ТНЕ GENUS *PSEUDOLESKEELLA* (BRYOPHYTA) IN RUSSIA РОД *PSEUDOLESKEELLA* (BRYOPHYTA) В РОССИИ Elena A. Ignatova¹, Oxana I. Kuznetsova², Alina V. Fedorova² & Micheal S. Ignatov^{1,2} Елена А. Игнатова¹, Оксана И. Кузнецова², Алина В. Федорова², Михаил С. Игнатов^{1,2}

Abstract

A taxonomic revision of the genus *Pseudoleskeella* in Russia has been addressed at the species level. Molecular phylogenetic analysis found a quite separate position of *P. tectorum* and *P. nervosa*, while *P. rupestris*, *P. catenulata* and *P. papillosa* appeared to be rather closely related. *Pseudoleskeella rupestris* is an extremely variable species in Russia, comprised partly by plants with short double or forked costae in some leaves which makes difficult its differentiation from *P. tectorum*; such morphotypes are described as *P. rupestris* var. *tenuis*. In the *Pseudoleskeella catenulata*-clade one specimen from Sakhalin was found contrastingly different by morphology, having very long acuminate leaves and only moderately thick-walled cells. It is described as a new species, *P. sachalinensis*. Thus, the genus *Pseudoleskeella* is represented in Russia by six species and one variety.

Резюме

Проведена таксономическая ревизия рода *Pseudoleskeella* в России, целью которой было уточнение таксономии на видовом уровне. Молекулярно-филогенетический анализ выявил изолированное положение *P. tectorum* и *P. nervosa*, в то время как *P. rupestris*, *P. catenulata* и *P. papillosa* оказались близкородственными видами. *Pseudoleskeella rupestris* является морфологически очень вариабельным видом, и в отдельных популяциях часть листьев имеет короткую двойную или вильчатую жилку, что усложняет их разграничение с *P. tectorum*; такие морфотипы описаны как новая разновидность *P. rupestris* var. *tenuis*. В кладе *Pseudoleskeella catenulata* один образец с Сахалина оказался контрастно отличающимся по морфологическим признакам, его листья имеют длинно оттянутую верхушку и клетки с умеренно утолщенными стенками. Он описан как новый вид, *P. sachalinensis*. Таким образом, род *Pseudoleskeella* представлен в России 6 видами и одной разновидностью.

KEYWORDS: Hypnales, molecular phylogeny, trnS-F, ITS, taxonomy, new variety, new species

INTRODUCTION

Pseudoleskeella Kindb. is a relatively small genus of pleurocarpous mosses; however, due to enormous morphological variation of its species, its taxonomy is not easy. Most Eurasian and North American floras in 20th century accepted only two species in the genus Pseudoleskeella, P. catenulata (Brid. ex Schrad.) Kindb. and P. tectorum (Funck ex Brid.) Kindb. (e.g., Lazarenko, 1955; Crum & Anderson, 1981). Some authors combined Pseudoleskeella with Leskeella (Limpr.) Loeske, thus adding one more species, P. nervosa (Brid.) Nyholm. Later this placement of the latter species was supported by molecular phylogenetic analyses (Gardiner et al., 2005), and became widely accepted. A fourth species of the genus is *P. papillosa* (Lindb.) Kindb. It differs from other Pseudoleskeella species in having massive papillae on its dorsal leaf surface, so it was rarely included in the genus Pseudoleskeella in 20th century, being more

commonly classified in *Heterocladium* Bruch, Schimp. & W. Gümbel. Molecular phylogenetic analysis has fixed the placement of *P. papillosa* in the genus *Pseudoleskeella* (Ignatov *et al.*, 2007). The fifth currently widely accepted species was introduced to wide usage by Wilson & Norris (1989). These authors elevated a variety *Pseudoleskeella nervosa* var. *sibirica* (Arnell) E. Lawton (originally described within *Leskea* Hedw.) to the status of species. Shortly after that, Hedenäs & Söderström (1991) found that *P. rupestris* (Berggr.) Hedenäs & L. Söderstr. is the earlier name for *P. sibirica* (Arnell) P.S. Wilson & D.H. Norris, and since that time the nomenclature of the group had temporarily stabilized.

