BRYOPHYTES — МОХООБРАЗНЫЕ

Rare and new bryophytes (Bryophyta, Marchantiophyta) for the Leningrad Region on outcrops of Devonian sandstones in the Luga River Basin (European Russia)

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Abstract. Outcrops of Devonian sandstones in the Leningrad Region represent a unique habitat for bryophytes. These outcrops are locally different in chemical composition, light and moisture conditions and serve as specific microhabitats for different bryophyte species and their communities. In this article, four rare liverwort and 12 rare moss species are reported from the outcrops of Devonian sandstones in the Luga River Basin which covers the southwestern part of the region. Description of habitats and distribution of each species are discussed. *Mesoptychia collaris* is new for the Leningrad Region. This specimen is described and illustrated by detailed photomicrographs. The discovery of *M. collaris* in the Leningrad Region is the southernmost in Northwestern Russia. Among the other rare species, *Tortula lingulata* is protected in Russia, *Atrichum flavisetum*, *Mesoptychia heterocolpos*, *Metzgeria furcata*, *Mnium hornum*, *Myurella julacea*, *Saelania glaucescens* are protected in the Leningrad Region. An analysis of species composition and distribution of bryophytes persuades us to distinguish the outcrops of Devonian sandstones in the Luga River Basin as important bryophyte refuges of the northwestern outskirts of the Russian Plain.

Keywords: *Mesoptychia collaris*, *Tortula lingulata*, bryophyte ecology, Devonian sandstone, hepatics, liverworts, mosses, protected species, East European Plain, Russian Plain.

Новые и редкие виды мохообразных (Bryophyta, Marchantiophyta) для Ленинградской области с выходов девонских песчаников в бассейне реки Луга

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Резюме. Обнажения девонских песчаников Ленинградской области служат уникальным местообитанием для мохообразных. Различаясь по химическому составу, характеру освещения и увлажнения, песчаники являются своеобразным убежищем для разных видов мохообразных

и их синузий. В работе описаны находки четырех редких видов печеночников и 12 редких видов мхов на обнажениях девонских песчаников бассейна р. Луга, охватывающего юго-западную часть Ленинградской обл. Для каждого вида приведены местообитания и географическое распространение. Находка *Mesoptychia collaris* является первой в Ленинградской обл. и самым южным местонахождением вида на Северо-Западе России. Образец *M. collaris* подробно описан и проиллюстрирован микрофотографиями. Семь редких видов имеют статус охраняемых: *Tortula lingulata* занесен в Красную книгу России, *Atrichum flavisetum*, *Mesoptychia heterocolpos*, *Metzgeria furcata*, *Mnium hornum*, *Myurella julacea*, *Saelania glaucescens* — в Красную книгу Ленинградской обл. Анализ видового состава и распространения мохообразных позволяет выделить обнажения девонских песчаников в бассейне р. Луга как ключевые местообитания мохообразных северо-западной части Русской равнины.

Ключевые слова: *Mesoptychia collaris*, *Tortula lingulata*, девонский песчаник, мхи, охраняемые виды, печеночники, экология мохообразных, Восточно-Европейская равнина, Русская равнина.

The northwestern outskirts of the Russian Plain is a relatively flat area covered by thick Quaternary deposits, with typical taiga vegetation. The local Quaternary deposits are well washed fluvioglacial sandy and sandy loam or moraines. There is typical south taiga vegetation in the study area (*Piceetum oxalidosum* and *Piceetum vaccinio-sum* forest types) (Safronova, Yurkovskaya, 2015). Such areas are usually less rich in bryophyte species compared with other landscapes. Pre-Quaternary deposits are exposed in narrow and deep valleys as gaps of landscapes. They are folds of space having other conditions than in plain: various substrate features, more constant air humidity, more stable moisture and temperature regime.

Outcrops of Devonian sandstones occasionally occur in valleys of streams throughout the territory of the Main Devonian Field. It covers the territory of the main part of the North-West portion of Russia, parts of Estonia, Latvia, Lithuania and the north of Belarus. The most extensive natural outcrops stretch along the rivers Velikaya, Shelon', Luga, Msta, Lovat', Kerest', Syas', Oyat', Svir', and their tributaries (Geologia..., 1971).

The Luga River Basin covers the southwestern part of the Leningrad Region. The Luga River is a typical lowland river and has numerous tributaries. Its sources are located in different often hardly accessible places. The water level in the Luga River varies much because the river collects spring melting and rain waters from an extensive area. The water level may change greatly seasonally and annually and differ in 2–3 meters. The water in the river reaches its minimum level from mid-June to mid-October (Uroven'..., 2022). The outcrops of Devonian sandstones distributed along banks of the Luga River and its tributaries represent a favorable substrate and various microniches for bryophytes. Changes in the water level of the Luga River may act as one of the factors of distribution of the bryophyte diaspores between the microniches.

Local Devonian sandstones have uniform particle size distribution but differ by chemical composition. A series of outcrops from poor white to deep red color was previously studied in the Leningrad Region (Engalychev, Panova, 2011). It is shown that the color of sandstone depends on the proportion of minerals in sandstone compo-

sition, primarily iron oxide. However, quantities of Al, K, Ti, Mn, Mg can increase together but not strictly proportional. Layering is common for sandstones. Different layers at one outcrop vary in content of some petrogenic oxides. The sandstone is a denser and more stable substrate than soil outcrops of the river banks in valleys. However, different layers at particular sandstone outcrop can significantly vary in density and strength.

Previous studies on bryophytes of Devonian sandstone outcrops in the southwest of the Leningrad Region were mostly held in the 1970–1990[s] and had floristic and ecological aims (Vyunova, 1974, 1975; Cherepanov, 1989, 1990; Potemkin, Cherepanov, 1993; Potemkin, 1995). All of the listed papers include the data about the records of rare species for the region. Our work on flora and vegetation of sandstones was started in 2015 and resulted in data of the new records of rare species discussed below. The goal of this paper is to present data on collection sites on sandstone outcrops, ecology and differentiation of revealed rare bryophyte species significant for further studies of bryophytes in the Leningrad Region and nature protection. Our study intends to provide an impetus for the further exploration of the Luga River Basin and outcrops of Devonian sandstones in the Leningrad Region and adjacent territories.

