Woessia lignicola (Ramalinaceae, lichenized Ascomycota) a new combination and a new lichen species to Asia and Russia

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Abstract. The epiphytic species *Woessia lignicola,* comb. nov., is newly reported for Asia and Russia from the Altai Territory (South Siberia). The species identity is supported by morphological examination and molecular-phylogenetic data (nrITS sequence). This finding extends the known distribution of the species eastward by more than 4000 km. In light of the recent resurrection of the genus *Woessia*, we propose the new combination *W. lignicola* (based on *Bacidina lignicola*).
Keywords: *Bacidina*, *Woessia,* biogeography, ITS, new record, taxonomy, Altai-Sayan Mountain system, Altai Territory, Salair Ridge.

Woessia lignicola (Ramalinaceae, lichenized Ascomycota) — новая комбинация и новый вид лишайника для Азии и России

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Резюме. Эпифитный вид *Woessia lignicola,* comb. nov., впервые обнаружен в Азии и России на территории Алтайского края (Южная Сибирь). Видовая принадлежность подтверждена морфолого-анатомическими и молекулярно-филогенетическими (последовательность nrITS) данными. Эта находка увеличивает известное распространение вида на восток более чем на 4000 км. В свете недавнего восстановления рода *Woessia* мы предлагаем новую комбинацию *W. lignicola* (на основе *Bacidina lignicola*).
Ключевые слова: *Bacidina*, *Woessia*, ITS, биоразнообразие, новые находки, таксономия, Алтае-Саянская горная страна, Алтайский край, Салаирский кряж.

Recent molecular phylogenetic studies have led to significant revisions within the lichen-forming family Ramalinaceae. Historically, the genus *Bacidina* Vězda was established to accommodate some species previously classified within the genera *Bacidia* De Not. and *Catillaria* A. Massal. (Vězda, 1991). The designated type species was *Bacidina phacodes* (Körb.) Vězda. Traditionally, *Bacidina* has been characterized by a thallus composed of goniocysts, a paraplechtenchymatous proper exciple, "*Lecanora*-type" asci, acicular or rarer more or less bacilliform ascospores, the absence of secondary metabolites, and filiform conidia (Vězda, 1983, 1991; Ekman, 2001; Kistenich *et al*., 2018; Fatima *et al*., 2021). Subsequent studies revealed considerable morphological diversity within the genus, including indistinct, granular, crustaceous, warted, areolate, microsquamulose to distinctly sorediate thallus (Ekman, 1996, 2023; Aptroot, van Herk, 1999; Coppins, van den Boom, 2002; Brand *et al*., 2009; Lumbsch *et al*., 2011; Czarnota, Guzow-Krzemińska, 2012; Ekman *et al*., 2012; Kondratyuk *et al*., 2019; van den Boom, Alvarado, 2019; van den Boom, Magain, 2020; van den Boom, 2021). Additionally, molecular data showed *Bacidina* s. l. to be non-monophyletic (Kistenich *et al*., 2018).

The genus *Woessia* D. Hawksw. et Poelt was recently resurrected based on robust multi-locus phylogenetic evidence (van den Boom, Alvarado, 2025). That study, utilizing sequences of mtSSU, LSU, and RPB1, recovered *Woessia* as a well-supported clade distinct from both *Bacidia* s. str. and *Bacidina* s. str. Consequently, several species previously classified in *Bacidina* were formally transferred to the resurrected genus *Woessia*, including its type species *W. fusarioides* Hawksw. et al. [current name *W. modesta* (Zwackh ex Vain.)

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van den Boom et Alvarado] and other well-known taxa such as *W. arnoldiana* (Körb.) Sérus. et Diederich, *W. chloroticula* (Nyl.) Puntillo et al., and *W. egenula* (Nyl.) van den Boom et Alvarado (van den Boom, Alvarado, 2025).