Despite of the above mentioned advances, the practical identification of *Pseudoleskeella* remains problematic, and large numbers of specimens remain named with a question mark, or with 'cf.', 'aff.' or 'sp.' Especially difficult was *P. rupestris* due to its enormous morphological variability. Wil-

¹ – Lomonosov Moscow State University, Faculty of Biology, Plant Ecology and Geography Dept., Leninskie Gory Str. 1–12, Moscow 119234 Russia. E-mail: arctoa@list.ru; ORCID (EI): 0000-0001-6287-5660; (MI): 0000-0001-6096-6315

² – Tsitsin Main Botanical Garden, Russian Academy of Sciences, Botanicheskaya Str., 4, Moscow 127276 Russia; ORCID (OK): 0000-0002-5513-1329; (AF): 0000-0001-7362-2124.



son & Norris (1989) described this species as having an intermediate position between three other species of the genus, i.e. *P. tectorum*, *P. catenulata* and *P. nervosa*.

Considering the powerful help offered by molecular phylogenetic reconstruction we applied this method for the elucidation of the *Pseudoleskeella* species diversity in Russia.

MATERIAL AND METHODS

Specimen selection. We selected the material from MHA, paying special attention to specimens which morphology is controversial, selecting few samples of most common phenotypes.

Amplification and sequencing protocols were essentially the same as in our previous moss studies, described in detail by, e.g., Gardiner *et al.* (2005) for ITS, and for the *trn*S–F region we used the primers *rps*4-166F and P6/7, as described in Wynns & Lange (2014).

Molecular analysis. Sequences were aligned using Bioedit (Hall, 1999). Preliminary tests showed no supported conflicts in trees inferred from separate analysis

Fig. 1. Bayesian tree of *Pseudoleskeella* based on nuclear ITS and plastid *trn*S–F sequences. Posterior probabilities and / MP bootstrap supports are shown at branches.

of nuclear ITS and plastid trnS–F regions, thus the concatenated dataset was used for the final analysis. Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with 10 000 000 generations. Supplementary maximum parsimony analysis was performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 1000 replications (N searches 100, starting trees per rep 100, max trees 100, do max).

Illustrations were made under stereomicroscope Olympus SZX-7 (digital camera Infinity 8-8) and Olympus CX43 (digital camera Infinity 1-2), with Z-stacking in Helicon Software (Kozub *et al.*, 2008).

RESULTS

Molecular phylogenetic analysis (Fig. 1) found a quite separate position for *P. tectorum* (PP=1 BS =98), sister to all other species, which clade is highly supported (PP=1 BS =98). Within the latter, the *P. nervosa*-clade is the first that branches off, with maximal support in Bayesian analysis, but with a low support in MP analysis (PP=1, BS =66). The sister clade to *P. nervosa* lacks support, and is formed by a grade of (1) the unsupported clade of *P. rupestris*; (2) the weakly supported clade of *P. papillosa* (PP=0.99, BS =52); (3) the moderately supported clade composed largely of specimens of *P. catenulata* (PP=1, BS =72).

Most specimens in the present analysis were sequenced *de novo*, but two were taken from the analysis of Gardiner *et al.* (2005). One of them was resolved as it was named in that publication (*P. papillosa* from the Urals), while another one, reported by Gardiner *et al.* (2005) as *P. tectorum*, appeared in the present analysis in a clade with *P. rupestris*.

Morphology of the sequenced specimens is discussed below.

TAXONOMY

The main result of the present study confirmed the monophyly of previously recognized species of the genus, thus this study includes only a few taxonomic novelties



leaves from upright shoots and 1-2 leaves from creeping shoots are shown. For specimen data, according to isolate numbers, see Appendix. Scale bars: 0.5 mm for leaves; 50 µm for cells.