Material and Methods

Liverworts and mosses were collected by E. V. Kushnevskaya and E. V. Smirnova from vertical surfaces (70–90°) and talus slopes of sandstone. In 2015 data were obtained during floristic studies of the Luga River Basin by the route method. This work was a part of comprehensive studies for the creation of a specially protected natural area "Yashchera-Lemovzha" (Materialy..., 2015). The route method is suitable for surveying large areas in a limited time. It includes a survey of the entire diversity of habitats in the territory. The sites of interest were preliminarily identified from the map, satellite images, earlier documents. Some outcrops were discovered during fieldwork. All bryophytes observed on the outcrops were recorded.

In 2018–2021 bryophytes were gathered during geobotanical studies of bryophyte communities of sandstone outcrops by sample plot method. The plots with an area of 60 cm^2 were arranged regularly with an interval of 60–70 cm within the natural boundaries of the communities. In small contours with an area less than 1500 cm^2, three sites were placed at similar distances to each other. The total number of sample plots per outcrop ranged from 66 to 146. We also collected floristic data between sample plots.

The locations of the studied outcrops are marked on a map (Fig. 1) and listed below. For coordinates, we used a geodetic system WGS 84.

Study area: 1: Luzhsky District, 1 km S of Psoed' Village, left bank of the Saba River, specially protected natural area "Geological Ordovician and Devonian Outcrops on the Saba River", red sandstone, 3500 m^2, [58°58′N, 29°05′E]; **2**: Volosovsky District, Hotnezha Village, right bank of the Lemovzha River, 1.8 km N of the confluence of the Luga and the Lemovzha rivers, red sandstone, 500 m^2, [59°07′N, 29°17′E]; **3**: Luzhsky

District, 2 km NW of Muraveino Village, left bank of the Luga River, right bank of Rastishenskii Stream, 150 m W of the confluence of the Luga River and the Rastishenskii Stream, red sandstone, 115 m^2, 59°00′40″N, 29°37′17″E; **4**: Luzhsky District, 1.7 km NW of Muraveino Village, left bank of the Luga River, 300 m SE of the confluence of the Luga River and the Rastishenskii Stream, red sandstone, 150 m^2, separate outcrop closest to Muraveino Village covered with moss vegetation, 59°00′30″N, 29°37′35″E; **5**: Luzhsky District, 800 m E of Bezhany Village, right bank of the Bezhanka River, 600 m E of the confluence of the Luga and the Bezhanka Rivers, red sandstone, 15 m^2, 58°58′19″N, 29°42′53″E; **6**: Luzhsky District, 1 km SW of Kemka Village, left bank of the Kemka River, 500 m E of confluence of the Luga and the Kemka rivers, white sandstone, 6 m^2, 58°56′39″N, 29°48′24″E; **7**: Luzhsky District, 1 km NE of Yashchera Village, left bank of the Yashchera River, 2 km NE of the confluence of the Luga and the Yashchera rivers, white sandstone, 3000 m^2, from 58°53′47″N, 29°50′25″E to 58°53′49″N, 29°51′01″E.

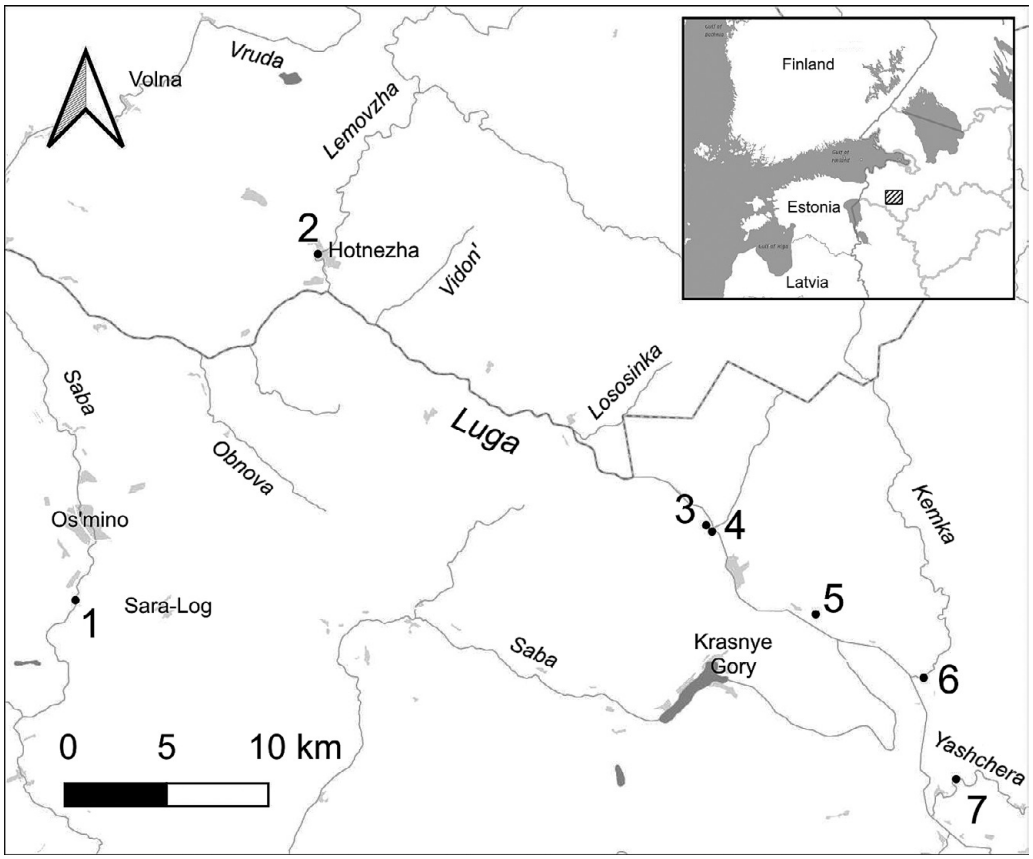

Fig. 1. Locations of the studied outcrops.

We noted the population size and its spatial distribution on the outcrop, species composition, substrate characteristics, and height above the river water level for every species. Registration of the substrate color was also important because it reflects the difference in chemical composition. The increase in K and Fe content is visible due to the intensity of the red color of the sandstone.

Photomicrographs of dry plants, leaves, and stem sections were made with MSP-2 var. 2 and MicroMed-6 microscopes (LOMO, St. Petersburg, Russia) and a Stylus Tough TG-5 camera (Olympus, Tokyo, Japan), using its macro and stacking modes.

The names of liverworts and mosses follow Hodgetts *et al.* (2020). Primary identification of collections was made by E. V. Smirnova and confirmed or revised by E. V. Kushnevskaya. Critical specimens of rare liverwort species were revised and mostly confirmed by A. D. Potemkin, of mosses by L. E. Kurbatova. The contribution of every author in identifications is evident from the list. The representative specimens are kept in the Bryological Herbarium of the Komarov Botanical Institute (LE).