Currently, the genera *Bacidina* and *Woessia* comprise approximately 60 worldwide-known species, 10 to 12 of which belong to the genus *Woessia* and have been newly described or resurrected in recent years (Fatima *et al*., 2021; Afshan *et al*., 2023; Ekman, 2023; van den Boom, Alvarado, 2025). Many of these recently recognized species have not been reported from Russia yet. One of the species recently described within the *Bacidina*/*Woessia* complex is *B. lignicola* S. Ekman known from dead wood in Scandinavia and Central Europe. Morphologically, it is very similar to *Woessia chloroticula*, recently recorded from the Salair Ridge, Russia (Kotkova *et al*., 2022), and to *Bacidina phacodes*. During a revision of Russian material of these morphologically similar species, we identified specimen matching the description of *B. lignicola*. Given the reinstatement of the genus *Woessia*, the taxonomic placement of this species requires revision. In this paper we (1) confirm the first record of *Bacidina lignicola* in Asia and Russia based on morphological and molecular (nrITS) data from the Altai Territory, (2) formally transfer *B. lignicola* to the genus *Woessia* to align its nomenclature with the current phylogenetic framework.

Material and Methods

Study area and material collection. The material was collected by the authors in Salair National Park on the Salair Ridge in the Altai Territory. The Salair Ridge is a low-mountain area within the northwest of the Altai-Sayan Mountain system with an area of 22500 km^2 with average elevations of 400–600 m a. s. l. and the highest mountain Mt. Kivda, 621 m a. s. l. (Lashchinskii *et al*., 2007; Bykov *et al*., 2021).

Morphological studies. The specimens were examined using a stereomicroscope (Zeiss Stemi 2000-C) and a compound microscope (Zeiss Axio Lab.A1). Anatomical examination was undertaken using hand-cut sections mounted in water. Measurements of morphological characters follow Vondrák *et al*. (2013), morphological terminology follows Ekman (2023).

Molecular studies. DNA extraction, amplification and sequencing followed the methods described by Davydov and Yakovchenko (2017). The primer sets were ITS1F (Gardes, Bruns, 1993) and ITS4 (White *et al*., 1990) The program Geneious 6.0 (Biomatters Ltd., New Zealand) was used for assembling sequences. Consensus sequences were exclusively compiled from double-stranded parts of the sequences.

The newly generated nrITS sequence of *Woessia lignicola* was supplemented with nrITS and mtSSU sequences related to *Woessia* and morphologically close *Bacidina* species referable from the phylogenetic studies of *Bacidina* s. l. (Vondrák *et al*., 2023, 2024; van den Boom, Alvarado, 2025) obtained from GenBank (Table 1). *Bellicidia incompta* (Borrer) Kistenich et al. was designated as the outgroup, because in the recent phylogenetic studies *Bellicidia* is closely related to *Bacidia* and *Bacidina* (e. g., Kistenich *et al*., 2018).

Sequence alignment was performed using the MAFFT algorithm (Katoh *et al*., 2005) on the GUIDANCE web server (Sela *et al*., 2015) with default settings. The aligned dataset was partitioned by locus ITS1, 5.8S, ITS2, and mtSSU, with each partition treated independently in the subsequent analysis.

Maximum likelihood (ML) analysis was conducted using RAxML 8.0.26 (Stamatakis, 2014) via raxmlGUI v.1.3.1 (Silvestro, Michalak, 2012). The GTRGAMMA model of evolution was applied to each partition. Branch support was assessed with 1000 rapid bootstrap replicates, and a majority-rule consensus tree was generated.

Results and Discussion

Phylogenetic placement and confirmation of identity. Phylogenetic reconstruction based on the combined dataset of nrITS and mtSSU sequences (Fig. 1) resolves four main clades with high statistical support: 1) a clade corresponding to the genus *Woessia*, including the type species *W. modesta* (82% BS); 2) a clade uniting *Bacidina violacea* and *B. populnea* (99% BS); 3) a clade corresponding to the genus *Bacidina*; and 4) a clade corresponding to the genus *Bacidia*. In addition to the confirmed members of *Woessia*, the *Woessia* clade includes *Bacidina assulata*, *B. lignicola*, *B. paradoxa*, and two putatively new *Bacidina* s. l. species (*Bacidina* sp. 2 and 3). *Bacidina adastra* and *B. pycnidiata* likely also belong to *Woessia* (Fig. 1). While a comprehensive taxonomic revision of all these taxa is beyond the scope of the present study and requires further investigation, the close morphological affinity of *Bacidina lignicola* to *Woessia chloroticula* prompted us to address its nomenclatural status. Consequently,