Fig. 3. *Pseudoleskeella rupestris* var. *tenuis* (from holotype): A, E–G: habit, dry; B: mid-leaf cells; C: upper leaf cells; D: basal leaf cells. Scale bars: 2 mm for A; 100 µm for B–D.

resulting from the discrepancy between the position of sequenced samples in the molecular phylogenetic tree and their morphology. Below we discuss separate morphological characters, which occurrences in different taxa are often incompletely described and may lead to species misidentification.

1) Double / forked costae

Traditionally, a double or forked costa was considered as a key character with P. tectorum, although a number of leaves with long single costae were observed in many populations (Fig. 2a). Wilson & Norris (1989) suggested for Pseudoleskeella to describe separately leaves from creeping shoots and from upright shoots. Although there is a common trend that leaves from creeping shoots often have poorly developed, occasionally double costae, we were unable to confirm that double costae can be found in P. catenulata. This is also rare in P. rupestris. Moreover, in the latter species there is a certain variation with respect to costal development. In the ITS tree (not shown), specimens of P. rupestris were found in three clades, without support, but rather consistent with their morphology. One of them includes plants with many leaves having short double costae, whereas plants from other clades have leaves with costae vanishing in the leaf acumina or shortly below them in leaves from both upright and creeping shoots. In the tree from the concatenated dataset (Fig. 1) the group of specimens with some leaves with double costae form the basal polytomy (OK3119, 3120, 3141, 3159 cf. Fig. 2B, 3), whereas especially robust plants with stout costae in all leaves are in a small, low supported clade (PP=0.98, BS<50, samples OK 3131, 3134, 3135, Fig. 4). In a view of such imperfect correspondence we suggest recognizing *P. rupestris* plants with occasion-al double costae at the rank of variety.

Pseudoleskeella rupestris var. **tenuis** Ignatov & Ignatova, var. nov.

Type: Russia, Republic of Sakha/Yakutia, Eveno-Bytantaisky District, Orulgan Range, upper course of Aenigan-Toolono Creek, 68°16', 128°25'E, 900 m alt., S-faced cliffs in narrow gorge, 6 Aug 2011 Ignatov 11-4533 (MHA 9060832). Holotype MHA, isotype MW. Figs. 2 '3120', 3.

Diagnosis: *Pseudoleskeella rupestris* var. *tenuis* differs from var. *rupestris* in having smaller plants, usually shorter (to 0.5–0.6 vs. 0.6–0.9 the leaf length) and thinner costae in leaves from erect shoots, and short, double vs. single costae in many leaves from creeping shoots.

Description: *Plants* small to medium sized, pale green or yellowish-green, in loose mats. *Stems* creeping to ascending and erect, 1.0–1.5 cm long, irregularly branched, terete-foliate; hyalodermis absent, central strand present. *Leaves from erect shoots* straight, 0.5–0.7×0.2–0.4 mm, from ovate bases \pm abruptly tapered into lanceolate, narrow, straight or slightly curved acumina; margins plane, subentire or finely serrulate above; *costae* single, thin, to 0.5(0.6) the leaf length or, in poorly developed plants, short and double; *cells* in mid-leaf rounded-polygonal or elongate-rhomboidal, 10–15×5–7 µm, with moderately thickened walls, smooth. *Leaves from creeping shoots* with wider bases and usually with short and double cos-



Fig. 4. *Pseudoleskeella rupestris* var. *rupestris* (A, C–D – from syntype of *Leskea sibirica*, LE; B – from Altai Mts., OK3134; E – from Primorsky Territory, OK3131; F – see Appendix for label data according to isolate numbers). A–B, E: habit, dry; C: stem leaf; D: mid-leaf cells; F: for each sample one leaf from upright shoot, one leaf from creeping shoot, and mid-leaf cells are given. Scale bars: 0.5 mm for leaves in F; 50 μ m for leaf cells in F.

tae or with short single costae. Sporophytes unknown.