Results

Our study resulted in a bryophyte inventory of Devonian sandstone outcrops in the abovementioned locations. The list of all recorded bryophytes is out of the scope of the present paper. The dominant bryophyte species of each location (Fig. 1), significant for the description of conditions in which the revealed rare species were gathered, are as follows: **1**: *Gymnostomum aeruginosum*, *Gyroweisia tenuis*, *Leptobryum pyriforme* (Hedw.) Wilson, *Pohlia proligera* (Kindb.) Lindb. ex Broth.; **2**: *Conocephalum salebrosum* Szweyk. et al., *Distichum capillaceum* (Hedw.) Bruch et Schimp., *Leptobryum pyriforme*, *Plagiochila porelloides* (Torr. ex Nees) Lindenb., *Pohlia* spp.; **3**: *Dicranella crispa* (Hedw.) Schimp., *Sphenolobus minutus* (Schreb. ex D. Crantz) Berggr., *Plagiochila porelloides*, *Plagiothecium rossicum* Ignatov et Ignatova; **4**: *Distichum capillaceum*, *Mnium stellare* Hedw., *Pohlia cruda* (Hedw.) Lindb., *Pseudoanomodon attenuatus*; **5**: *Mesoptychia heterocolpos*, *Pohlia* spp.; **6**: *Brachythecium* spp., *Metzgeria furcata*, *Pogonatum urnigerum* (Hedw.) P. Beauv.; **7**: *Mylia taylorii* (Hook.) Gray, *Pogonatum urnigerum*, *Pohlia proligera*, *Sphenolobus minutus*, *Tetraphis pellucida* Hedw.

The annotated list of new and rare (protected, and substrate-specific species with a scattered distribution) bryophytes for the Leningrad Region is presented below. Data for every species include collecting site number (Fig. 1), its frequency on the outcrop (sporadic, rare, unique), presence of sporophytes (S-, S+) and asexual reproduction devices, type of substrate, associated species (listed in order of decreasing of their abundance), collection date, collector, names of authors, who identified and revised specimen, and collection number if the specimen was included in the herbarium collection. Protected species easily identified in the field were not collected. The frequency of species is based on the number of records and their abundance on any particular outcrop. The species, occurring regularly as an admixture or irregularly but in big patches on the outcrop, are defined as sporadic. The species, occurring irregularly in small patches, are rare. The species, found once per outcrop, are unique. The exclamation

mark (!) denotes the species protected in Russia (Krasnaya..., 2008), the asterisk (*) marks the species protected in the Leningrad Region (Krasnaya..., 2018).

Division Marchantiophyta

Geocalyx graveolens (Schrad.) Nees — **1:** rare, S-, on outcrop of red sandstone with *Bryoerythrophyllum recurvirostrum*, *Brachytheciastrum velutinum* (Hedw.) Ignatov et Huttunen, etc., 27 VIII 2018, *Kushnevskaya*, *Smirnova*, det. *Smirnova*; **3:** rare, S-, on outcrop of red sandstone with *Blepharostoma trichophyllum* (L.) Dumort., *Plagiochila porelloides*, etc., 11 VIII 2020, *Smirnova*, LE B0022653; **7:** sporadic, S-, on outcrop of white sandstone with *Mylia taylorii*, *Bryoerythrophyllum recurvirostrum*, *Pohlia proligera*, *Sphenolobus minutus*, *Blepharostoma trichophyllum*, etc., 3 V 2018, *Kushnevskaya*, *Smirnova*, det. *Smirnova*, rev. *Kushnevskaya*, LE B0022654.

The specimens of *Geocalyx graveolens* were encountered on different types of sandstone. It occupies the partly shaded outcrops at a height of 1–5 m above their bases at different distances from the water surface (0–15 m to the surface of the summer water level of the adjacent water stream).

The species has boreal subcircumpolar distribution (Konstantinova, 2000). It usually grows on rotten wood, bases of trees, soil, and is considered a specialized species characteristic of habitats with constantly high air humidity (Vyyavlenie..., 2009).

Mesoptychia collaris (Nees) L. Söderstr. et Váňa [≡ *Leiocolea collaris* (Nees) Schljakov = *Leiocolea alpestris* (Schleich. ex F. Weber) Isov.] — **3:** rare, S-, on outcrop of red sandstone with *Tortula lingulata*, *Gyroweisia tenuis*, *Distichum capillaceum*, etc., 13 VIII 2020, *Smirnova*, det. *Potemkin*, rev. *Smirnova*, *Kushnevskaya*, LE B0022651 (Figs 2, 3).

Morphology of the examined specimen (LE B0022651). Plants small, 0.5–1.3 mm wide and (3)5–7 mm long, green to yellow and brown. Stem pellucid in dorsal part, brown in ventral part, of thin-walled cells, ca. 9–10 cells high and 200 μm in diam. Rhizoids brownish, ± numerous. Leaves plane to slightly concave, widest in the median part, about (300)500–650 μm long and wide, with V-like broad sinus in larger leaves slightly reflexed at the bases, 0.2–0.25 of the length; dorsal margin of leaves ± straight to slightly convex, ventral margin ± evenly convex; ventral lobe broader and slightly longer than dorsal lobe; lobes and occasionally distal leaf margin bleached. Cells thin-walled with variable bulging to occasionally rather small acute trigones, 17–25 × 20–35 μm in the median part of leaves, ± elongated near ventral leaf base, (20)25 × 25–37(20) μm, near ventral margin up to 15 × 55 μm. Leaf surface obscurely striolate papillose, to the leaf base particularly. Underleaves small, ca. 300 μm long, indistinct, subulate, 2-seriate near the base and uniseriate in distal part, with lateral uniseriate cilia. Dioicous. One plant with unfertilized gynoecium and vestigial perianth without adjacent male bracts confirming its doiocous state was found (Fig. 3A).