Table 1

Collection and GenBank accession numbers of the specimens used in the phylogenetic analysis in this study

Species and № in phylogenetic tree	Specimen numbers	GenBank accession numbers	
		ITS	mtSSU
Bacidia abisistens	BG, *Ekman 3223*	AF282085	MG925845
B. arceutina	PRA, *Vondrák 24590*	OQ717709	OQ646107
B. caucasica	GLM, *Otte 0048447*	MW523553	MW506388
B. laurocerasi	PRA, *Vondrák* 22972	OQ717714	OQ646109
B. polychroa	PRA, *Vondrák 26081*	OQ717313	OQ682869
B. rosella	PRA, *Vondrák 26028*	OQ717314	OQ682870
B. rubella	PRA, *Vondrák 26027*	OQ717316	OQ682871
Bacidina acerina 1	PRA, *Vondrák 24355*	OK332880	OK465494
B. acerina 2	PRA, *Vondrák 20656*	OK332878	OK465492
B. adastra 1	PRA, *Vondrák 24569*	OK332938	-
B. adastra 2	Herb. *Malíček 13928*	OQ717318	-
B. assulata 1	PRA, *Palice 30714*	OQ717321	-
B. assulata 2	PRA, *Vondrák 24106*	OQ717721	OQ646116
B. assulata 3	PRA, *Vondrák 24102*	OQ717722	OQ646115
B. caerulea	BG, *Ekman 3579*	OP256853	-
B. friesiana	BG, *Ekman 3401*	AF282101	-
B. paradoxa 1	PRA, Palice *26142*	OQ717326	OQ682876
B. paradoxa 2	PRA, *Palice 33646*	OQ717327	OQ682877
B. phacodes 1	PRA, *Vondrák 25994*	OQ717322	-
B. phacodes 2	PRA, *Vondrák 24463*	OQ717723	-
B. piceae	PRA, *Palice 32287*	OQ717724	OQ646117
B. populnea	UPS, *L-1009299*	OP256855	-
B. pycnidiata	Herb. *Malíček 2553*	KX239034	-
B. violacea	PRA, *Palice 31173*	OQ717328	-
Bacidina sp. 2 (1)	Herb. *Malíček 15981*	OQ918723	OQ920110
Bacidina sp. 2 (2)	PRA, *Vondrák 24921*	OK332885	OK465501
Bacidina sp. 3	PRA, *Vondrák 24573*	OK332886	OK465503
Bellicidia incompta	PRA, *Vondrák 23534*	OQ717713	OQ646108
Woessia arnoldiana 1	PRA, *Vondrák 24753*	OQ717717	OQ646112
W. arnoldiana 2	BG, *Ekman 3157*	-	MG925854
W. brandii	GPN, *Czarnota 7599*	KX239029	-
W. chloroticula 1	PRA, *Palice 32914*	OQ717320	-
W. chloroticula 2	B, *Sipman 55079*	-	JQ796833
W. chloroticula 3	PRA, *Vondrák 26080*	OQ717319	OQ682874
W. delicata	*Sérusiaux s. n.* (LG, DNA 369)	JQ796854	JQ796834
W. egenula	LG, *van den Boom 39665*	-	JQ796836
W. inundata	BG, *Ekman 3187*	-	MG925855
W. lignicola 1	PRA, *Vondrák 24312*	OQ717719	OQ646113
W. lignicola 2	PRA, *Vondrák 25879*	OQ717720	OQ646114
W. lignicola 3	ALTB, ***Davydov 23847***, ***Storozhenko***	**PZ103500**	-
W. lignicola 4	UPS-L, *Ekman 941645*	OP256857	-
W. modesta 1 (type)	DUKE-AFTOL-ID 1845	-	DQ986810
W. modesta 2	GPN, *Czarnota 7246*	JN972447	-
W. modesta 3	GPN, *Czarnota 5275*	JN972445	-
W. neosquamulosa 1	UPS, *van den Boom 24182*	OP256854	-
W. neosquamulosa 2	LG, *van den Boom 39692*	-	JQ796838
W. terricola	BR, *van den Boom 55461*	-	MW622008

Note: the newly generated sequence is in bold.