Other specimens examined: Perm Province, Bezgodov 16 Jul 2017 #194 (MHA9049390); 28 Jul 2017 #325, #329 (MHA9018309, MHA9018303); 15 Jul 2017 #143 (MHA 9049420); 9.VIII.2005 #106, #53 (MHA9046519, (MHA9049520). Altai Republic, Ignatov 32/29, 32/30, 32/31 (MHA9046619, MHA9046337, MHA9046620). Republic of Sakha/Yakutia, Orulgan Range, Ignatov 11-4363, 11-4071 (MHA9046637, MHA9046634).

This variety grows on rocks (limestones, aleurolites, shists), in the Urals at 180–760 m elev., in Orulgan Range, Yakutia at 670 m, in Altai at 2150–2200 m.

Differentiation: Pseudoleskeella rupestris var. tenuis



Fig. 5. Dorsal leaf surface of *Pseudoleskeella tectorum* (A, from OK3136 & B–C, from OK3123) with scattered papillae and *P. papillosa* (D, from OK3140) showing massive, prominent papillae in upper angle of each cell; E - P. *papillosa* (see Appendix 1 for label data according to isolate numbers). Scale bars in E: 0.2 mm for leaves; 50 µm for cells.

is similar to *P. tectorum* (cf. Fig. 2) but that species usually has leaves with widely ovate bases and comparatively short acumina, whereas leaf bases of *P. rupestris* var. *tenuis* are usually narrower ovate and the acumina are longer (however, these characters occasionally overlap). In optimally developed plants of *P. tectorum* costae in the majority of leaves are forked or double, while in *P. rupestris* var. *tenuis* costae are single in leaves from upright shoots and forked or double in leaves from creeping shoots. Similarly, this character separates *P. rupestris* var. *tenuis* from var. *rupestris*, the latter variety always having leaves from all shoots with single, stronger and longer costae (cf. Fig. 2B vs. Fig. 4). The isotype of *P. sibirica* (Fig. 4A, C–D) has all leaves with long, single costae, thus it belongs to *P. rupestris* var. *rupestris*.



Forked or double costae also occur *P. papillosa*, but this species is very different in small size of plants and prominent, massive papillae on the dorsal side of the leaves (Fig. 5).

2) Papillose laminal cells

This is another character used in keys of *Pseudoles-keella*, specifically for the identification of *P. papillosa*. This species has conspicuous papillae over most cells (Fig. 5D). Papillae are occasionally observed on leaves of *P. tectorum* as well, especially if the stem with undetached leaves is put in the microscope slide (Fig. 5A–C). These



Fig. 6. *Pseudoleskeella papillosa* (A – from Yakutia, OK3148; B – from Murmansk Province, OK3140) showing brood branches clustered at the upper ends of shoots.

Fig. 7 (on opposite page). *Pseudoleskeella sachalinensis* (A–E, H–R, from holotype), *P. rupestris* (F–G, from Altai Mts., MHA9131270) and *P. catenulata* (S, see Appendix for label data according to isolate numbers). A–B: habit, dry; C–F: upper leaf cells; G, I, L–N: leaves from upright shoots; K, O, P: leaves from creeping shoots; H: stem transverse section; J: mid-leaf cells; R: basal leaf cells; S: for each specimen one leaf from upright shoot and one from creeping shoots are shown; for 3137and 3139 upper leaf cells are shown and for 3262 - mid-leaf cells. Scale bars: 2 mm for A; 1 mm for B; 0.5 mm for G, I, K–P, leaves in S; 100 μm for C–F, H, J, R, cells in S.





Fig. 8. Mid-leaf cells of *Pseudoleskeella catenulata* (A – from Dagestan, OK3137) and *P. rupestris* (B – from Anabar Plateau, OK3130; C – from Altai Mts., OK3134). For specimen data see Appendix. Scale bar: 50 µm for all.

papillae are less numerous, and not so sharply delimited, as their 'slopes' are more gentle.