The species is represented by rather typical but small and impoverished plants growing on rather dry sandstone in conditions of partial shade. The collection site at the outcrop is located 3 m from the adjacent water stream. Leaf lobes are mostly

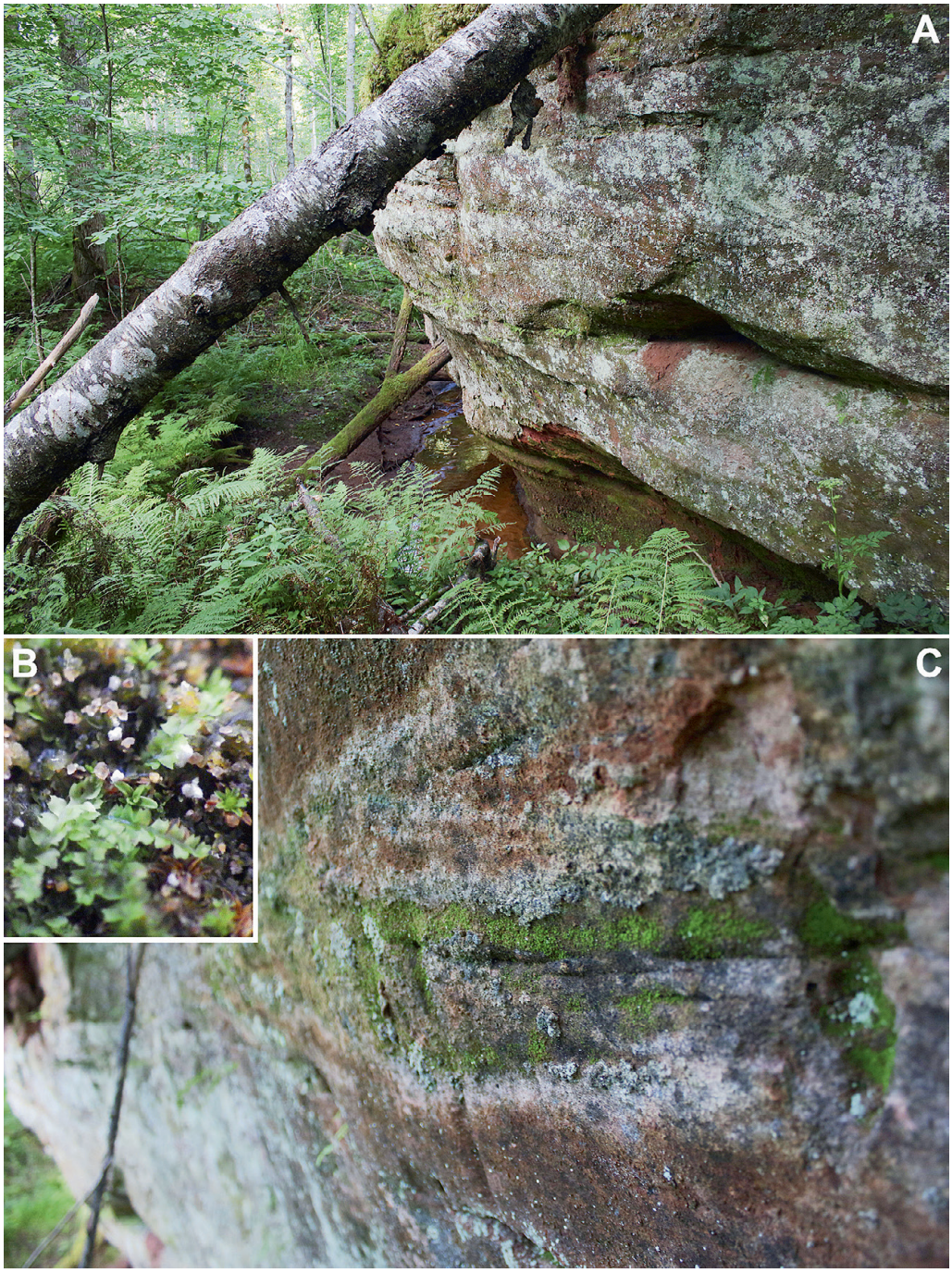

Fig. 2. Collection site of *Mesoptychia collaris* (A, C) and live plants from location 3 (B).

