerve*_Altai_306 HQ890525; *S. tenuinerve*_Sakhalin_233 HQ890524; *S. trichodon*_var_*nutans*_Austria_71 HM053953; *S. trichodon*_var_*nutans*_Caucasus_114 HM053954; *S. viride*_USA_Maryland_102 HM053958; *S. viride*_USA_Missouri_104 HM053957.