3) Brood branches

Most moss floras key out *P. nervosa* as the only species characterized by the presence of fragile branches with minute leaves clustered in leaf axils near shoot tips. However, we found similar brood branches in many collections of *P. papillosa* from Russia (Fig. 6). Unlike *P. nervosa*, they are less tightly crowded, thus looking less 'stellate'. Anyway, in some cases strict following of a key may result in erroneous identifications.

4) Bistratose leaf margins

Leaf margins are commonly unistratose in most species of *Pseudoleskeella*. However, in the Caucasus and Crimea there are plants with partly bistratose leaf margins which were described as *Leskeella incrassata* (Lindb. ex Broth.) Broth. This species is indistinguishable from *P. nervosa* in all other characters. Similar plants also occur sporadically in southern Europe. Molecular-phylogenetic data do not support the taxonomic recognition of *L. incrassata* (specimens from the Caucasus, OK3143– 3146 have bistratose margins, while specimens from Sakhalin and from Nizhhy Novgorod are unistratose).

5) Thick-walled cells

This character is somewhat difficult to demonstrate and apply. Pseudoleskeella catenulata is usually keyed out as a species with thickest cell walls within the genus; it also has short leaf acumina, often with subobtuse apices, but morphotypes with slightly longer acumina and acute apices are not rare. These latter plants can be confused with short-leaved plants of extremely variable P. rupestris (compare Fig. 7S and Fig. 4C, F). However, P. catenulata always has leaves with costae to 0.5-0.6 the leaf length, while in P. rupestris costae extend far above mid-leaf, becoming weakly delimited from adjacent cells in the leaf acumina. Cell wall thickness is also helpful, as leaf cells of P. rupestris are usually much thinner-walled (cf. Fig. 4D vs. Fig. 9A'). If it is difficult to estimate if cells are thick- or thin-walled, another distinguishing character can be used: the leaf cell areolation of P. catenulata is not contrasting between juxtacostal and marginal areas (Fig. 8A), whereas in P. rupestris rhomboidal and elliptical, thinner-walled cells in mid-leaf differ contrastingly from several rows of quadrate to transversely rectangular, thicker-walled marginal cells (Fig. 8B-C).

The clade of *P. catenulata* in the molecular phylogenetic tree is well supported (Fig. 1), but it includes one

specimen from Sakhalin Island differing from other specimens of this clade in morphology. It has very long acuminate leaves and only moderately thickened cell walls, in contrast to leaves with short acumina and thick-walled cells of *P. catenulata*. DNA was extracted twice from this specimen in order to exclude possible errors; two identical sequences were obtained. This plant is described below as a new species.

Pseudoleskeella sachalinensis Ignatov & Ignatova, spec. nov.

Type: Russia, Sakhalinskaya Province, Sakhalin Island, Smirnykh District, Nature Reserve "Vaida Mountain", 49°52'N, 143°28'E, 450 m alt., on rocks in fir forest, 21 Aug 2006 *Ignatov & Teleganova 06-323* (MHA9046548). Holotype MHA, isotype MW.

Diagnosis: *Pseudoleskeella sachalinensis* is similar to *P. rupestris* var. *rupestris* in having leaves with long acumina, long single costae, and elongate-rhomboidal leaf cells, but differs in having leaves from erect stems with even longer acumina, constituting ca. 0.5–0.7 the leaf length (0.3–0.5 the leaf length in *P. rupestris* var. *rupestris*) and longer cells in distalmost leaf portion: 4–6:1 vs. 2–4:1.

Description: *Plants* medium-sized, green or yellowish-green, in loose mats. *Stems* creeping and ascending to erect, 1.0–1.5 cm long, hyalodermis absent, central strand present. *Leaves from erect shoots* straight or slightly falcate-secund, 0.7–1.0×0.2–0.4 mm, from an ovate base \pm abruptly tapered into long, narrow lanceolate, straight or slightly curved acumina constituting ca. 0.5– 0.7 the leaf length; margins plane, entire or serrulate in places; *costae* single, thin, to 0.6–0.8 the leaf length; *cells* in mid-leaf elongate-rhomboidal, 19–35×6–8 µm, towards margins shorter, rhomboidal, quadrate and transversely rectangular, firm-walled, smooth; upper cells of leaf acumina oblong, 16–35 µm long, 4–6:1. *Leaves from creeping shoots* slightly smaller, with wider bases, costa single. *Sporophytes* unknown.