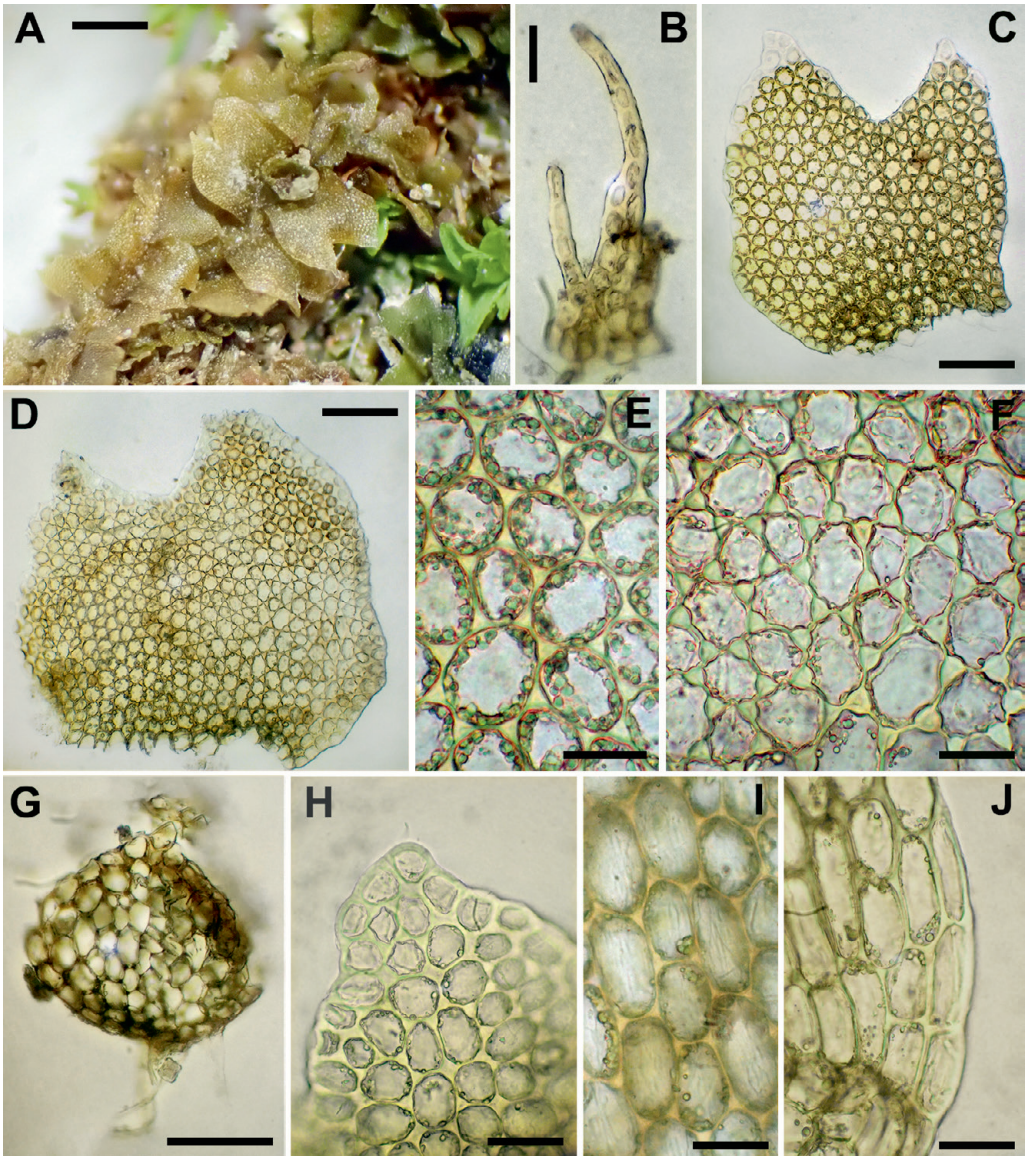

Fig. 3. *Mesoptychia collaris* (13 VIII 2019, *Smirnova*, LE B0022651).
A — plant with unfertilized gynoecium and young perianth; B — underleaf; C, D — leaves; E, F — median leaf cells; G — stem transverse section; H — leaf lobe; I — cells of median leaf base with striolate papillae; J — ventral leaf base.
Scale bars: A — 400 μm; B — 50 μm; C, D, G — 100 μm; E, F, E — 25 μm; H, J — 45 μm.

bleached and have cells with variable and not characteristic of this species often strongly convex trigones. That may result from the dry or other unfavorable habitat conditions (Potemkin, Sofronova, 2009: 96).

Distribution. *Mesoptychia collaris* is an arctoboreomontane subcircumpolar species with sporadic occurrence in Europe (Konstantinova, 2000).

This is the first record of *Mesoptychia collaris* for the Leningrad Region. The nearest locations are known from the old collections gathered by Finnish researchers in the 19th century: in the south of the Republic of Karelia near Sortavala (Bakalin, 1999) and by S. O. Lindberg in Southern Finland near Helsinki (Hassel, 2022). No records of *M. collaris* known to us were reported in those areas later. In the list of Finnish bryophytes (Pihlaja, Ulvinen, 2021), the abovementioned S. O. Lindberg record of *M. collaris* based on a specimen from TRH is not mentioned, and this species is listed for the northern provinces of Finland only.

Differentiation. *Mesoptychia collaris* might be confused with more widespread *M. badensis* (Gottsche ex Rabenh.) L. Söderstr. et Váňa and *M. heterocolpos*, known from similar habitats in the Leningrad Region, and with *M. gillmanii* (Austin) L. Söderstr. et Váňa reported from territories of the Republic of Karelia adjacent to the Leningrad Region and occurring in wet calcareous rocks and eutrophic mires. It differs from *M. badensis* in common (vs. rare) brownish pigmentation and stiffer (vs. more delicate) structure, presence (vs. usual absence) of underleaves, distinct acute to bulging (vs. vestigial) trigones, striolate verruculose (vs. usually smooth) leaf surface and smaller cells in the median part of leaves, 18–34 × 22–42 μm vs. 25–40 × (20)30–45(50) μm. Our plants of *M. collaris* differ from *M. gillmanii* in smaller size (0.5–1.3 mm vs. 1.5–3.5 mm wide), smaller cells (mostly 18–25 μm vs. 27–40 μm wide in the median part of leaves), and sex distribution (dioicous vs. paroicous). *Mesoptychia collaris* is distinct from *M. heterocolpos* without gemmae in ± elongated leaf cells in the proximal part of larger leaves (vs. ± isodiametric) and often straight to slightly concave (vs. ± convex) sinus margins.

Sterile specimens of *Mesoptychia collaris* might be confused also with sterile specimens of some species of *Nardia* Gray. It differs from *Nardia* in the broader ventral (vs. dorsal) lobe, striolate papillose (vs. smooth) leaf surface.

***Mesoptychia heterocolpos** (Thed. ex Hartm.) L. Söderstr. et Váňa [≡ *Lophozia heterocolpos* (Thed. ex Hartm.) M. Howe ≡ *Leiocolea heterocolpos* (Thed. ex Hartm.) H. Buch] — **4:** sporadic, abundant, S-, with gemmae, on outcrop of red sandstone with *Plagiochila porelloides*, *Plagiomnium cuspidatum* (Hedw.) T. J. Kop., *Chionoloma tenuirostre*, *Bryoerythrophyllum recurvirostrum* (Hedw.) P. C. Chen, etc., 19 VIII 2021, *Smirnova*, rev. *Kushnevskaya*, LE B0022652; **5:** sporadic, abundant, S-, with gemmae, on outcrop of red sandstone, 14 VIII 2015, *Kushnevskaya*.

These records confirm the first record of this species by Potemkin (1995) from the sandstone bank of the Luga River near Muraveino Village. The populations are in a good state and plants have abundant gemmae, suggesting further records of *Mesoptychia heterocolpos* in the Luga River Basin are likely to be discovered. The total area of mats of this liverwort exceeds 1 m^2. *Mesoptychia heterocolpos* grows on the solid parts of red sandstone of nearly a vertical slope. Both outcrops are somewhat distant from the open water surface and moderately shaded by floodplain deciduous forest. The liverwort is most abundant from the base of the outcrop up to 1.5 m.

Mesoptychia heterocolpos has a rather broad ecological amplitude (Potemkin, Sofronova, 2009) and arctoboreomontane circumpolar distribution (Konstantinova, 2000). In the Leningrad Region, it was also found only on Devonian sandstone, like in Great Britain, where it usually occurs on base-rich substrates like base-rich sandstones and calcareous cliffs (Mosses..., 2010).

***Metzgeria furcata** (L.) Corda — **6:** rare, S-, on outcrop of white sandstone, 7 V 2015, *Kushnevskaya*, field observation.

Metzgeria furcata was previously known from the Luzhsky District (Krasnaya..., 2018) and these records were associated with *Ulmus* spp. bark and rocks in floodplain elm forests. Near the mouth of the Kemka River, it was also located in the floodplain elm forest but grew on a wet sandstone surface at the base of a small outcrop near water.

Metzgeria furcata is a widespread but locally rare species. It sporadically occurs from Svalbard to New Zealand (Potemkin, 2011). In the Leningrad Region, this species is rare. It grows in habitats with constantly high air humidity on the bark of broad-leaved trees, granite rocks and stones, bases of trunks, rare on deadwood (Potemkin, 2011), and is considered a specialized species characteristic of habitats with constantly high air humidity (Vyyavlenie..., 2009).