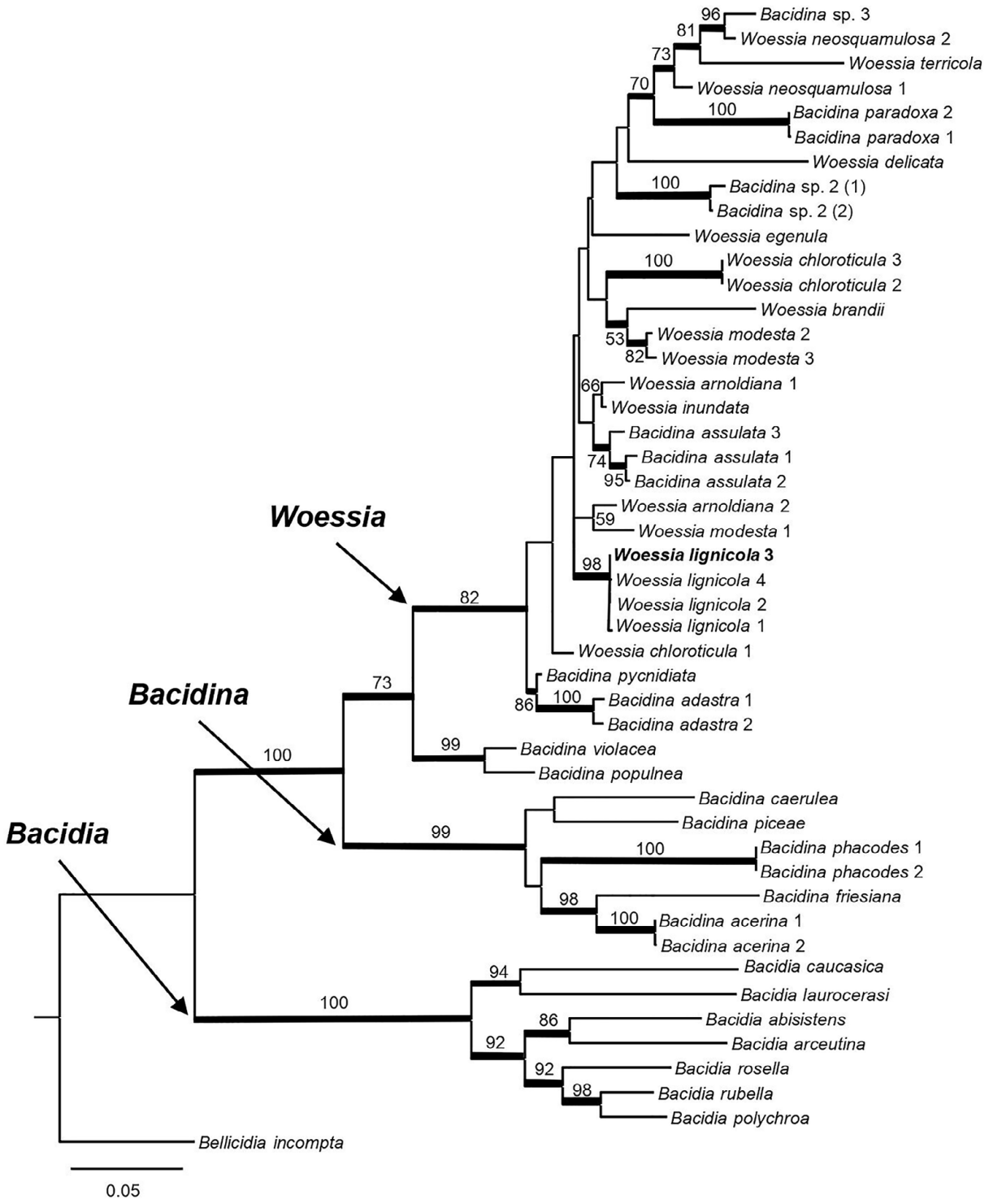

Fig. 1. Phylogenetic relationships among *Woessia* and *Bacidina* s. l. species based on a ML + rapid bootstrap combined analysis of ITS1-5.8S-ITS2 and mtSSU. Numbers on branches represent maximum likelihood bootstrap values (BS; ⩾ 70% is bold). The newly generated sequence from Russia is highlighted in bold. Corresponding GenBank accession numbers are provided in Table 1.

we propose the new combination *Woessia lignicola* below.