Pseudoleskeella sachalinensis is currently known only from the type locality.

Differentiation: Pseudoleskeella sachalinensis differs from all other species of the genus by the longest – ca. 0.5-0.7 the leaf length – leaf acumina, and especially long – 4–6:1 – cells in the uppermost leaf portion. Leaf acumina of *P. rupestris* are usually shorter, composed of shorter cells. However, in some morphotypes of *P. rupestris* leaf acumina in proportion to leaf length approach those of *P. sachalinense* and are similarly narrow acumi-



Fig. 9. A–B – *Pseudoleskeella catenulata* (A – from Dagestan, OK3137; B – from Perm Territory, OK3139) and *P. sachalinensis* (C–E, from holotype). A–E: habit, dry; A' & D': mid-leaf cells.

nate (Fig. 7G). In this case, the difference in cell length and width of acumina are important distinguishing characters: a number of long cells in leaf acumina is larger in *P. sachalinensis* and the acumina are 2–4 cells wide for a longer distance than in *P. rupestris* (cf. Fig. 7C–E vs. F).

KEY TO IDENTIFICATION OF PSEUDOLESKEELLA IN RUSSIA

- Leaf cells smooth or weakly prorate or only a few cells with single, small or large papillae at the upper cell ends
 2
- 2. Costae single, percurrent; axillary brood branches usually present; corticolous, rarely saxicolous

Costae single, forked, or double, extending 0.2–0.9

- Leaves broadly ovate or broadly ovate-triangular at the base, abruptly tapered to acumina that are 35– 50% the leaf length 1. *P. tectorum* In Russia *P. tectorum* is known from most well explored mountain areas and some lowlands where calcareous outcrops are more or less numerous.
 - Leaves ovate or ovate-oblong at base, somewhat abruptly tapered to acumina that are 45–70% the leaf
 - length 4. *P. rupestris* var. *tenuis* This variety is known from scattered localities in the Urals, Altai Mountains, Yakutia, and Sakhalin Island.
- Leaf apices acute, often blunt; acumina 0.2–0.4(– 0.5) the leaf length; leaf cells 1–1.5:1, thick-walled

- Leaves from creeping shoots often with double or forked costae; leaves from upright shoots with costae to 0.3–0.5(–0.7) the leaf length
- Leaf acumina 0.5–0.7 the leaf length; upper leaf cells elongate-rectangular, 4–6:1...... 5. *P. sachalinensis* Russian Far East (Sakhalin Island).
- Leaf acumina 0.3–0.5(–0.7) the leaf length; upper leaf cells rhomboidal, irregularly polygonal, and rect-

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APPENDIX: sequenced specimens of *Pseudoleskeella* (all from Russia), with GenBank (ITS, trnS–F) and Isolate numbers.