Division Bryophyta

***Atrichum flavisetum** Mitt. — **4:** unique, abundant, S+, on outcrop of red sandstone, 15 VIII 2020, *Kushnevskaya*, LE B0024641.

The nearest records are located in the Luzhsky District (Krasnaya..., 2018): 58°53′48.9″N, 29°51′01.5″E, on soil, 16 VIII 2015, *Kushnevskaya*; 58°58′19.5″N, 29°42′52.8″E, on soil, 5 V 2015, *Kushnevskaya* (Materialy..., 2015).

In the Leningrad Region, *Atrichum flavisetum* is rare and usually found in river and stream valleys and on moraines, on the soil on the roots of fallen trees (authors' observations; Krasnaya..., 2018).

Atrichum flavisetum is widespread in Eastern Asia, Siberia, Russian Far East and has a limited distribution in Europe. Its typical habitats are vertically arranged soil outcrops (Ignatov *et al*., 2017). In the Leningrad Region, it is considered a specialized species characteristic of old broad-leaved forests on fertile soils (Vyyavlenie..., 2009).

In the vegetative stage, it is impossible to distinguish *Atrichum flavisetum* from *A. undulatum* (Hedw.) P. Beauv. which also appears on the outcrops. So we could clearly identify only one big tuft and several shoots where sporophytes were present.

Campylophyllopsis calcarea (Crundw. et Nyholm) Ochyra [≡ *Campylidium calcareum* (Crundw. et Nyholm) Ochyra ≡ *Campylium calcareum* Crundw. et Nyholm] — **1:** unique, S-, on outcrop of red sandstone with *Pohlia cruda*, *Mnium stellare*, *Leptobryum pyriforme*, 19 VIII 2019, *Smirnova*, rev. *Kurbatova*, *Kushnevskaya*, LE B0024642.

Our specimen has equally thickened yellowish alar cell walls and short double costa in stem leaves. It could be a feature of a particular specimen.

Two records of *Campylophyllopsis calcarea* were known for the region previously: from the specially protected natural area "The Lava River canyon" (15 V 2005, *Ukrainskaya*, LE) and from a sand bank of Hogland Island (Karttunen, 1986), but the nearest location is known in St. Petersburg from the Duderhof Hills Nature Reserve (18 IX 2007, *Kurbatova*, LE). We gathered a mat of *C. calcarea* with an area of 2 cm^2 in a dry crack of the unshaded sandstone at a distance of 20 m from the summer water level of the adjacent water stream.

The species is widely distributed in the countries of Central and Northern Europe. In European Russia, it is common for the limestones of the southern regions: in steppes, forest-steppes and partly in broad-leaved forests. It grows mainly in shaded places in various moisture conditions (Ignatov, Ignatova, 2004).

Chionoloma tenuirostre (Hook. et Taylor) M. Alonso et al. [≡ *Oxystegus tenuirostris* (Hook. et Taylor) A. J. E. Sm.] — **4:** sporadic, S-, on outcrop of red sandstone with *Mnium stellare*, *Rhizomnium punctatum* (Hedw.) T. J. Kop., *Distichum capillaceum*, etc., 18 VIII 2021, *Smirnova*, det. *Kushnevskaya*, rev. *Smirnova*, *Kurbatova*, LE B0024643.

Chionoloma tenuirostre grows on the dry base of the shaded outcrop, filling the gaps between other bryophytes. The nearest published location of this species is in the vicinity of Osmino Village, on stones along a stream in a ravine (Vyunova, 1974). According to our observations, this species usually occurs on stones of acidic and neutral rocks in mixed forests. In some cases, it is noted for the banks of forest streams.

The species is widely distributed throughout the world but unevenly recorded in European Russia: in the Caucasus, the Urals and the North-West (Leningrad, Tver and Murmansk regions, Republic of Karelia) (Moss..., 2022).

Encalypta vulgaris Hedw. — **2:** unique, S-, on outcrop of red sandstone with *Distichum capillaceum*, *Leptobryum pyriforme*, etc., 27 VIII 2018, *Kushnevskaya*, *Smirnova*, det. *Smirnova*, rev. *Kushnevskaya*, *Kurbatova*, LE B0024644; **3:** unique, S-, on outcrop of red sandstone with *Myurella julacea*, *Distichum capillaceum*, *Pohlia cruda*, *Mnium lycopodioides*, etc., 13 VIII 2020, *Smirnova*, LE B0024645.

In the Leningrad Region, *Encalypta vulgaris* was previously known from the Tosna River (Abramov, 1955) and the vicinity of Osmino Village (Vyunova, 1974). Our specimens occupied moderately shaded outcrops at a height of 1–8 m above the summer water level of the adjacent water stream.

Encalypta vulgaris is widespread in Europe and registered in Asia, North and South America, Australia, Africa. In literature, it is mentioned for base-rich substrates such as limestones and calcareous soil (Ignatov *et al*., 2017).

Gymnostomum aeruginosum Sm. — **1:** sporadic, S-, on outcrop of red sandstone with *Leptobryum pyriforme*, *Conocephalum salebrosum*, *Bryoerythrophyllum recurvirostrum*, 27 VIII 2018, *Kushnevskaya*, *Smirnova*, det. *Smirnova*, rev. *Kushnevskaya*, *Kurbatova*, LE B0024648.

This record is the second report for the Leningrad Region. The nearest location is known in the vicinity of Lemovzha Village (20 km NE of our record) on a sandstone

outcrop (Sofronova *et al*., 2016). It occupies partly shaded outcrops at a height of 1–8 m above the summer water level of the adjacent water stream.

Gymnostomum aeruginosum is rather common for mountain regions of Russia, but sporadically appears on flat landscapes. It prefers calcareous rocky substrates. In North-Western European Russia, the species was also recorded from the Republic of Karelia, Vologda, Tver, Arkhangelsk and Murmansk regions (Moss..., 2022).

Gyroweisia tenuis (Hedw.) Schimp. — **1:** sporadic, abundant, S-, with gemmae, on outcrop of red sandstone with *Leptobryum pyriforme*, 27 VIII 2018, *Kushnevskaya*, *Smirnova*, det. *Smirnova*, rev. *Kushnevskaya*, LE B0024646; **3:** rare, S-, with gemmae, on outcrop of red sandstone with *Mesoptychia collaris*, *Tortula lingulata*, *Distichum capillaceum*, 13 VIII 2020, *Smirnova*; **4:** rare, S-, with gemmae, on outcrop of red sandstone, 16 VIII 2021, *Smirnova*, LE B0024647.