Within the *Woessia* clade, the newly generated sequence from Russia (PZ103500) groups with high statistical support (BS = 98) with reference sequences from the type material of *W. lignicola* from Sweden (OP256857) and the Czech Republic (OQ717719, OQ717720), confirming the identity of our specimen as *W. lignicola*. According to the distance matrix, the Russian ITS sequence differs from the Swedish sequence by a single nucleotide and is identical to the Czech sequences.

Morphological distinction from similar species. *Woessia lignicola* has previously been confused with *Bacidina phacodes* and *Woessia chloroticula* due to superficial similarities in apothecium size, coloration, and overlapping substrates. However, detailed anatomical examination reveals consistent differences in thallus structure, apothecia, proper exciple, and conidia, allowing for reliable separation of these species (Ekman, 2023). While *W. lignicola* and *Bacidina phacodes* share a similar anatomical structure, the main differences lie in apothecial shape and hymenium height. *Woessia lignicola* and *W. chloroticula* can be distinguished by differences in the external and internal structure of their apothecia (Ekman, 2023). Key diagnostic characters are summarized in Table 2.

The examined specimens of *Woessia lignicola* and *W. chloroticula* clearly differ in apothecial color, the structure of the apothecial margin, and the thickness of the proper exciple. The Russian specimen of *W. lignicola* (Fig. 2) is characterized by pale pinkish to pale orange apothecia, a hymenium 37–43 μm tall, constituting 25–40% of the total apothecium height, that does not correspond to the known literature (Ekman, 2023), in which the height of the hymenium is 10–20%, a distinctly radiating proper exciple, and colorless, acicular, 0–5–7-septate, straight ascospores 25.0–30.0–42.0 × 1.2–1.4–1.7 μm (n = 20). Pycnidia were not detected.

Specimens examined. *Woessia lignicola*: **Russia, Altai Territory:** Togul'skii District, Salair Ridge, headwaters of the Malaya Mostovaya River at 10 km NEE from the Novokamenka settlement, 53°23′28″N, 86°27′39″E, 400 m a. s. l., *Abies sibirica* Ledeb. dominated subnemoral forest, on fruit body of polyporoid fungus on bark of *Populus tremula* L., 15 IX 2022, *Davydov 23847*, *Storozhenko*, ALTB.

Woessia chloroticula: **Russia, Altai Territory:** Zarinskii District, Salair Ridge, at 13 km to NE from the Novoiushino, Togul River basin, 53°42′07″N, 85°59′44″E, 335 m a. s. l., linden (*Tilia sibirica* Bayer) forest, on bark of *Padus avium* L., 22 VIII 2020, *Davydov 21314*, *Storozhenko*, det. *Storozhenko*, *Yakovchenko*, *Davydov*, ALTB; *ibid*., 53°41′41.1″N, 86°00′05.8″E, 315 m a. s. l., fir-poplar (*Abies sibirica-Populus tremula*) subnemoral forest, on fruit body of polyporoid fungus, 23 VIII 2020, *Davydov 21306*, *Storozhenko*, ALTB.

Bacidina phacodes: **Russia, Altai Territory:** Togul'skii District, Salair Ridge, at 13 km to NE from the Novoiushino, Togul River bassin, 53°42′03.9″N, 85°59′38.3″E, 330 m a. s. l., linden (*Tilia sibirica*) forest, on bark of *Populus tremula*, 24 VIII 2020, *Davydov 21730*, *Storozhenko*, ALTB.