Pseudoleskeella tectorum ON677966 ON693987 OK3138: Yakutia, Moma, Ignatov & Ignatova 18-1880, MHA9029410; ON677967 ON693988 OK3122: Krasnoyarsk Terr., Anabar Plateau, Fedosov 05-551, MHA; ON677968 ON693989 OK 3123: Yakutia, Ust-Nera, Ignatov & Ignatova 15-1506, MHA9046606; ------ON693993 OK3125: Dagestan, Gunib, Ignatov & Ignatova 09-517, MHA9046597; ------ ON693994 OK3126: Perm Terr., Bezgodov 28 Sept 2003 #144, MHA9025021; ------ ON693995 OK3128: Volgograd Prov., Ignatov 8 Aug 1999, MHA9046556; ON677969 ON693990 OK 3136: Altai, Ignatov & Ignatova 12-369, MHA9046435; ON677970 ON693991 OK 3154: Altai, Tabozhok, Ignatov & Ignatova 30/80, MHA9046491; ON677971 ON693992 OK 3162: Altai, Ignatov & Ignatova 12-369a, MHA9046435; ON677972 ------ OK 3091: Altai, Ignatov & Ignatova 21-449, MHA; Pseudoleskeella nervosa ------ ON693996 OK3143: Dagestan, Gunib, Ignatov & Ignatova 09-175, MHA9045403; ON677973 ON693997 OK3144: Ingushetia, Ignatov et al. 18-927, MHA9026637; ON677974 ON693998 OK3145: Ingushetia, Ignatov et al. 18-1000, MHA9026687;ON677975 ON693999 OK3146: Kabardino-Balkarian Rep., Ignatov et al. s.n., MHA9046445; ON677976 ------ OK3149: Sakhalin, Chamga, Ignatov & Teleganova 06-667, MHA9046463; Pseudoleskeella catenulata ON677977 ON694000 OK3260: Dagestan, Gunib, Ignatov & Abakarova 11-375, MHA9046174; ON677978 ON694001 OK3262: Yakutia, Sette-Daban, Ignatov & Ignatov 16-1272, MHA 9022351; ON677979 ------ OK3265: Komi Rep., Pechero-Ilychsky Nature Reserve, Bezgodov & Kucherov 5 July 2000 #300, MHA 9046580; ON677980 ON694002 OK3266: Perm Terr., Lysva, Bezgodov 12 Aug 2005 #185, MHA9046573; ON677981 ON694003 OK3137: Dagestan, Gunib, Ignatov & Ignatova 09-763, MHA9046165; ON677982 ON694004 OK3139: Perm Terr., Bezgodov 18 May 2012 #12, MHA9046132; Pseudoleskeella papillosa ON677983 ON694005 OK3148: Yakutia, Allah-Yun, Ignatov 00-182, MHA9046467; ON677984 ON694006 OK3150: Bashkortostan, Baisheva 13-2-34, MHA9046471; ON677985 ON694007 OK3151: Chelyabinsk Prov., Ibatullin 28 Aug 2011, MHA9046472; ON677986 ON694008 OK3140: Murmansk Prov., Umba, Ignatov & Ignatova 12-76, MHA9046473; ----- ON694009 OK3152 Khabarovsk Terr., Botchi, Ignatov & Ignatova 13-995, MHA9046482; ON650756 ------ IM2008: Krasnoyarsk Terr., Anabar, Fedosov 08-382, MHA9060718; Pseudoleskeella rupestris ON677987 ON694010 OK3124: Altai, Ignatov & Ignatova 21-349, MHA; ON677988 ON694011 OK3130: Anabar Plateau, Fedosov 08-549, MHA9046554; ON677989 ------ 3264: Altai, Kosh-Agach, Ignatov 32/31, MHA 9046619; ON677990 ON694012 OK3141: Perm Terr., Bezgodov 31 July 2017 #441, MHA9018283; ON677991 ON694013 OK3120: Yakutia, Orulgan, Ignatov 11-4533, MHA 9046645; ON677992 ON694014 OK3119: Sakhalin, Vaida, Ignatov & Teleganova 06-314, MHA9046552; ON677993 ON694015 OK3259: Altai, Ongudai, Ignatov & Ignatova 21-174, MHA9121253; ON677994 ON694016 OK3131: Primorsky Territory, Ignatov & Ignatova 13-1364, MHA9046555; ON677995 ON694017 OK3134: Altai, Ignatov & Ignatova 12-465, MHA9046535; ON677996 ON694018 OK3135: Perm Terr., Bezgodov 1 Aug 2017, MHA9018302; Pseudoleskeella sachalinensis ON677997 ON694019 OK3133 & ON677998 ON694020 OK3255: Sakhalin, Vaida, Ignatov & Teleganova 06-323, MHA9046548. Received 28 April 2022 Accepted 23 May 2022