On the outcrops, it mostly grows into dense and occasionally sparse monospecies groupings on dry parts of red outcrops in various light conditions. All our specimens have brown clavate gemmae near shoot bases, which makes possible a certain identification of this species. It was already known from the sandstone outcrops of the Saba River (Vyunova, 1974) and was also found on sandstone banks of the Oredezh and the Vruda rivers, which are tributaries of the Luga River (Sofronova *et al*., 2015).

Gyroweisia tenuis has a scattered distribution in Europe, North America, North Africa. It is a common floristic element of plant communities on outcrops of wet carbonate rocks (Ignatov, Ignatova, 2003).

***Mnium hornum** Hedw. — **3:** unique, S-, on outcrop of red sandstone, 14 VIII 2019, *Smirnova*, rev. *Kushnevskaya*, *Kurbatova*, LE B0024649.

In the Leningrad Region, *Mnium hornum* away from the coast of the Gulf of Finland is very rare. The discovery of this species on the Luga River sandstone outcrop is the southernmost occurrence in the region. Our specimen was gathered on the shaded sandstone near the water in the small stream valley.

Mnium hornum is mentioned for various substrates in oceanic regions of Europe. In Russia, it is found mainly in the Kaliningrad Region (Ignatov *et al*., 2017). In the Leningrad Region, it is more common for wet soil outcrops and is considered an indicator species characteristic of deciduous floodplain forests (Vyyavlenie..., 2009).

Mnium lycopodioides Schwägr. — **3:** unique, S-, on outcrop of red sandstone with *Distichum capillaceum*, *Pohlia cruda*, *Encalypta vulgaris*, etc., 13 VIII 2020, *Smirnova*, rev. *Kushnevskaya*, *Kurbatova*, LE B0024650.

Our specimen was encountered on the loose part of shaded sandstone near water. In the southwest of the Leningrad Region, this species was previously known from other substrates: mostly on soil, less often on rocky substrates. The information about distribution in this part of the region is based on specimens from the vicinities of Kaibolovo Village (19 IV 2007, *Kurbatova*, LE), Siverskaya Railway Station (as *Mnium riparium* Mitt., 23 VIII 1971, *Vyunova*, LE), Krasnye Gory Village (as *M. ambiguum* H. Müll., 23 VII 1972, *Vyunova*, LE), Poddub'e Village (as *M. ambiguum*, 12 VIII 1972, *Vyunova*, LE), Nikolaevskoe Village (as *M. ambiguum*, 2 VIII 1972, *Vyunova*,

LE), published records from the canyon of the Suma River (Leushina *et al*., 2011) and Cheremenetsky Nature Reserve (Ocherki..., 1992).

Mnium lycopodioides is considered arcto-alpine and widely distributed in the Northern Hemisphere. In Russia, it occurs sporadically especially in mountain regions, rarely on the slopes of ravines in plain regions (Ignatov *et al*., 2017).

***Myurella julacea** (Schwägr.) Schimp. — **3:** rare, S-, on outcrop of red sandstone with *Mesoptychia collaris*, *Tortula lingulata*, *Distichum capillaceum*, etc., 13 VIII 2020, *Smirnova*, rev. *Kushnevskaya*, LE B0024651; **4:** sporadic, S-, on outcrop of red sandstone with *Distichum capillaceum*, *Tortula lingulata*, etc., 15 VIII 2020, *Kushnevskaya*.

Myurella julacea occupies shaded places of the outcrops at a height of 1–4 m above the sandstone bases at different distances from the water surface (0–20 m to the surface of the summer water level of the adjacent water stream).

Previously, this species was known in the region from the Karelian Isthmus (Leushina *et al*., 2011) and Mshinskoye Nature Reserve (Vyunova, Kuzmina, 1991). *Myurella julacea* is not typical for warm plain regions and ordinarily grows on fine soil on carbonate rocks (Ignatov, Ignatova, 2004).

Pseudoanomodon attenuatus (Hedw.) Ignatov et Fedosov [≡ *Anomodon attenuatus* (Hedw.) Huebener] — **4:** sporadic, abundant, S-, on outcrop of red sandstone with *Plagiomnium cuspidatum*, *Mnium stellare*, *Conocephalum salebrosum*, *Homalia trichomanoides* (Hedw.) Brid., *Pohlia cruda*, etc., 15 VIII 2020, *Kushnevskaya*, det. *Smirnova*, rev. *Kushnevskaya*, LE B0024652.

Pseudoanomodon attenuatus is known near the Geological Station Zhelezo which is located upstream of the Luga River, where it grows on dead wood and rocks in the deciduous forest (Vyunova, 1975). In our case, it grows on a red sandstone at a height over 1.5 m above the outcrop base. This moss covers several square meters of the outcrop shaded by floodplain deciduous forest and appears on the bark of the adjacent broad-leaved trees. Extensive mats retain and accumulate a large number of soil particles.

There are also specimens of this species from the vicinities of Shchugovitsy Village in the Volosovsky District (14 V 1985, *Ignatov*, LE), Shcheleiki Village in the Podporozhsky District (23 IV 2004, *Leushina*, LE), and several references from the Karelian Isthmus (Brotherus, 1923; Piippo, 1982).

In the Leningrad Region, *Pseudoanomodon attenuatus* occurs on the bark of old broad-leaved trees, shaded rocks and stones, and is considered an indicator species characteristic of old broad-leaved forests (Vyyavlenie..., 2009).

***Saelania glaucescens** (Hedw.) Broth. — **3:** rare, S-, on outcrop of red sandstone with *Sphenolobus minutus*, *Dicranella crispa*, *Lophozia ventricosa* (Dicks.) Dumort., *Blepharostoma trichophyllum*, etc., 11 VIII 2020, *Smirnova*; **4:** rare, S+, on outcrop of red sandstone with *Leptobryum pyriforme*, *Pohlia proligera*, *Bryoerythrophyllum recurvirostrum*, *Blepharostoma trichophyllum*, etc., 14 VIII 2021, *Smirnova*, LE B0024653; **7:** unique, S+, on outcrop of white sandstone with *Sphenolobus minutus*, *Plagiochila porelloides*, *Blepharostoma trichophyllum*, *Schistochilopsis incisa* (Schrad.) Konstant., etc., 3 V 2018, *Kushnevskaya*, *Smirnova*, rev. *Kurbatova*, LE B0024654.