Table 2

Key diagnostic characters of similar *Woessia* and *Bacidina* species

Character	*Woessia lignicola*	*Bacidina phacodes*	*Woessia chloroticula*
1. Substrate and thallus	Primarily fresh stumps of conifers (*Picea abies*, *Pinus sylvestris*) and hard wood; thallus thin or thick, of scattered convex areoles or continuous and warted	Soft bark of deciduous trees; thallus thin to irregularly warted or scurfy, confined to bark crevices	Diverse substrates: wood, bark, rock, metal, moribund bryophytes; thallus thin, filmy or of discrete granules
2. Apothecia: size, shape, color	0.15–0.44 mm diam, convex, pale pinkish (becoming brownish-orange in herbarium)	Less than 0.4 mm diam., effuse, pale pink	0.15–0.25 mm diam., flat, pale greyish yellow or pale brown-grey
3. Apothecial margin	Usually slightly paler than disk, smooth, soon excluded	Paler than disk, smooth, soon excluded	Slightly paler than disc, almost hairy, persistent
4. Hymenium and hypothecium height	Hymenium makes up 10–20% (Ekman, 2023) and 25–40% (for author's specimen) of apothecium height, mostly colorless; thick hyphal cushion below hypothecium. Hypothecium colorless	Hymenium makes up 30–40% of apothecium height, mostly colorless; no hyphal cushion. Hypothecium colorless	Hymenium relatively tall (35–50% of apothecium height), mostly colorless, without special thickening. Hypothecium pale
5. Proper exciple structure	Excipular hyphae distinctly radiating, cell lumina up to 12 × 4 μm	Excipular hyphae weakly radiating; cell lumina up to 7.0 × 3.3 μm	Exciple paraplectenchymatous, hyphae not radiating, with vesicle-like lumina, cell lumina up to 7 × 4 μm
6. Conidia	Acicular, straight, non-septate or weakly 1–3-septate, 22.0–43.0 × 1.2 μm	Acicular, straight, resembling ascospores, 3–7-septate, (24)28–50(60) × 1.0–1.5(2.0) μm	Mostly filiform, occasionally pyriform, curved, non-septate, 19.0–48.0 × 0.8–1.0 μm
7. Pycnidia	Abundant, 50–130 μm diam., immersed to semi-immersed	Sparse, 120–200 μm diam., immersed	Sparse, 40–90 μm diam., immersed or semi-immersed