Saelania glaucescens was found mainly in unshaded places of the outcrops at a height over 2 m above the summer water level of the adjacent water stream. All shoots have strong glaucous coloration due to a species-specific wax cover on leaves.

Only one record of *Saelania glaucescens* from the Kingisepp District in the south of the region was published (Andrejeva, 2014). Other specimens of this species were collected on the Karelian Isthmus and in the northeast of the Leningrad Region (Krasnaya..., 2018). Thus, the records from the Luzhsky District expand the known distribution range of this species in the Leningrad Region to the south and to the east.

Saelania glaucescens is documented from many countries of Western Europe, Central and Eastern Asia, North America, and other regions. This moss is more typical for mountain areas and prefers fine soil on rocks (Ignatov *et al*., 2017).

!Tortula lingulata Lindb. — **1:** rare, S+, on outcrop of red sandstone with *Leptobryum pyriforme*, *Brachytheciastrum velutinum*, etc., 30 VIII 2019, *Smirnova*, rev. *Kushnevskaya*, *Kurbatova*, LE B0024655; **3:** rare, S+, on outcrop of red sandstone with *Mesoptychia collaris*, *Gyroweisia tenuis*, *Distichum capillaceum*, 13 VIII 2020, *Smirnova*, LE B0024656; **4:** sporadic, abundant, S+, on outcrop of red sandstone with *Distichum capillaceum*, *Leptobryum pyriforme*, etc., 15 VIII 2020, *Kushnevskaya*, LE B0024657.

We found *Tortula lingulata* specimens growing on moderately dense, shaded, slightly damp parts of red sandstone. The patches of *T. lingulata* were mostly monospecific without sporophytes, although individual shoots with sporophytes were rarely found. In the Leningrad Region, this species was previously known from two published locations, i. e., sandstone outcrops of the Saba River (Vyunova, 1974) and the Sablinka River (Abramov, 1959). All records for the region are associated with Devonian sandstones.

Tortula lingulata has mainly European distribution. It is known from Estonia, Latvia, Russia, Ukraine, Georgia, Czech Republic and Germany (Ingerpuu *et al*., 2008). Some authors (Krasnaya..., 2008; Ingerpuu *et al*., 2008; Košnar, Kolař, 2009) classify *T. lingulata* as a substrate-specific species of sandstones with neutral-alkaline pH reaction of a substrate.

In this list, we have reported detailed annotations only for the new records of 16 rare species collected by the authors of this study. Therefore, there are published data, for which we updated information about the state of populations of rare species. *Bazzania trilobata* (L.) Gray and *Mylia taylorii* were previously reported on white sandstone from location 7 (Fig. 1) (Potemkin, Cherepanov, 1993). Both species grow in this location now, forming extensive mats at a height of 1–5 m above the summer water level of the adjacent water stream (22 XII 2019, *Kushnevskaya*, *Smirnova*). In the studied locations, we also made the first records of other species that we published earlier. *Arnellia fennica* (Gottsche) Lindb. was previously collected extremely close to locations 3 and 4 on sandstone from the same Luga River bank at a height of 1 m above the summer water level (Potemkin, 1995). *Liochlaena subulata* (A. Evans) Schljakov and *Solenostoma confertissimum* (Nees) Schljakov were published earlier by Smirnova

et al. (Sofronova *et al.*, 2021). *Liochlaena subulata* was gathered from red sandstone from location 3 at a height of 1–2 m above the summer water level, and *S. confertissimum* was gathered on white sandstone from location 7 at a height 2.5 m above the summer water level of the adjacent water stream.

Discussion

The outcrops of Devonian sandstones that are denuded on a relatively small part of the landscape have become the refuge of some rare species. The probability of colonization of the sandstones by these species is very low, but in some cases, it nonetheless occurs. The outcrops of Devonian sandstones have a remarkable suite of bryophytes in comparison to other substrates: dead wood, soil, tree bark and others (Materialy..., 2015; Kushnevskaya, 2018).

The properties of sandstone as a substrate are due to its chemical composition, rock strength, humidity regime and decreased competition on vertical surfaces free from vascular plants. The chemical composition of red-colored outcrops is characterized by a high content of metals (Engalychev, Panova, 2011). Some layers can contain a moderate amount of calcium, but it was not common in our study site. There are also no outcrops of calcium rocks in the studied part of the Leningrad Region, and highly specialized calcicolous species were not found. However, some species that prefer calcium-enriched substrates can exist on outcrops with a lower amount of calcium. The nine following species are cited by other authors (Ignatov, Ignatova, 2003, 2004; Krasnaya..., 2008; Potemkin, Sofronova, 2009; Krasnaya..., 2018) as calcicolous species of varying degrees of persistence: *Arnellia fennica*, *Campylophyllopsis calcarea*, *Encalypta vulgaris*, *Gymnostomum aeruginosum*, *Gyroweisia tenuis*, *Mesoptychia collaris*, *Mesoptychia heterocolpos*, *Myurella julacea*, *Tortula lingulata*. We found all of these species on red-color sandstones. The sensitivity of these bryophytes to amounts of calcium and metals is a subject of future studies.

Some of the rare bryophytes we encountered can be characterized as species with typical suffusion distributional rarity in a portion of their range yet be quite abundant elsewhere (Cleavitt, 2005). Populations of such species can decline rapidly as they move away from the main area of distribution of the species. In our case, such species vary in their distribution patterns. Different combinations of ecological conditions in sandstone outcrop microniches are causing bryophyte composition that consists of species with mostly more northern and/or mountainous (*Arnellia fennica*, *Gymnostomum aeruginosum*, *Mnium lycopodioides*, *Myurella julacea*, *Saelania glaucescens*, *Solenostoma confertissimum*), more southern (*Campylophyllopsis calcarea*, *Pseudoanomodon attenuatus*), more suboceanic (*Mnium hornum*), and more southern and suboceanic distribution patterns (*Bazzania trilobata*, *Metzgeria furcata*).

Conclusions

The outcrops of Devonian sandstones represent a set of various niches favorable for rare bryophytes. The preservation of bryophyte habitats on outcrops of Devonian sandstones depends on their position above water level, substrate stability, low

competition with the vascular plants on the vertical surfaces. Our results show that the Luga River Basin may represent a temporary or long-lasting refuge for the selected bryophyte species. These facts point to the importance of further studies of the outcrops of Devonian sandstones in the Leningrad Region and in the Luga River Basin in particular.

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