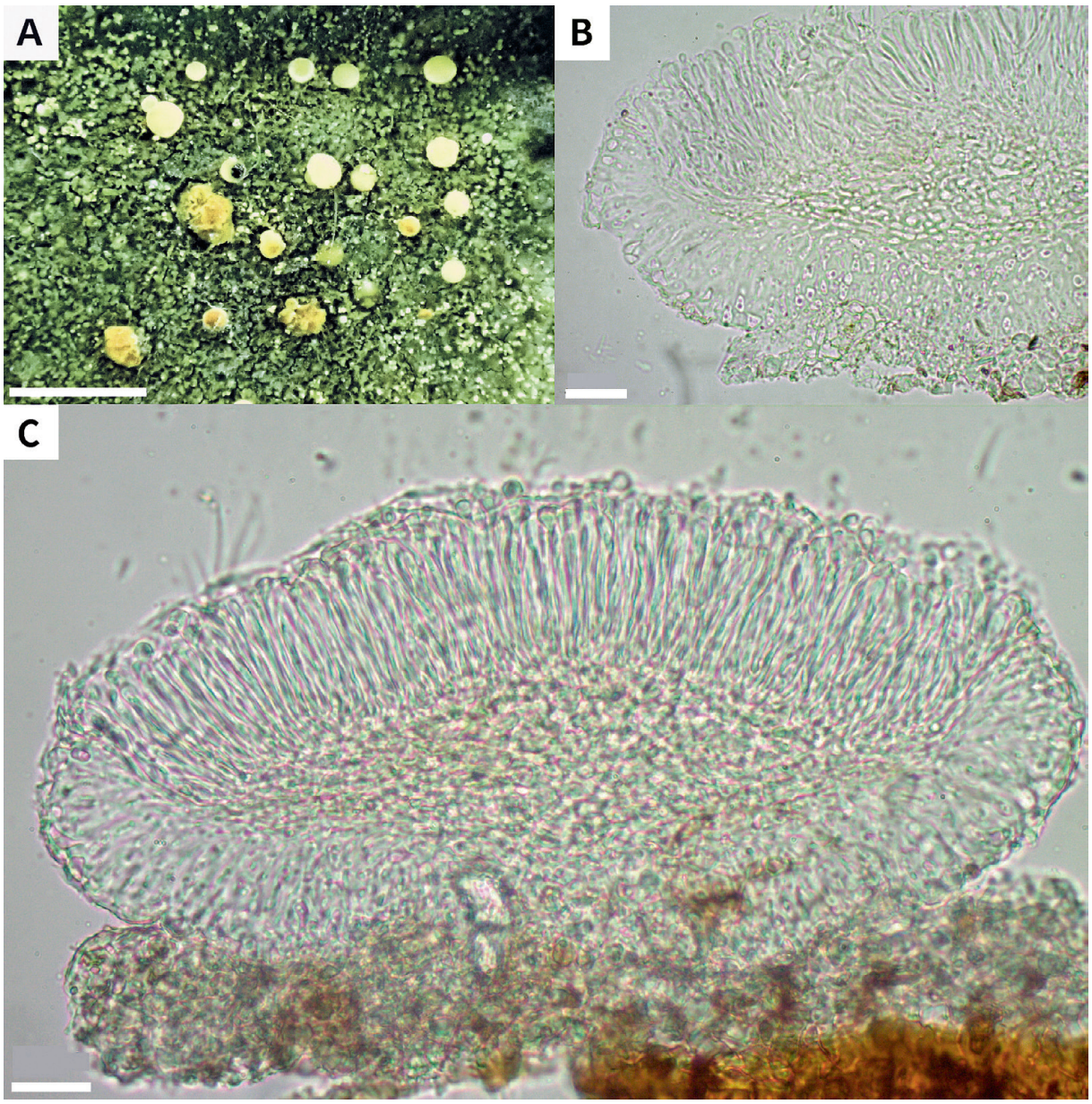

Fig. 2. Russian specimen of *Woessia lignicola* (ALTB, *Davydov 23847, Storozhenko*): A — habitus; B — anatomical structure of the proper exciple; C — apothecial structure. Scale bars: A — 1 mm, B, C — 20 μm.

Distribution and ecology. *Woessia lignicola* was previously known only from scattered localities in Northern and Central Europe — Norway, Finland, Poland, Germany and the Czech Republic, where it occurs primarily on recently dead wood of conifers and hardwoods in humid, shaded forests (Ekman, 2023). Our discovery in the Salair Ridge (the Altai Territory) represents a significant eastward range extension of more than 4000 km, marking the first record for Asia and Russia. Here the species was found in a low-mountain area within the Altai-Sayan system in old-growth mixed forests. This suggests that *W. lignicola* may have a broader boreal distribution across Eurasia, possibly linked to relict forest refugia. The disjunct distribution pattern resembles that of several other epiphytic lichens with European-Siberian ranges (Davydov, Printzen, 2012; Davydov, Konoreva, 2017), highlighting the importance of South Siberia and particularly Altai as a biogeographic corridor and refugium for temperate and boreal lichen species (Davydov, Printzen, 2012). Further studies in Siberia and the Russian Far East are needed to clarify full distribution of *W. lignicola*.

Taxonomy. In accordance with the revised generic delineation within the Ramalinaceae proposed by van den Boom, Alvarado (2025), which recognizes *Woessia* as a distinct genus, we formally transfer *Bacidina lignicola* to the genus *Woessia*. The new combination is proposed below.

Woessia lignicola (S. Ekman) Storozhenko, Davydov et Yakovchenko, comb. nov.

MycoBank No.: MB862208

Basionym: *Bacidina lignicola* S. Ekman, Nordic Journal of Botany 2023 (e03846): 12 (2023).

Type: Sweden, Gästrikland, Torsåker par., Hofors herrgård, the park S of the manor, 50°33′05.7″N, 16°17′50.0″E, 120 m a. s. l., on *Ulmus* stump, 23 IX 2018, *S. Ekman 5749*, UPS L-971089 holotype, not seen.

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Contribution of the authors. Yu. V. Storozhenko — collection and study of samples, data analysis, writing; E. A. Davydov — organization of expedition, collection of samples, methodology, data analysis, writing; L. S. Yakovchenko — methodology, sample examination, data analysis. All the authors have read and agreed with the final submitted version of the manuscript.

Conflicts of Interest. The authors declare no conflict of interest.

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